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CHAPTER 7

Electrical and magnetic readings of mental functions

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Ever since Berger's (1929) discovery that brain electrical activity (electroencephalogram (EEG)) can be measured at the human scalp, it has been assumed that in these voltage fluctuations are hidden the mysteries of the workings of the human mind. While classical neurophysiologists questioned the likelihood that such "simple" fluctuations could be the key to the complexities of understanding, talking, reasoning, imagining and supposing, the past 70 years have proven otherwise. A large body of evidence has shown that electrical and magnetic activity (human or otherwise) encode information about brain states and brain processes and, by inference, about mental states and mental processes. The exact mapping from neural structures to sensory, perceptual and cognitive processes and states is not at all transparent, but all neuroimaging techniques are based on the assumption that such mappings exist and are decipherable.

In this chapter we examine the nature of the mapping between perception, movement and cognition on the one hand and electrical and magnetic activity at various scalp locations on the other. In this regard, it is important to remember that the brain's currency at a neurophysiological level is electrochemical activity. It is the pattern of electrical activity at the scalp that doctors and scientists alike take to be a sign of how and how well the brain is functioning. As we will document, electrical and magnetic activity can be used within the context of psychological experiments to assess the brain's sensitivity to various experimental manipulations, and thereby to constrain psychological theories of various cognitive and behavioural phenomena. The chapter starts with a few references to some basics of electrical (event-related potentials (ERPs)) and magnetic (event-related fields (ERF)) recording. This is followed by a short tutorial on the physiology and physics of electrical and magnetic activity, a discussion of the types of inference that can and cannot be drawn from such measurements, and a cursory overview of the most widely used terms in cognitive electrophysiology. We conclude with a few specific examples of cognitive ERP and ERF research.

7.1 EVENT-RELATED ACTIVITY: ELECTRICAL (ERPS) AND MAGNETIC (ERFS)

An ERP/ERF experiment requires a willing participant, electrodes for recording the brain wave activity or a magnetometer, some means of presenting stimuli, amplifiers and a digitizer that turns the analogue data into a digital form for storage, further representation and analyses. Technical details about electrodes, electrode placement, amplifiers, magnetic recordings, digitization and analyses can be found in a number of articles and books (Cooper et al. 1974, Regan 1989, Hamalainen et al. 1993, Rugg & Coles 1995).

There are many ways to look at electrical and magnetic activity in both the temporal and spatial domains. The emphasis of this chapter is on scalp activity, specifically that which is time-locked or synchronized to some external stimulus or event. Typically, the earliest or so-called "exogenous" components of the ERP are used in a clinical setting to assess the integrity of the peripheral or central nervous system, although they are clearly essential for understanding cognitive effects as well (for more in-depth discussion see Desmedt 1988, Starr & Don 1988, Regan 1989). Since the evoked response to a single stimulus at the scalp is quite small (5-10uV), it must be extracted from the background activity via averaging. Averaging enhances the signal (or whatever is invariant from trial to trial) and reduces what is random (noise) to nearly zero, improving the signal-to-noise ratio by a factor proportional to the square root of the number of trials. Since the assumptions of averaging are often violated, single-trial ERP data have also been examined using pattern recognition techniques, cross-correlation, Woody filter and step-wise discriminant analysis (e.g. Glaser & Ruchkin 1976, Gevins & Remond 1987), although averaging remains the most common technique.

7.1.1 How ERPs are generated by the brain

The net flow of current across the neural membrane generates an electric potential in the conductive media both inside and outside the cells. It is this electric potential that forms the basis for the electrophysiological recordings made both invasively, by lowering electrodes into the brain, and non-invasively, by placing electrodes on the scalp for EEG/ERP (Nicholson & Freeman 1975, Nunez 1981). The same transmembrane current flows are also responsible for the magnetic fields recorded outside the head for MEG (the magnetoencephalogram). Viewed from outside the neurons, each patch of membrane acts as a tiny current source or sink, depending on whether the net local current flow is outward or inward, respectively. The electric potential Φ and magnetic field $\vec{\mathbf{B}}$ are given by the following linear differential equations (Hamalainen, et al. 1993)

$$\nabla \cdot (\sigma \nabla \Phi) = \nabla \cdot \vec{\mathbf{J}}^i \tag{1}$$

$$\nabla \cdot \vec{\mathbf{B}} = 0 \tag{2}$$

$$\nabla \times \vec{\mathbf{B}} = \mu_0 \left(\vec{\mathbf{J}}^i - \sigma \nabla \Phi \right) \tag{3}$$

where $\vec{\mathbf{J}}^i$ are the impressed currents, corresponding to microscopic non-Ohmic transmembrane currents due to ionic concentration gradients, and σ represents the electrical conductivity.[1] Φ, $\vec{\mathbf{B}}$ and $\vec{\mathbf{J}}^i$ all vary as functions of both space and time, while σ is assumed to vary as a function of space but not as a function of time. These equations can, in principle, be used to calculate the potential and magnetic field anywhere inside or outside the head for any arbitrary distribution of neural membrane currents. It is not essential to understand the details of these equations for the purposes of this chapter. However, it is important to understand certain simple properties of these equations for the subsequent discussion:

(a) Both the electric potential and the magnetic field at time t depend on the membrane currents only at time t; in other words, the propagation of the potential and magnetic fields is essentially instantaneous.

(b) All three equations are linear, i.e. if $\vec{\mathbf{B}}_1, \vec{\mathbf{J}}^i_1, \Phi_1$ and $\vec{\mathbf{B}}_2, \vec{\mathbf{J}}^i_2, \Phi_2$ both satisfy the equations, then so must $c_1\vec{B}_1 + c_2\vec{B}_2$, $c_1\vec{J}^i_1 + c_2\vec{J}^i_2$, and $c_1\Phi_1 + c_2\Phi_2$ where c_1 and c_2 are scalar constants. Hence, the potential and magnetic field produced by a weighted sum of two current source distributions are equal to a weighted sum of the fields produced by each current source distribution alone.

Consequently, the electric potential and magnetic field generated by a particular spatial distribution of current sources and sinks can be computed either by adding up the individual contributions of each current source and sink in the entire source space or, alternatively, by partitioning the source space into a number of regions, calculating the contributions of all the sources and sinks within each region, and then adding together the contribution of each region. In either case, the resultant field is the same. For simplicity we will assume that the sources and sinks are inside an infinite homogeneous conductor; that is, that the conductivity σ is constant. Although an infinite homogeneous conductor is not a very good model of a human head, as the conductivity of brain, skull and air are quite different, on the whole the principles we discuss below generalize to more realistic conductors.

The potential produced by a single current source within such a homogeneous conductor is given by

$$\Phi_1 = \frac{s}{4\pi\sigma r} \tag{4}$$

where s is the strength of the current source (or sink, if s is negative), and r is the distance from the source to the measuring point. First, let us consider the case of a current source and a current sink of equal strength s, located at distances r_1 and r_2, respectively, from the measuring point. The potential produced by this dipole can be calculated by adding the separate contribution from each source and sink,

$$\Phi_2 = \frac{s}{4\pi\sigma r_1} - \frac{s}{4\pi\sigma r_2} = \frac{s}{4\pi\sigma}\left(\frac{1}{r_1} - \frac{1}{r_2}\right) \tag{5}$$

However, if the distance between the dipole and the measuring point is several times greater than that between the dipole sink and source, the equation can be simplified as follows:[2]

$$\Phi_2 \approx \left(\frac{1}{4\pi\sigma}\right)\frac{s\vec{\mathbf{d}}\cdot\vec{\mathbf{r}}}{r^3},\ r \gg d \tag{6}$$

where $\vec{\mathbf{d}}$ is the vector from the dipole source to the sink, and $\vec{\mathbf{r}}$ is the vector from the centre of the dipole to the measuring point. Note that, while the potential produced by a source or sink (monopole) falls off as r^{-1} with distance, the potential produced by a dipole falls off more rapidly, specifically as r^{-2}. The potential produced by any arbitrary collection of sources and sinks can be expressed in terms of a multipole expansion:

$$\Phi \approx \Phi_1 + \Phi_2 + O\left(r^{-3}\right) \tag{7}$$

where Φ_1 is a monopolar term, as in Equation 4, Φ_2 is a dipole term, as in Equation 6, and $O(r^{-3})$ represents so-called quadropolar, octopolar and higher order terms which fall off as r^{-3}, or faster, with distance. Hence, we see that the electric potential produced by a collection of current sources and sinks within a region can be approximated closely by considering only the monopolar and dipolar terms, as long as the size of the region is small relative to the distance at which the measurements are made.

Now, recall that the current sources and sinks in the brain correspond to currents flowing through neural membranes. Since the total amount of current leaving a cell must equal the total amount of current entering the cell, the monopolar term in the multipole expansion of the source-sink distribution of a cell must equal zero. Thus, under these circumstances, where activity of neurons in a patch of tissue is observed at a distance much greater than the linear extent of the patch, only the dipolar term of the multipole expansion need be considered. In short, the distribution of sources and sinks within such a patch can be represented by a single so-called "equivalent dipole" located in the middle of the patch.

If the sources and sinks are distributed in an approximately radially symmetric fashion within the patch of tissue, the dipole term vanishes. This is known as a "closed field" source configuration. For example, if we assume that all the dendrites of the neurons illustrated in the top row of Figure 7.1 are activated to a similar extent, on average, then the current sources and sinks in a given cell will be distributed in an approximately radially symmetric fashion, and the resulting dipole moment vanishes. In other words, no potential would be recorded at a distance. Figure 7.1 also shows two other examples of closed fields, where the net dipole moment of the collection of cells is zero, either because the cells are oriented in a random fashion (middle row), or because the activity of the cells is not synchronized (bottom row).

In summary, we see that a patch of brain tissue produces an externally observable electric potential or magnetic field if, and only if, (a) the average distribution of sources and sinks within the neuron in the patch is distributed in a non-radially symmetric fashion, (b) the neurons are aligned in some systematic fashion, and (c) the neurons are activated in a synchronized fashion, as illustrated in Figure 7.2. The neocortex is one of the main structures of the brain which satisfies all these constraints. It is organized as a large folded sheet a few millimetres thick. About 70% of the cells in the neocortex are pyramidal cells which have apical

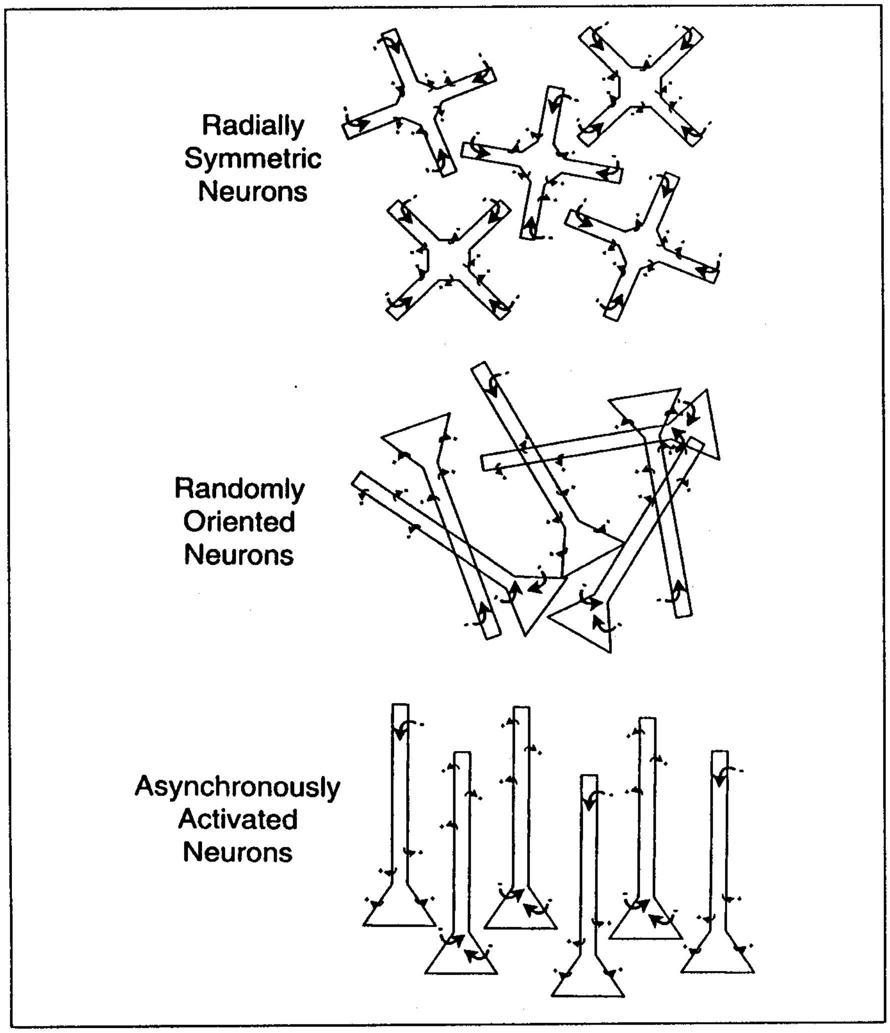

FIG. 7.1. Examples of self-cancelling or closed field source configurations. Neurons which are radially symmetric, randomly oriented or asynchronously activated do not produce externally observable electric or magnetic fields.

dendrites extending from the soma towards the surface of the sheet, which gives the cortex a columnar appearance. When the proximal parts of the apical dendrites of a cell are activated, currents flow into the cell around the soma, and currents flow out of the cell at more distal sites, thus creating an approximately dipolar source-sink configuration oriented perpendicularly to the cortical sheet (Nunez 1981). Similarly, if

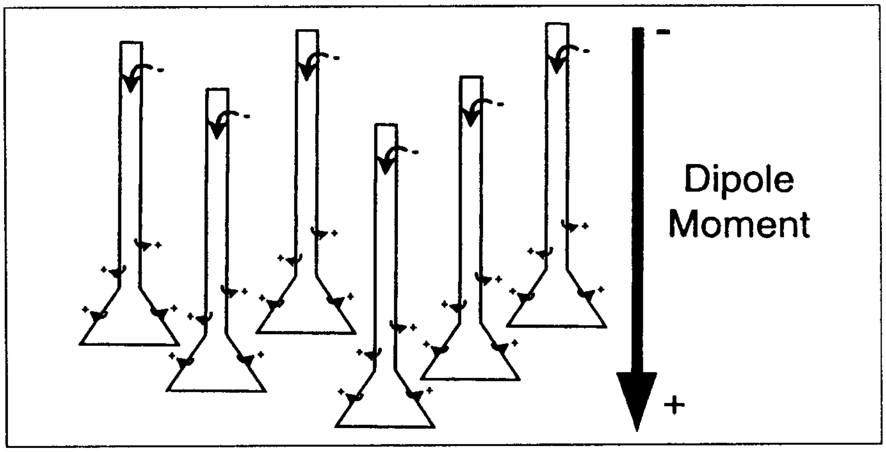

FIG. 7.2. Open field source configuration. Neurons which are non-radially symmetric, spatially aligned and synchronously activated add up to produce externally observable electric and/or magnetic fields.

the distal parts of the dendrites are activated, a dipole field of the opposite orientation is generated. Of course, the potential and magnetic field produced by a single cortical pyramidal neuron are quite weak, but those produced by a patch of cortex containing hundreds of thousands of such cells may be strong enough to be detected even at a considerable distance from the patch. These are believed to be the primary source of scalp-recorded ERPs and associated ERFs.

Since non-invasive measurements of electric potential and magnetic field are made at a distance of at least 1 cm from the nearest cortex and the thickness of the cortex is, at most, a few millimetres, we can approximate the source-sink distribution within a patch of cortex by a single equivalent dipole located in the middle of the patch and oriented perpendicularly to it. For that given dipole the electric potential $\Phi_i(t)$ measured at the ith electrode at time t can be expressed as

$$\Phi_i(t) = e_i s(t) \tag{8}$$

where s(t) is the strength of the dipole, and e_i is a scalar constant which depends on the location and orientation of the dipole as well as on the conductive properties of the head. Similarly, the magnetic field $\vec{\mathbf{b}}_i(t)$ measured at the ith sensor location can be expressed as

$$\vec{\mathbf{b}}_i(t) = \vec{\mathbf{m}}_i s(t) \tag{9}$$

where $\vec{\mathbf{m}}_i$ is a three-vector constant which depends on the location and orientation of the dipole and the conductive properties of the head (Grynszpan & Geselowitz 1973, Cuffin & Cohen 1977, Oostendorp & van Oosterom 1989). Since a magnetic sensor (superconducting quantum interference device (SQUID)) does not measure the magnetic field vector at a point, but rather the scalar magnetic field component in some particular direction, we can rewrite Equation (9) as

$$b_i(t) = m_i s(t)\,, \tag{10}$$

where b_i is the scalar magnetic measurement, and m_i is a scalar coefficient relating the dipole strength s to the measurement. Because of the linear nature of the forward equations we can express the electric potential and magnetic field generated by the entire cortex as

$$\Phi_i(t) = \sum_j^p e_{i,j} s_j(t) \tag{11}$$

and

$$b_i(t) = \sum_j^p m_{i,j} s_j(t) \tag{12}$$

where p is the number of patches, s_j is the strength of the equivalent dipole in patch j, and $e_{i,j}$ and $m_{i,j}$ are scalar constants relating the jth patch to the ith electric and magnetic recording sites, respectively. Note that Equations (11) and (12) are of exactly the same form, i.e. the instantaneous electric and magnetic measurements are both linearly related to the instantaneous dipole strengths. This makes it possible to combine these equations into a single equation for the combined electric and magnetic measurements

$$\vec{\mathbf{x}}(t) = \sum_j^p \vec{\mathbf{g}}_j s_j(t)\,, \tag{13}$$

where $\vec{\mathbf{x}}$ is an n-dimensional vector of combined electric and magnetic measurements (where n is the total number of sensors, electric plus magnetic), and $\vec{\mathbf{g}}_j$ is a so-called gain vector specifying the electric and magnetic measurement at each sensor generated by a unit of dipole strength at the jth patch.

Equation (13) can be written even more compactly, in matrix form, as

$$\vec{\mathbf{x}}(t) = \mathbf{G}\vec{\mathbf{s}}(t) \tag{14}$$

where $\mathbf{G}$ is an n by p matrix whose jth column is the gain vector $\vec{\mathbf{g}}_j$ for the jth dipole, and $\vec{\mathbf{s}}$ is a vector of dipole strengths.

Although, as we have seen, electric and magnetic signals are generated by the brain in a very similar way, the two types of measure do provide somewhat different views of the underlying brain activity. This is because the electric and magnetic recordings are affected differently by factors such as head shape, and dipole location and orientation.[3] For instance, the magnetic field strength falls off much more rapidly with the depth of a dipole than does the electric potential. Furthermore, while the electric potential is affected by dipoles of any orientation, the magnetic field is mainly sensitive to the tangential component of the dipole moment, i.e. the portion of the dipole oriented tangentially to the scalp. a purely radially oriented dipole, regardless of depth, produces almost no magnetic field outside the head.

In practical terms, this means that MEG is mostly sensitive to superficial, largely tangentially oriented dipoles. Given that the primary source of the MEG and EEG are the cortical pyramidal cells, oriented perpendicularly to the cortical sheet, it follows that the MEG is mostly sensitive to activity in the superficial parts of the sulci, and much less sensitive to activity on the crowns of gyri or in the depths of sulci. While the MEG provides only a limited view of brain activity compared with the EEG, it has the advantage of being largely unaffected by skull and conductive inhomogeneities in the intervening tissue. This makes the magnetic field easier to model quantitatively than the electric potential, for which the exact shape and conductive properties of the head have to be taken into account.

In summary, the MEG mostly provides information about the synchronous activation of parallel-oriented populations of pyramidal cells located superficially within cortical sulci. The EEG provides a broader picture of underlying neuronal activity, which includes both superficial and deep sources at various orientations relative to the scalp. However, since the EEG and MEG provide somewhat complementary information about the same underlying brain activity, the broadest picture of this activity can be obtained by combining the two kinds of measure (Wood et al. 1985, Dale & Sereno 1993).

7.1.2 What can be inferred from ERPs?

In this section we discuss how ERPs can be used to make inferences about cognitive processes and their associated neural activity. The classical approach has been to identify certain so-called "components" of the ERP, usually positive or negative peaks with characteristic scalp distributions and latencies, which can be shown to be reliably correlated with particular experimental manipulations. It is often assumed that, since such a peak is correlated with a particular cognitive process, it can in fact be used as a physiological index of that process. Based on this reasoning, it follows that the timing of the process can be inferred from the latency of the corresponding peak, and the degree of activation or "strength" of the process can be inferred from the amplitude of or area under the peak. Moreover, according to this view, the question of whether two experimental conditions involve the same cognitive process reduces to the question of whether both conditions evoke the same component. It may be worthwhile to examine more closely the assumptions implicit in this reasoning.

Before doing so, however, it is important to note that there is no single, universally accepted definition of an ERP component. In some cases, "component" merely refers to a peak or a trough in the waveform. According to one of its more common usages, which we will call "functional", "component" refers to a delineated waveform feature whose approximate polarity, latency and scalp distribution are predictable from experimental (psychological) manipulations (Donchin 1979); in this view, the fact that an ERP is generated by the brain is taken to be irrelevant. At the other extreme, in a more "physiological" view, an ERP component is presumed to be the reflection of the activity of a particular generator or set of generators in the brain (Nunez 1981). Although few researchers start by explicitly defining their usage of the word "component", the majority seem to have adopted aposition which is intermediate between or a combination of the "functional" and "physiological" usages. Let us examine the assumptions of this generic combined usage of the term.

From the discussions in the previous section, recall that neural activity in a particular location in the brain produces a characteristic spatial pattern of electric and magnetic measurements (cf. the gain vector in Eq. (13)). The definition of a "component" in terms of a characteristic scalp distribution thus implies that the neural activity associated with a particular component has a characteristic spatial distribution within the brain. The strength of such a component is often defined in terms of the peak measurement at a particular electrode within a particular latency range. This component strength is then used to infer something about the brain's sensitivity to some experimental variable. However, the idea that a peak measured at a given electrode reflects only the activity of a particular process implicitly assumes that the potential recorded at that electrode is affected by that process, and by that process alone. This assumption is potentially troubling, since we know that even highly localized foci of activity within the brain may produce widespread potential distributions on the scalp, and it is highly unlikely that there would only be a single process active at any given moment.

We will show the consequences of this assumption via a number of simple simulations. Let's imagine, for instance, that three processes (L, R and M) involve neural activity at different locations, and that the current distributions in the tissue activated by each can be approximated by radially oriented dipoles on the left (L), right (R) and middle (M) of the brain, respectively. The scalp distributions of the potential generated by each of these dipoles in a homogeneous spherical head are shown on the left in Figure 7.3; the simulated ERP waveforms from 16

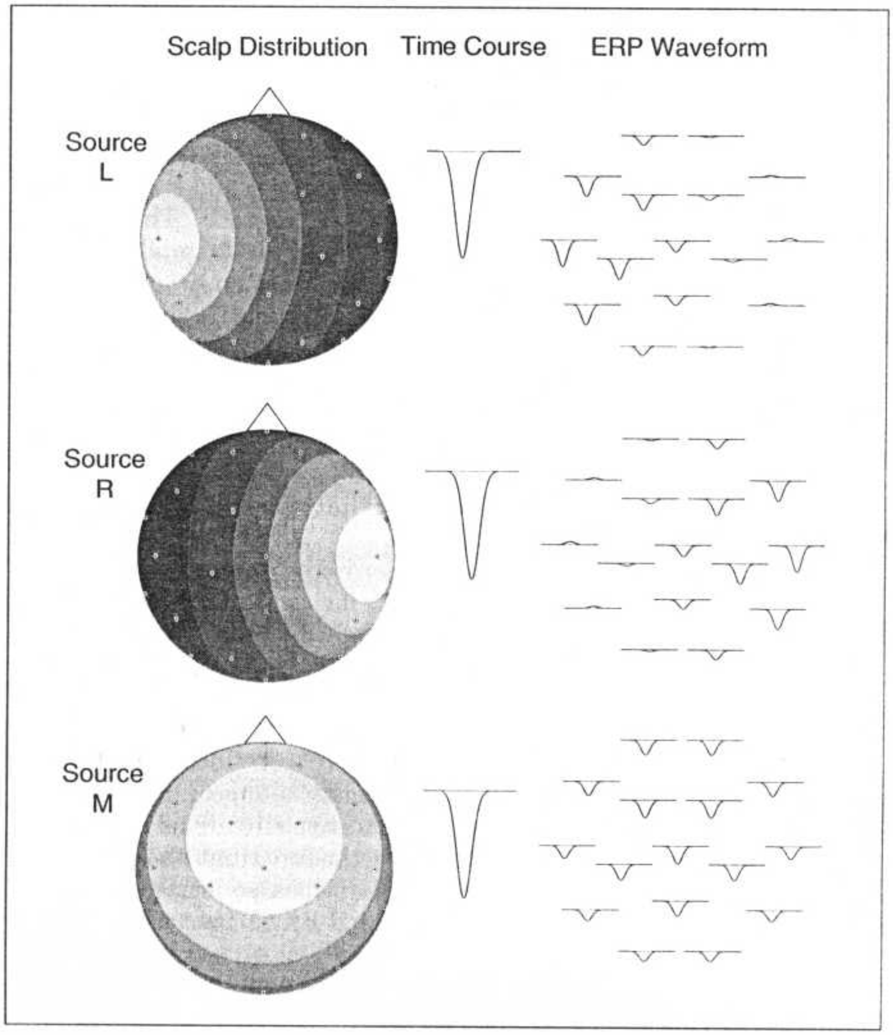

FIG. 7.3. Scalp distribution, time-course and resulting ERP waveform for three different simulated neural generators. Sources L, R and M are represented by radially oriented dipoles located on the left, right and middle of the head, respectively.

different locations on the scalp generated by each of these dipoles are shown on the right. Clearly, the scalp distributions of the potentials generated by these three dipoles overlap greatly. In fact, dipole M would affect peak amplitude at all the electrodes. Thus, there is no simple measure at any electrode that can be used as a pure index for the activity of any of the three processes.

It may be argued that different components can be distinguished based on their scalp distributions, since the potentials generated by each of the dipoles L, R and M are quite distinguishable. However, consider the example shown in Figure 7.4 wherein the processes L and R are both activated but with slightly different latencies. The scalp distributions produced by the. combination of these two dipoles, as shown on the bottom at three different latencies, is quite different from either one alone. In fact, the combined scalp distribution of L and R looks somewhat similar to that produced by dipole M (see Fig. 7.3). This example also illustrates another common misconception in ERP analysis based on peak amplitude or area measurements. It is often assumed that a peak reflects the same process at all electrodes, such that differences in peak latency at various locations can be taken to reflect propagation of the process from one side of the head to the other. However, the current example shows that continuous changes in peak latency across the scalp may instead be due to multiple fixed dipoles with different but overlapping time-courses. In fact, as we shall see later, changes in scalp distribution over time necessarily imply that several generators with different time-courses must be involved.

The fact that different brain generators produce widespread, overlapping potential distributions makes it essential to have a method for extracting the signal produced by each generator. As we see in the next section, if the scalp distribution of each generator is known, then the contribution of each generator is given by a weighted sum of the potentials recorded at each electrode, with the weights given by the least-squares solution. This makes it possible to determine the time-course of activation of each generator, and in turn to determine whether or not the same generator is involved in different experimental conditions. By this account, the contribution to the ERP of a particular source can be thought of as a component, and we can investigate how this component is affected by various experimental manipulations.

Unfortunately, however, we usually do not know the scalp distributions of all the generators involved in a given experiment. The problem of finding these scalp distributions is essentially equivalent to localizing all the generators, which, as we see in the next section, is a decidedly non-trivial problem. Nonetheless, as we show next, it is still

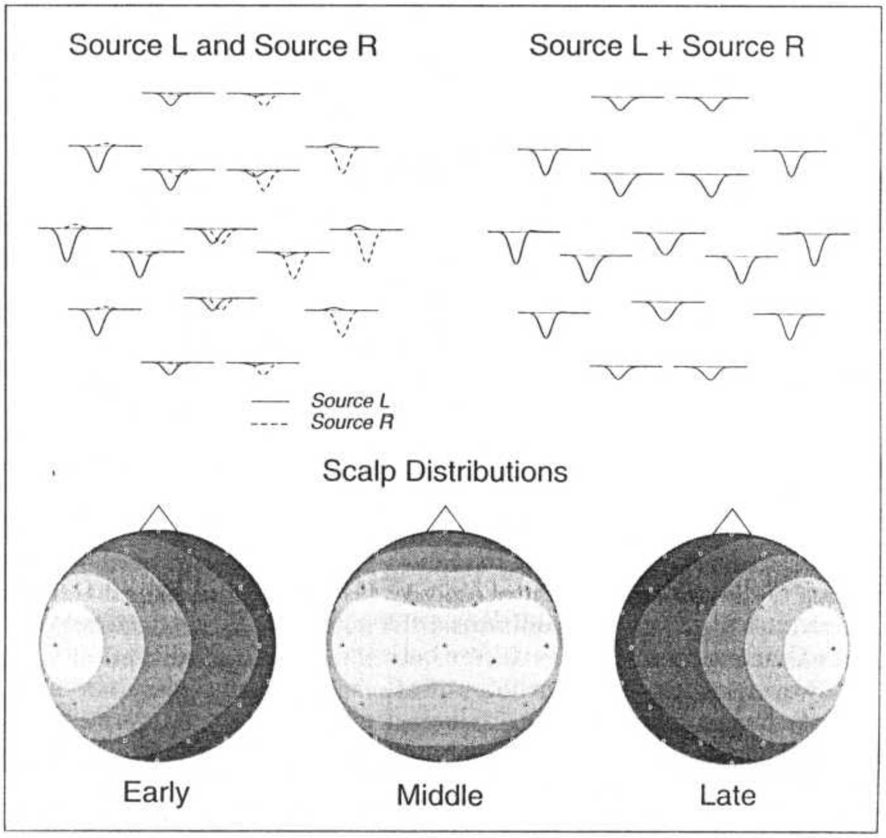

FIG. 7.4. Spatial superpositioning of ERP waveforms produced by the two generators L and R. The difference in latency between sources L and R results in a gradual change in scalp distribution over time.

possible to draw certain important inferences about the underlying brain activity from ERP recordings without localizing the sources.

First, let us compare the ERPs from two experimental conditions (A and B). If A-ERP and B-ERP are (statistically) indistinguishable (across all electrode sites), then we can safely conclude that the pattern of data appears consistent with the hypothesis that the two conditions are identical. But can we safely offer this as evidence or proof that the brain activity evoked by the two conditions is identical? No! There are several reasons, other than the actual identity of the underlying neural activity, as to why the ERPs from two conditions could appear to be identical. For example, the EEG and MEG simply may not be the correct techniques for detecting the difference because the configuration of active generators generate no dipole moment (so-called closed fields). Another possible way we could easily be led astray would be if the measurements were not sensitive enough due to inappropriate temporal and/or spatial sampling, a poor recording technique or a similar factor.

Conversely, if the A-ERP and B-ERP do differ reliably, then it is safe to conclude (or as safe as science ever allows us to be) that the brain activity and the mental activities it subserves are different in the two conditions. For the moment we need not concern ourselves with either the nature or the cause of the difference. The fact is that the ERP difference indicates that some difference exists and, sometimes, being able to conclude that two conditions are different is a critical finding in and of itself. Any such ERP difference, obtained when by all psychological accounts the conditions were expected to be identical, should lead to a reformulation of the current working hypothesis that supports or at least allows the difference.

Of course, identifying a difference is merely the first step in a much longer process of ERP analysis. At a minimum, we can use the timing of the onset of an ERP difference to make additional inferences about the timing of the associated mental activity. If time t is the earliest time at which ERPs from the two conditions differ significantly, then we can conclude that the brain activity differs between the two conditions at time t. However, we may not conclude that there was no difference in brain activity before time t, because such differences simply may not be detectable with ERPs, as discussed above. In other words, the onset of the latency of the ERP difference must be taken as an upper limit on the time by which the brain must have processed the stimuli sufficiently to distinguish them.

It is also possible to make some inferences based on the spatial distribution of the ERPs. If a given condition involves only a single generator, then the ERP waveform for that condition must have the same scalp distribution across its entire extent. That is,

$$\vec{\mathbf{x}}(t) = \vec{\mathbf{g}} \cdot \mathbf{s}(t)$$

for all time points t, where $\vec{\mathbf{x}}(t)$ is the electric or magnetic recording vector, $s(t)$ is the strength of the generator and $\vec{\mathbf{g}}$ is the gain vector for the generator. Practically speaking, this means that if the scalp distribution changes over time we can conclude that there must be more than a single generator involved. In fact, we can go further than that by applying principal component analysis (PCA) to determine the minimum number of spatial basis vectors needed to account for the waveforms (Donchin 1979, Press et al. 1990). If a given set of ERP waveforms requires k basis vectors, i.e. PCA finds k significant "components",[4]

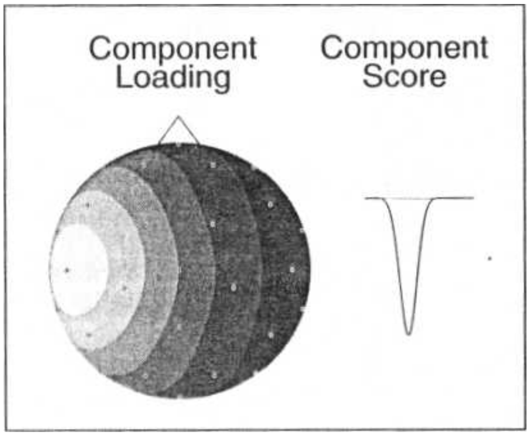

FIG. 7.5. Result of applying spatial PCA to the ERP waveform produced by the single generator L. Note that the component loading and score accurately reflect the scalp distribution and time-course, respectively, of source L as shown in Figure 7.3.

then there must be at least *k* generators involved. Applying this PCA to the ERP produced by a single generator L in Figure 7.3 yields a single significant principal component, with the scalp distribution (known as the "loading") and time-course (known as the "score") shown in Figure 7.5. Note that the spatial distribution and time-course of this principal component are the same as that of generator L. Applying this analysis to an ERP waveform produced by two generators, such as the sum of dipoles L and R shown in Figure 7.4, yields two significant components, with the scalp distributions and scores shown in Figure 7.6. Note that, while the number of principal components in this case accurately reflects the number of generators,[5] the scalp distributions of the principal components and their scores do not reflect the actual scalp distributions and time-courses of the generators. This illustrates the point that PCA may be useful for providing a (lower) estimate of the number of generators, even though the principal component vectors do not necessarily correspond to the scalp distributions of actual sources, and their scores do not necessarily correspond to the time-courses of the actual sources.

In order to determine the actual scalp distributions and time-courses of activation of the generators of our observed ERPs and ERFs, we first have to determine the locations of these generators. In the next section we examine this so-called "source localization problem" more closely.

7.1.3 Source localization

Recall that if the locations and orientations of a set of *k* dipoles are known, then the combined electric and/or magnetic measurements can be expressed as a weighted sum of *k* gain vectors $\vec{\mathbf{g}}_j$ (see equations (13) and (14)),

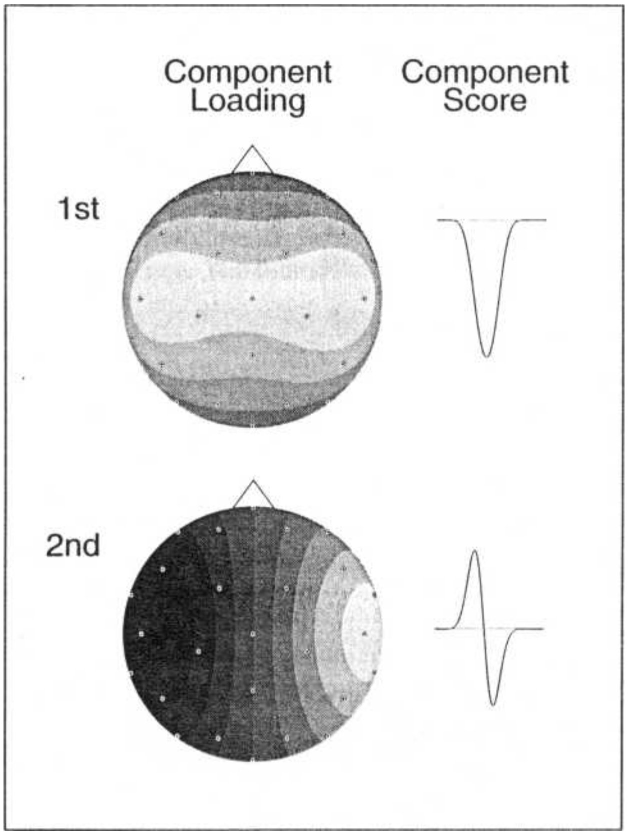

FIG. 7.6. Result of applying spatial PCA to the ERP waveform produced by the two generators L and R. Note that, while the number of principal components (two) accurately reflects the number of sources, the component loadings and scores do not reflect the scalp distribution or time-course of either generator.

$$\vec{\mathbf{x}}(t) = \sum_{j}^{k} \vec{\mathbf{g}}_j \cdot \vec{\mathbf{s}}_j(t) = \mathbf{G}\vec{\mathbf{s}}(t) \tag{15}$$

where the gain vectors $\vec{\mathbf{g}}_j$ depend on the locations and orientations of the dipoles, the locations of the sensors, and the shape and conductive properties of the head (Grynszpan & Geselowitz 1973, Cuffin & Cohen 1977, Nunez 1981, Oostendorp & van Oosterom 1989, Hamalainen 1993). Thus, the so-called "forward problem" of determining the electric potential and magnetic field produced by a given set of dipoles has a well-defined and unique solution. On the other hand, the so-called "inverse problem" of determining the locations, orientations and time-courses of the set of dipoles producing the electric and magnetic recordings is ill posed, i.e. it has no unique solution. In other words, there are, in general, infinitely many distributions of dipoles inside the brain which are consistent with any set of electric and/or magnetic recordings (Nunez

1981, Sarvas 1987). In order to overcome this fundamental ambiguity, it is necessary to impose some additional constraints on the solution.

The most common approach to this problem is to model the generators as some fixed number of so-called "equivalent dipoles", each representing the activity within some volume of tissue. The electric and magnetic recordings can be expressed as

$$\vec{\mathbf{x}}(t) = \sum_{j}^{k} \vec{\mathbf{g}}_j\left(\vec{\mathbf{r}}_j, \vec{\mathbf{d}}_j\right)\vec{s}_j(t) \qquad (16)$$

where k is the number of equivalent dipoles, $s_j(t)$ is the strength of the jth dipole, and the gain vector $\vec{\mathbf{g}}_j\left(\vec{\mathbf{r}}_j, \vec{\mathbf{d}}_j\right)$ for the jth dipole is an explicit function of the dipole location $\vec{\mathbf{r}}_j$ and orientation $\vec{\mathbf{d}}_j$. The dipole locations, orientations, and strengths can be estimated by the method of least-squares (Oostendorp & van Oosterom 1989, Scherg 1989), i.e. by minimizing the error measure

$$E = \int_{t_0}^{t_1} \mathrm{d}t \left\| \vec{\mathbf{x}}(t) - \vec{\mathbf{x}}_{obs}(t) \right\|^2$$

where $\vec{\mathbf{x}}_{obs}(t)$ is the observed electric and magnetic recording, and $\vec{\mathbf{x}}(t)$, the predicted recording, is given by Equation (16). Note that, while the relationship between dipole strength and electric or magnetic recordings is a simple, linear one, the recordings depend on the dipole location and orientation in a non-linear way. No efficient method for minimizing such non-linear cost functions is known, making it impractical to localize more than a few dipoles using this approach. Moreover, in general, it is impossible to know *a priori* how many equivalent dipoles to use.

Another approach to the inverse problem is to model the brain electric or magnetic generators as an essentially continuous dipole distribution, rather than as some pre-specified number of discrete equivalent dipoles. As discussed in a previous section, most of the observed electric and magnetic recordings are thought to be generated by post-synaptic currents in the apical dendrites of cortical pyramidal cells. Hence, we may assume that the dipole moment is zero everywhere except in the cortical gray matter, and that the local dipole moment is oriented perpendicularly to the cortical sheet. Given these assumptions, the inverse problem reduces to one of estimating dipole strength everywhere over the folded cortical surface.

Since dipole strength and electric or magnetic recordings are linearly related, the problem is a linear one. However, the number of dipole patches needed adequately to represent the cortical surface is much greater than the number of electric and/or magnetic sensors that can practically be applied, and hence the problem remains underdetermined. A common way to deal with this problem is to choose the so-called "minimum-norm solution", that is, the "shortest" dipole strength vector $\bar{\mathbf{s}}(t)$ satisfying

$$\bar{\mathbf{x}}_{obs}(t) = \mathbf{G}\bar{\mathbf{s}}(t)$$

(Hamalainen & Ilmoniemi 1984, Smith et al. 1990, Wang et al. 1992, Dale & Sereno 1993). The minimum-norm solution $\hat{\mathbf{s}}(t)$ is given by

$$\hat{\mathbf{s}}(t) = G^{\dagger}\mathbf{x}(t) \tag{18}$$

where $$\mathbf{G}^{\dagger} = \mathbf{G}^{T}\left(\mathbf{G}\mathbf{G}^{T}\right)^{-1}$$

is the Moore-Penrose pseudo-inverse of the gain matrix **G**. Although the minimum-norm constraint does provide a unique solution to the inverse problem, there is no guarantee that the solution is the correct one. In order further to disambiguate the inverse problem in a principled way, it is essential to impose additional constraints that are based on biological insights (Dale & Sereno 1993).

A particularly promising source of such additional constraints is functional imaging techniques, such as functional magnetic resonance imaging (fMRI) and, to a lesser extent, positron emission tomography (PET) (see Ch. 6). Although these techniques provide little information about the fine-grained temporal sequence of brain activity, they do provide information about average brain activity with relatively high and uniform spatial resolution (Belliveau et al. 1991, Ogawa et al. 1992). It seems reasonable to assume that the bioelectrical activity which is responsible for the observed electric and magnetic recordings is also likely to cause changes in metabolic and haemodynamic processes, which can be seen using fMRI or PET. The so-called linear estimation approach (Smith et al. 1990), of which minimum-norm estimation is a special case, makes it possible to use such functional imaging data as "soft" constraints on the inverse solution (Dale & Sereno 1993), thus potentially combining the spatial resolution of fMRI and the temporal resolution of EEG and MEG.

7.2 THE TERMS USED IN COGNITIVE ELECTROPHYSIOLOGY

By contrast to every other brain imaging technique, cognitive ERP research has a respectable history - 30 years of research unearthing the sensitivity of scalp activity to sensory, perceptual, motor and cognitive processes. It is important to note that much of this work was carried out during a period when there were no electrode caps (i.e. each electrode was placed by hand) and amplifiers and computing power were prohibitively expensive. Moreover, by today's standards, the computers were excruciatingly slow and, perhaps for related reasons, few sophisticated analytical or graphical techniques existed. As a consequence, an undue emphasis was placed on looking at the ERP waveform, specifically at the largest effects on peaks and troughs that could readily be discerned with the eye. In the previous section we detailed why this approach may be problematic. However, whatever might have been missed, the effects that have been reported tended to be the largest, the most reliable and undeniably real; thus, each must be explained by any viable theory of the function under study. Moreover, despite the technical differences between the various brain imaging techniques, it is our belief that much time can be saved by using this history to guide contemporary research in brain imaging for cognitive purposes. No single chapter could do justice to all the published observations on ERPs and their implications. Thus, this section is intended not to encourage continued peak labelling, but rather to provide the reader with an idea of the vast data base on cognitive ERP effects via quick reference to most of the terms in the various cognitive domains that can serve as keywords in library searches.

7.2.1 Event-preceding negativities including the CNV, O-wave, E-wave, PINV and SPN

The behaviourist tradition led to the discovery of the first of many "endogenous" ERP components linked to some cognitive process. While the primary aim of this research was to use exogenous evoked potential (EP) components to examine effects of conditioning on sensory processing, one of the more startling findings was a scalp negativity during the interval between a warning stimulus and the warned event (Fig. 7.7). Grey Walter et al. (1964) called this shift the *contingent negative variation* (CNV) or *expectancy wave* to underscore that it was the contingency between the stimuli and not the processing of either *per se* that was critical for its elicitation.

The early research revealed that the CNV varies systematically in its distribution across the scalp as a function of stimulus modality, task parameters and response requirements. Nonetheless, the negativity is referred to as *the* CNV, presumably to highlight the functional equivalence of the underlying processes, although there is no consensus as to exactly what these are. The proposals include cortical excitability, wherein the specific region of the cortex about to receive information was prepared to do so, arousal, attention, uncertainty, preparedness,

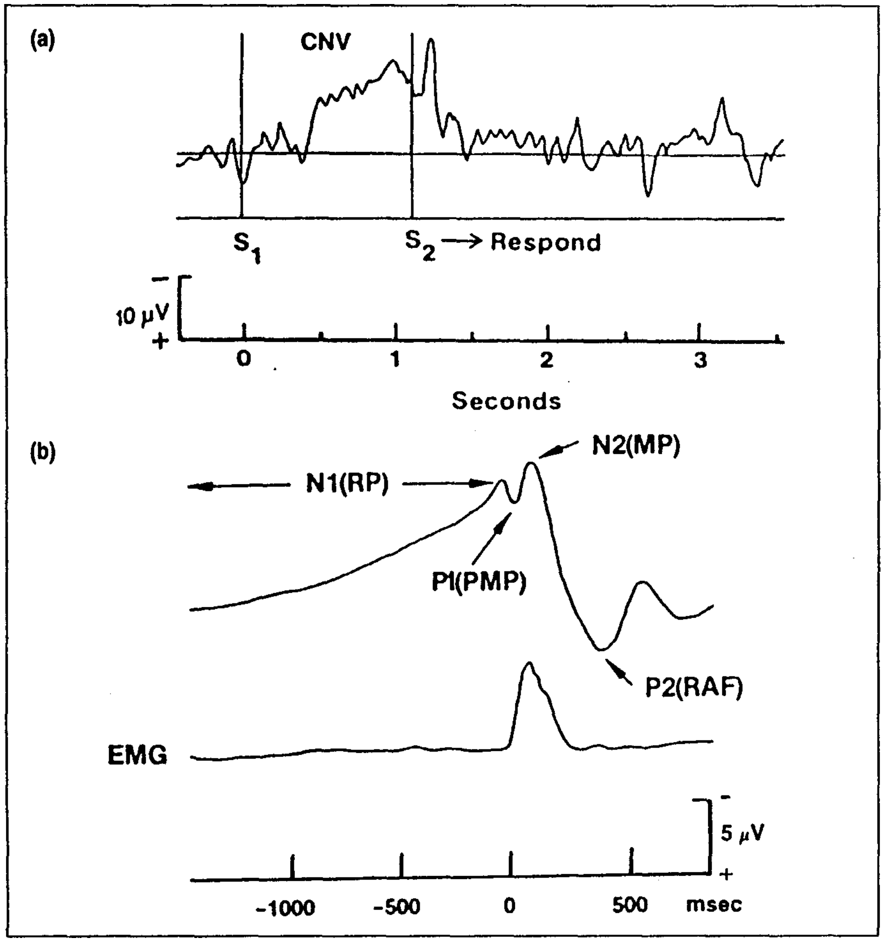

FIG. 7.7. (a) The slow negative potential, called the contingent negative variation (CNV), which builds during the interval between two stimuli. (b) The basic components of a movement-related potential elicited by a voluntary hand or arm movement. The waveform is labelled according to two of the more common nomenclatures. RP, readiness potential; MP, motor potential; PMP, pre-motion positivity, RAF, reafference potential. Movement onset is at zero. Between the movement-related potential and the time-line is the muscle activity (electromyogram) recorded from the responding arm. This figure was originally published as Figure 3 in Was and Hillyard (1985). Reprinted by permission of Lippincott/Harper & Row.

receptiveness, resource mobilization, level of effortful involvement and motivation (for a review see McCallum & Curry 1993).

In the 1970s, studies with long foreperiods led to the suggestion that the CNV did not index a single cognitive process but rather the sum of an *orienting* or *O-wave* that reflected processing of the warning stimulus and an *expectancy* or *E-wave* that developed in anticipation of the impending stimulus and/or response. To this day, it remains an open question whether there exists a subcomponent to the CNV that is not strictly tied to either the stimuli or the upcoming response but only to the contingency between the two. A recent proposal equates the "true" CNV with the *stimulus preceding negativity* (SPN) (e.g. Damen & Brunia 1994).

Typically, the CNV resolves (i.e. returns to baseline) or falls into a late positive component. However, under certain circumstances or in some patient populations (e.g. schizophrenic, neurotic), it is maintained for some time following the imperative stimulus, and is thus referred to as the *post-imperative negative variation* (PINY).

More recent classifications of slow potentials (longer than 1 s in duration) distinguish between those related to preparation, anticipation and expectation (largest at parietal sites) and those related to holding information in working memory (largest at frontal sites). Such investigations are based on the working hypothesis that the topography of the slow waves reflects the relative activity of cortical areas involved in solving the problem at hand, while their durations and amplitudes index the duration and degree of effort invested in particular processing steps, respectively (e.g. Roesler & Heil 1991).

7.2.2 Movement-related activity including the RP or BSP, LRP or CMA, MPN and ERN

At about the same time as the discovery of the CNV, a slow negative shift with a somatotopic distribution along the central sulcus was observed preceding self-paced voluntary movements; this was called the *Bereitschaftspotential* (BSP) or *readiness potential* (RP) (see Fig. 7.7b). Subsequently, movement-related potentials (MPs) were analysed into a series of subcomponents preceding and following movement onset (e.g. Shibasaki et al. 1980).

The movement potential component of greatest cognitive interest has been the RP, as it represents brain activity the generation of which is endogenous rather than stimulus driven. The RP starts approximately is prior to a voluntary movement at the scalp, subdurally (Neshige et al. 1988) and in magnetic recordings (e.g. Cheyne et al. 1991, Kristeva et al. 1991). Given that the RP precedes movement onset, varies with responding member, specific features (force, speed and complexity) of the impending movement, and performance, it has been taken as an index of motor preparation. Some researchers prefer that the RP be replaced by a more neutral term such as *movement-preceding negativity* MPN (Bocker et al. 1994) so as to mirror its counterpart, the stimulus-preceding negativity.

The RP prior to hand movements is larger over contralateral than ipsilateral central sites. This fact has been used to derive a measure called the *lateralized readiness potential (LRP)* or *corrected motor asymmetry (CMA)* from activity time-locked to the stimulus. Specifically, the LRP derivation is based on the notion that the late half of the CNV in a warned reaction-time task must include the RP. One common method (among several) of calculating the LRP involves: (1) recording from left and right central sites for movements with each hand; (2) subtracting the potential ipsilateral to the responding hand from the potential contralateral to it; and (3) averaging the values for the two hands. The resulting average measure is the LRP. In this way asymmetrical activity that is the same for both left- and right-hand movements is eliminated while the activity associated with side of movement remains (reviewed in Coles et al. 1995).

Studies of the LRP led to the discovery of the the *error-related negativity (ERN)* on those trials in a choice reaction-time task in which the wrong response was executed (e.g. Gehring et al. 1993, Falkenstein et al. 1995); presumably the ERN reflects a system involved in the detection of and compensation for response errors.

7.2.3 Information processing effects including P300, P3a, P3b, novel P3, LPC, N200, SW, MMN, P165, Na and Dm.

The other ERP component routinely used to analyse the structure of the human information processing system was discovered as the heyday of the behaviourist tradition was drawing to a close and the information processing approach to cognition was taking hold. From the information processing point of view, cognition is an ordered sequence of processing stages, each of which performs a specific mental operation and takes a measurable amount of time to complete. Psychologists have been challenged to discover the stages (representations and processes), their durations and their order of occurrence. The great hope of the information processing approach is that psychological functions can be mapped onto brain functions via the language of information, defined in terms of reduction in uncertainty.

In the late 1960s, a positive ERP component with a peak latency around 300ms (P300) was offered as a correlate of stimulus uncertainty because its amplitude varied inversely with stimulus uncertainty and its latency indicated when the uncertainty was reduced (for reviews see Pritchard 1981, Donchin & Coles 1988, Johnson 1988). The important finding was that exactly the same physical stimulus sometimes did and sometimes did not elicit a P300 depending upon the task demands and decisions rendered, i.e. upon its informational value. For instance, a large P300 is elicited by the presence of a stimulus that is unexpected as well as by the absence of one that is expected.

The relationship between the P300 and expectancy has been studied most extensively in the *oddball task*. In this paradigm individuals are asked to detect improbable (5-25%) targets or "oddballs" that occur unpredictably in a random sequence of non-target, non-oddball, so-called "standard" or background stimuli. Although the oddball task is considered the prototypical P3-eliciting paradigm, even in this task the ERPS to targets often contain both an early, frontally distributed positivity (P3a) and a later, larger and posteriorly distributed postivity (P3b) (e.g. Squires et al. 1975). These two subcomponents of the P3 often overlap and are difficult to disentangle. Other components characteristic of ERPs to oddballs include a modality-dependent negativity (N200) preceding the P300 (e.g. Simson et al. 1977), and a subsequent *slow wave* (SW) that is positive posteriorly but negative frontally (e.g. Ruchkin et al. 1982) (Fig. 7.8).

As long as people pay some attention to the stimulus sequence, the amplitude of P3 to the oddballs is inversely related to its probability of occurrence, with contributions from its probability within a given period of time (*temporal probability*), globally across an entire block

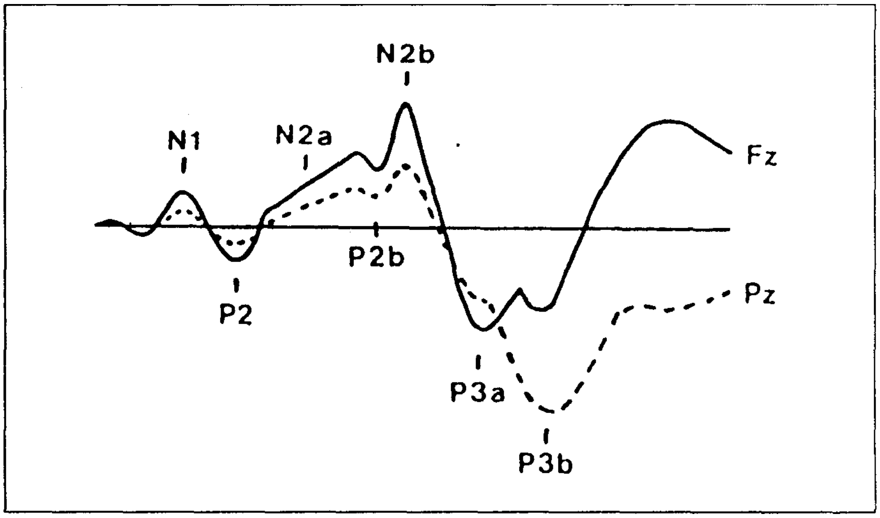

FIG. 7.8. Schematic representation of the component structure for the ERP to a deviant stimulus under detection conditions including the N2a (MMN), N2b, P3a, P3b and SW components. The solid line represents recordings from a midline frontal site and the dashed line the recording from a midline parietal site. Reprinted from Naatanen et al. (1982) with kind permission of Elsevier Science NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

of trials (*global probability*), and more locally in terms of both the immediate stimuli (*local probability*) and the fine structure of the stimulus sequence (*sequential probability*). It is important to note, however, that it is subjective not objective probability that is the more critical determinant of P3 amplitude (reviewed in Picton & Hillyard 1988). For example, in an oddball task when more than two different stimuli are used, P300 amplitude is determined by the probability of the relevant stimulus category rather than the probability of each individual stimulus. In short, the P300 seems to index the operation of adaptive brain systems that anticipate the occurrence of significant environmental events and react to unexpected discrepancies therein. Specific proposals have suggested that the P300 reflects updating of working memory (Donchin & Coles 1988), cognitive closure (Verleger 1988) and transfer of information to consciousness (Picton 1992).

Remarkably similar P300s are recorded in the visual, auditory and tactile modalities in a variety of paradigms. Again, it is the presumed functional significance of the positivity and the experimental conditions that lead to its elicitation, rather than the identity of its underlying neural generators that serve as the criteria for defining a P300. As yet there is no general consensus on the generator(s) of the P300, although a number of sites, including the hippocampus, parietal regions, locus coeruleus and temporoparietal junction, have been proposed, examined and implicated (see e.g. Swick et al. 1994).

The peak latency of the P300 to task-relevant stimuli varies from around 300 to 1000ms as a function of the difficulty of the categorization. By contrast to RT (reaction time) measures, the peak latency of the P3b is disproportionately sensitive to stimulus evaluation (encoding, recognition, classification) relative to response selection and execution processes (e.g. Magliero et al. 1984). Accordingly, P3b latency has been taken as an upper limit on the time it takes to reach the perceptual decision that an informative event has occurred. The latency of the preceding N200 likewise varies positively with the difficulty of the discrimination for stimulus categorization (Ritter et al. 1979).

Identifying a positivity as *the* P3 is problematic. Most researchers have skirted the problem by referring to any positivity after 300ms as a *late positive component* (LPC) or simply a member of the P3 family. Others have placed greater emphasis on a topographical criterion, although often implicitly in combination with sensitivity to experimental manipulations: thus, the "true" P3b or parietal P3 is sensitive to probability and task relevance, while the P3a or frontal P3 is smaller, earlier, and presumably does not require attention. It is unclear by these criteria whether the P3a differs from the *novel* P3 which also is early, has a frontal maximum and is elicited by infrequently occurring "novel" events such as dog barks interspersed in a sequence of tones in an oddball task (Courchesne et al. 1975). Similarly controversial is whether the so-called *difference related to memory* (Dm) is merely a modulation in P3 amplitude or an endogenous event that just happens to overlap with the P3, although one can use the measure regardless of the answer. The Dm refers to the greater late positivity during encoding (study) of items that will later be remembered, relative to those that will not; it is hypothesized to reflect some aspect of elaborative processing (Paller et al. 1987). The Dm and P3b have different scalp distributions, as do Pas in different situations (Johnson 1993).

The N200 component, often preceding the P3b, since its discovery, has experienced a similar fractionation (Ma, N2b, N2c) based on its different distributions and functional roles (sensory processing, orienting). By some accounts, the N2a in an oddball task is also known as the *mismatch negativity* (MMN), since its amplitude is a function of the degree of mismatch between different standard stimuli (Naatanen 1992), even if the stimuli are being ignored (see Fig. 7.8). Other components such as the *P165* and *Na* also have been identified following various subtractions of ERPs to targets and non-targets in variants of the oddball task with and without attention (Goodin et al. 1978, Ritter et al. 1982).

7.2.4 Attention-related effects including N1, Nd, processing negativity, P1 and selection negativity

A major issue that arose from the view of the mind as a limited-capacity information processor was the exact location of the "attentional" bottleneck. Electrophysiological studies designed to address this issue have implicated both early (N1 and P2) and later components of the ERP. Initially, the larger negativity observed in response to exactly the same stimuli when they were attended than inattended was called the *N1 attention effect* and presumed to be a physiological index of an early selection process. Experiments in the late 1970s, however, showed that neither the onset nor the duration of this enhanced negativity always mirrored that of the exogenous N1 component; the effect was early for easy selections but later for more difficult ones. As this effect of auditory attention was best visualized by subtracting the ERPs to stimuli when unattended from those to the same stimuli when attended, it was called the *Nd* or *negative difference*; the same effect is sometimes also referred to as the *processing negativity* (for a review see Naatanen 1992). Nd amplitude is presumably some function of the amount of processing resources allocated for focused or divided attention, although the nature of the processing resources remains unknown. It is now argued that the Nd comprises an early frontocentral phase and a later more frontal phase (Naatanen 1992).

ERP studies of selective attention have also been conducted in vision. Relative to unattended stimuli, those in the focus of attention produce enhanced sensory-evoked P1 (80-100ms) and N1 (140-190ms) components in tasks involving sustained attention, spatial cueing and visual search. The P1 effect has a focus over the ventrolateral extrastriate cortex, while the N 1 effect has a somewhat more dorsal focus over occipito-parietal cortex. Selection among stimuli based on features such as colour, spatial frequency, contour, size and shape is accompanied by a larger, longer latency negativity between 150-350ms over posterior sites and is called the *selection negativity* (SN) (for a review see Hillyard 1993).

7.2.5 Language-related effects including N400, N280 or LPN, P600 or SPS, and LAN

When people read sentences such as "He shaved off his moustache and city" versus "He shaved off his moustache and beard", the most striking feature of the ERP to the anomalous (as opposed to the expected congruent) word is a negativity starting around 200ms and peaking around 400ms (N400); (Fig. 7.9). An N400 is reliably elicited by semantic anomalies in written text and speech at different points in a sentence as well as in a variety of languages, including the handshapes of American Sign Language (for a review see Kutas & Van Petten 1994). Despite this family resemblance, N400s do differ in latency and scalp distribution, even within presumably similar experimental tasks. The problem of uniquely identifying a negativity as an N400 is further exacerbated by comparisons across paradigms employing single words in unstructured lists, word pairs related along various dimensions, and sentences in tasks requiring different decisions (such as lexical decisions, grammatical judgement).

All word-like stimuli elicit some N400 activity, its amplitude being sensitive to a variety of factors including frequency of usage, repetition and predictability. ERPs to words also contain a negativity at around 280ms (N280) which, unlike the right posterior predominance of the N400, has a maximum over left frontal sites (Neville et al. 1992). The functional significance of this negativity (also known as the *lexical processing negativity* (LPN)), is unknown, although its latency does vary systematically with the frequency of the eliciting word (King & Kutas 1995a) (see Fig. 7.9).

At least three different classes of ERP events have been described in association with more syntactic aspects of sentence processing: (a)

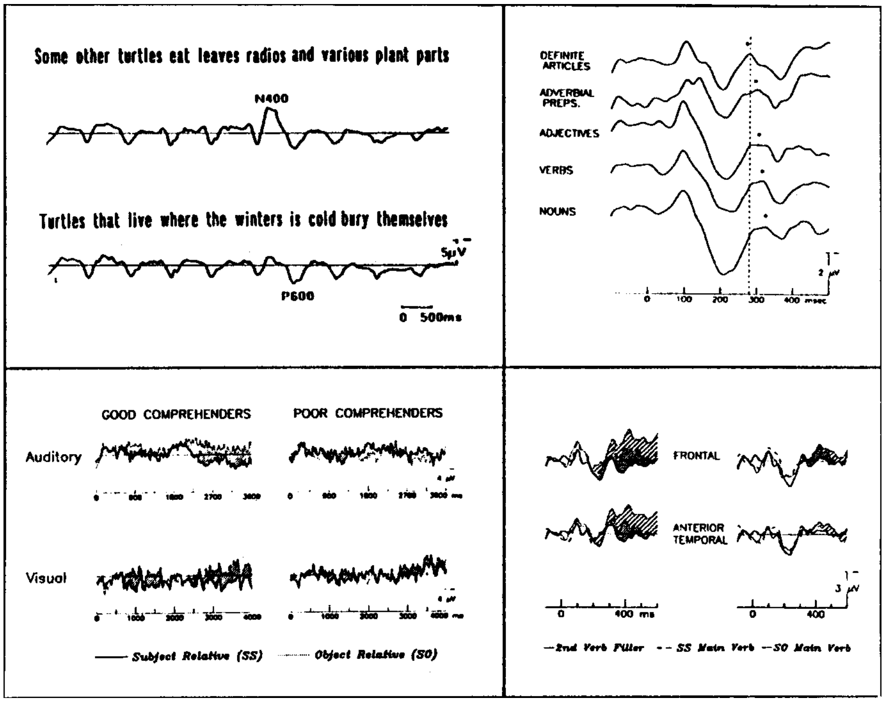

FIG. 7.9. Various ERP effects elicited during language processing. (Top left) Over sentence average ERP data showing an N400 elicited by semantic violations and a P600 elicited by grammatical violations occurring in written text read one word at a time for comprehension. (Top right) The lexical processing negativity (LPN) to various word classes, showing how LPN (previously known as N280) varies in latency with frequency and length. From King & Was (1995a). (Bottom left) Over sentence averages for written and spoken sentences with embedded relative clauses for good and poor comprehenders. Auditory and visual data are from two different subject groups. Data from Mueller et al. (1977). (Bottom right) Left anterior negativity (LAN) for main clause verbs in three different sentence types, two with embedded relative clauses (subject and object relatives, SS and SO, respectively) and one with no clauses (filler). Data from King and Kutas (1995b).

the *P600* or *syntactic positive shift* (sps), which may be a member of the P3 family, but is elicited by some types of grammatical error (see Fig. 7.9); (b) a frontocentral negativity with a left hemisphere tendency, which is also seen in word pair studies; and (c) a *left anterior negativity* (LAN) from 300 to 700ms or so, elicited by words that signal the need for reference back to an item earlier in the sentence (see Fig. 7.9), which at a non-linguistic level may be related to working-memory usage (for a general review and further references see Kutas & Kluender 1994, Kutas & Van Petten 1994, Osterhout & Holcomb 1995).

7.3 EXAMPLES OF ERP STUDIES IN COGNITIVE NEUROSCIENCE

7.3.1 Mental chronometry

People generally take (a) longer to reject "brane" than "hime" as words in the English language, (b) longer to pronounce "dough" than "cough", (c) longer to name the colour of the ink in which a word is printed if the word refers to a different colour than if it refers to the same colour, (d) longer to respond to a particular letter (H) when it is surrounded by a different letter (SSHSS) than when it is surrounded by the same letter (HHHHH), and (e) longer to respond to a stimulus to the right of fixation with the left hand and a stimulus to the left of fixation with the right hand than vice versa. Understanding these patterns of behaviour continues to be a significant component of experimental psychology and cognitive neuroscience.

According to the information processing framework, the answer to each of these questions is a matter of pinpointing the stage(s) at which there is interference that contributes to the slowed RT. Both RT and ERP measures are useful in this regard; in particular, ERPs provide dependent variables that are sensitive to the activity of relatively circumscribed parts of the processing system. For example, variables such as stimulus-response compatibility that alter the timing of response processes typically have very little, if any, effect on P3 latency, whereas manipulations that increase the difficulty of perceptual discriminations and categorizations do.

This said, how can such observations be used to determine why RTs in some of the conditions outlined above are slowed relative to others? In brief, several laboratories have done so by comparing the effects of manipulations like these on RT, P3b latency, electromyographic (EMG) or muscle activity, and LRP measures (for a review see Coles et al. 1988). Whenever P3 latency (defined by functional and distributional criteria) is unchanged while RT is prolonged, then the prolongation is attributed to some aspect of response selection or execution rather than before it. On the other hand, when P3 latency and RT are both prolonged, then the onus is placed on some aspect of stimulus evaluation (with or without the involvement of response-related processes). Moreover, whenever response-related processes are implicated, then the nature and time-course of their contributions can be delineated by examining the temporal relations among the EMG, the actual response and the LRP. Such data have been used to pinpoint the locus of interference in a number of paradigms wherein some "incongruence" or "conflict" has resulted in a delayed overt response. The LRP is taken to reflect response preparation and its timing an indication of when; moreover, its polarity can be taken as a sign of what response has been prepared.

On the whole, the patterns of brain, muscle and behavioural activity in conflict situations have revealed that on many incongruent trials, the incorrect response had in fact been activated before the correct one. The results of these experiments indicate that information flow is not always discrete (all-or-none) in the strictest sense, as partial analysis of the stimulus does indeed affect the response system (for reviews see e.g. Coles et al. 1988, 1995). The ERP data have thus been instrumental in diverting the research focus from choosing between all-or-none versus continuous models to the delineation of the factors that determine when each is the more appropriate characterization. Data from these types of experiment have also demonstrated that different stimulus features are not only processed independently of each other but also at different rates. It is likely that it is from this temporal patterning of feature selection that an apparent information processing structure emerges.

It is important to note that these ERP components are most useful in answering questions of this type when used in combination with, rather than instead of, the more traditional chronometric measures. That said, the P3 and LRP are especially valuable indices of informational transactions because they can be measured even on trials where no response need be made, as in the NO-GO trials of a GO/NO-GO paradigm

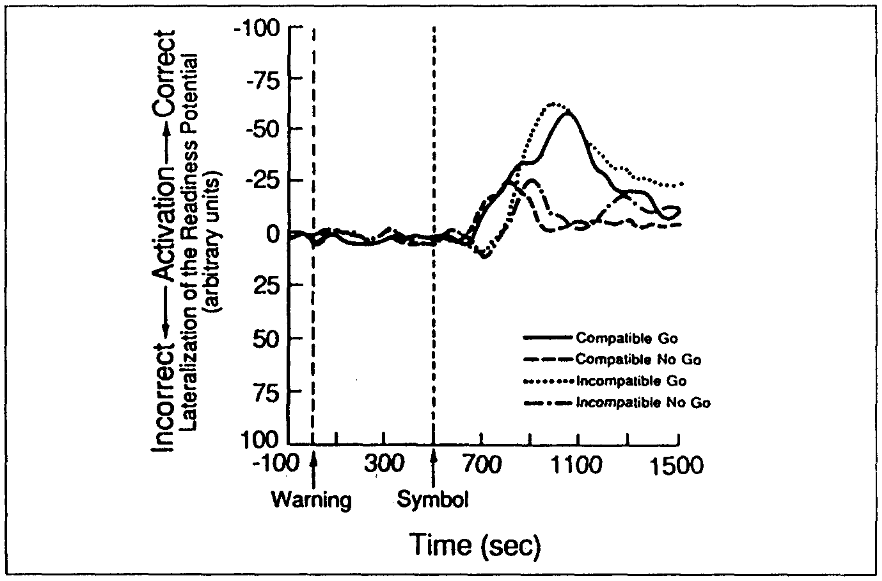

FIG. 7.10. Lateralized readiness potential (LRP) on GO/NO-GO trials. Note the presence of significant LRP on NO-GO trials. From Osman et al. (1992) with permission of the authors and publisher.

(e.g. Osman et al. 1992) (Fig. 7.10). We can determine the tune-course of feature extraction and information use by placing contingencies on how people respond to certain stimulus configurations. In a typical example, response contingencies are set so that one hand is equated with stimuli in one location and the other hand with stimuli in a different location, but whether or not a response is actually required depends on stimulus colour. The latency and polarity of the LRP under such circumstances can be used to determine whether colour is processed before or after location in space. This general logic can be used to test other hypotheses about the relative timing of distinct processes in a variety of complex acts such as speech production. Moreover, even when a person responds, LRP parameters can be used to reveal if and when they changed their mind, so to speak.

7.3.2 Attention

ERPs have been particularly useful in investigating the timing, level of analysis and anatomical loci of attentional selection in the brain. The beauty of the ERP technique in this endeavour is that it allows an examination of stimuli that are unattended with the same resolution as those at the centre of attention. ERP data have thus provided an unparalleled look at the suppressed processing of feature and semantic information when unattended in vision, audition and somatosensation, as well as information about just how effective attentional selection is (i.e. the width of the attentional beam or spotlight); the natures of the processing of both attended and unattended information have been found to vary depending on the input modality, stimulus features and task (for references see e.g. Hillyard 1993).

ERP and MEG data have provided some of the strongest evidence for early selection of sensory inputs based on spatial location; that is, an effect of focused auditory attention as early as 20ms post-stimulus under conditions of high sensory load (Woldorff et al. 1993). These data are in line with those observed for attention-sensitive single units from primary auditory cortex in monkeys. The magnetic data implicated the auditory cortex of the supratemporal plane (in or near Heschl's gyrus). Subsequent attention-related effects also appear to emanate from different regions of the auditory cortex depending on the nature of the selection required.

A variety of neuroimaging and neuropsychological studies have led to the view that there are many parts to the neural circuitry responsible for co-ordinating attentional resources during visual analyses, including the dorsolateral prefrontal cortex, the anterior cingulate, the posterior parietal lobe and the pulvinar nucleus of the thalamus (Posner & Dehaene 1994). It remains to be seen which of these structures contribute to the scalp-recorded activity. Much of the current-day ERP/ERF research is aimed at defining the nature and time-course of attentional control by the anterior and posterior attentional systems over sensory projection areas.

An elegant example of how ERPs have been used to delineate attention-related processes can be seen in the work of Woods et al. (1991). These researchers recorded ERPs to all events and reaction times to some in a multidimensional dichotic listening variant of a prototypic ERP selective attention paradigm. Specifically, people were asked to attend to tone bursts of a designated pitch in a particular ear and to respond to occasional (20%) stimuli that were 20 ms shorter in duration than the more frequent (80%) standard stimuli; thus, target stimuli were defined by three features - ear of delivery (right or left), pitch (250, 1000 or 4000hz) and duration (short or long). The relevant comparisons involved the ERPs to the standard stimuli when attended versus when inattended. This clever design allowed the authors to use the different ERP patterns to determine whether the brain was sensitive to differences in tone frequency (as would be expected from previous data), and also whether the brain processes pitch and location information differently and, if so, what the time-courses of the processing of each of these features and their conjunction might be.

The ERPs to tones of different pitches differed at 100ms (N100 component) regardless of attention in a way that reflected tonotopic organization in the eliciting area. By contrast, the attention effects for pitch, ear of delivery, and the pitch-ear conjunction, although statistically different from each other, did not show tonotopy, thereby implicating the involvement of non-tonotopic regions of the auditory cortex. The attention-related differences (Nd) for both pitch and location started fairly early (80-120ms) and showed slightly different topographies; thus, we can infer that these two features were analysed independently and in parallel starting by 80 ms at the latest. After 120 ms, in addition to the pitch and location Nds, conjunction-specific Nds appeared, indicating that conjunction processing lagged individual feature analysis somewhat. By 400ms, the Nds to individual features disappeared, leaving Nd activity strictly in response to stimuli that had both the relevant pitch and location (Fig. 7.11). The different Nd distributions indicated that, whereas either individual feature Nd could be accounted for by the activation of auditory cortical fields, the conjunction Nd (400-900ms) implicated the frontal lobes.

7.3.3 Language

One domain of cognition that has been revolutionized by the advent of various neuroimaging techniques is language. Whatever else language

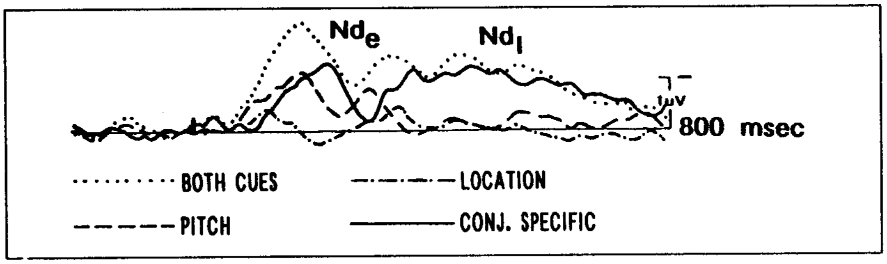

FIG. 7.11. Timing of feature processing including time-courses of Nd frequency, Nd location, Nd to both frequency and location and Nd that is conjunction specific. Nd refers to negative difference: e, early, l, late. Modified from Woods et al. (1994) with permission of the authors and publisher.

may be it is a compelling process that takes place in real time and in a large part outside of awareness until the input makes sense or not. Neuropsychological and neuroimaging data have implicated many areas of the brain (other than the classical Broca's and Wernicke's areas) in language processing. While these different areas may not all be active simultaneously, the relevant processes must overlap considerably in time. It is for this reason in particular that ERP/ERF activity which tracks language as it is being decoded and interpreted has been especially informative (for further discussion see Kutas & King 1996).

An elegant example of how ERPs can be used to investigate psycholinguistic questions can be found in the work of Garnsey et al. (1989). These researchers exploited the fact that semantic anomalies elicit N400s in order to evaluate two alternative hypotheses about the strategies that guide sentence parsing when there is a momentary ambiguity about syntactic structure. "Parsing" refers to the process of figuring out the syntactic relations between words in a sentence (i.e. who did what to whom). In English, determining the grammatical function (e.g. subject, object) of each word in a sentence is usually relatively easy, as this information is correlated with word order. However, there are exceptions; for instance, in *wh*-questions, where the questioned element occurs at the beginning of a sentence (e.g. *Which customer did the secretary call?*), there is no way of knowing what the grammatical function (subject, object, object of preposition) of the questioned element (*Which customer*) is until later in the sentence.

Sentence processing theorists have opposing hypotheses about what the parser does in cases where the function of an element is ambiguous. For instance, in the example above, the noun phrase *which customer* might automatically be assigned as the direct object of the clause, if the parser follows a "first resort" strategy. In this case, the disambiguating information in the verb "call" which occurs later in the sentence would tell the parser that its initial assignment was correct, because *which customer* is the direct object of call. However, if the parser were following a "last resort" strategy, then no grammatical role would be assigned to "which customer" until more information was available. Both strategies have costs and benefits. The first resort strategy is effective if *which customer* is the direct object; however, if it is not, as in "Which customer did the secretary call *about*?", then the parser incurs a great computational penalty in reanalysing "which customer" as the object of a preposition instead. The last resort strategy is necessarily less efficient in the early, ambiguous region of the sentence, but ensures no delays whenever the function of "which customer" is not the expected one.

Garnsey et al. constructed sentences with embedded *wh*-questions wherein the questioned element was either plausible or implausible as a direct object of the subsequent verb.

(a) The businessman knew which customer the secretary *called* _______ at home.
(b) The businessman knew which article the secretary *called* _______ at home.

These were randomly interspersed with simple declarative control sentences which either did or did not contain a semantically anomalous word. The beauty of this design is that the noun phrase "which article" in (b) isn't plausible as a direct object and will therefore elicit an enhanced N400 wherever in the sentence the parser assigns it as such. If the first resort strategy is in effect, the N400 will be observed early, namely at the verb "call", which is the first place the parser might assign a direct object role. On the other hand, according to the last resort strategy, the N400 should not appear until later in the sentence at the word "at", when it becomes unambiguous that "which article" serves the direct object role.

An N400 was observed at "called" and this was taken as evidence for the first resort strategy. Note that, in this example, the N400 is not to be taken as a direct reflection of role assignment, but rather of the incongruity that is either a consequence of making an implausible role assignment or of evaluating the possibility of that assignment. While other viable interpretations for this outcome have since been proposed,6 these are independent of the choice of the N400 as a measure, and the Garnsey et al. study remains a good example of how ERPs can be used to limit the number of viable explanations for certain linguistic phenomena.

Examples of this type are increasing daily. Equally powerful is the use of ERPs to investigate speech comprehension and aspects of parsing and integration beyond the level of individual words (Kutas & King 1996) in reading and listening to sentences with simple and complex syntax. What is remarkable is how similar sentence-level ERP effects are for written text presented one word at a time and for natural speech (e.g. Osterhout & Holcomb 1993, Mueller et al. 1997). Such data have also shown the necessity of taking individual differences in comprehension skills into account from the earliest stages of sensory analysis through comprehension (King & Kutas 1995b) (see Fig. 7.9, bottom right).

7.3.4 Memory: electrophysiological data on encoding and retrieval processes

ERPs are sensitive indicators of physical, perceptual and conceptual changes in the environment, both intentional and/or conscious and involuntary and/or unconscious. Clearly, an appreciation of change requires some trace or memory of past events. ERPs have been used to investigate aspects of the formation, maintenance (repetition) and retrieval of such memory traces (for reviews see Kutas 1988, Johnson 1995, Rugg 1995).

The earliest ERP studies of memory dealt with the timing of retrieval from short-term memory. Later ERP studies of memory focused on the amplitude of the P3 during encoding as a predictor of subsequent memory performance. These investigations were motivated by the hypothesis that P3 amplitude reflected the updating of one's mental model of the "environment" and evidence from intracranial recordings that potentials in the amygdala-hippocampal regions of humans co-occurred with the scalp-recorded P3 component. The story was somewhat complicated by the fact that humans and monkeys with damage to the medial temporal lobe did not necessarily show reduced P3 amplitudes at the scalp. While this issue remains unsettled, studies conducted to test the updating of working memory hypothesis of the P3 have nonetheless contributed to our understanding of memory and the brain. Proponents of the levels of processing framework had predicted that under most circumstances items that were processed more "deeply" (meaningfully) would be better remembered than items that were processed at only a shallow level (orthographically or phonologically in the case of words). Such predictions were confirmed by many studies wherein the nature of encoding was manipulated; the behavioural data allowed the inference that the way in which a stimulus is encoded is a critical determinant of the probability of its recognition or recall. However, the ERP data recorded in such tasks demonstrated more directly that the brain processes during encoding were in fact different within 200-300ms of stimulus presentation. Moreover, ERPs recorded during the study phase sorted as a function of subsequent memory performance have revealed different classes of people including those who choose to use "maintenance" versus "elaborative" rehearsal strategies to remember (e.g. Fabiani et al. 1990). Again, while this should come as no great surprise, ERPs provide more precise online evidence of the timing of these strategic choices.

Much current ERP research is aimed at testing various hypotheses about the proposed implicit/explicit distinction in long-term memory. By definition, amnesics do not perform as well as non-brain-damaged individuals on traditional tests of recognition and recall, and yet there are situations wherein the accuracy or speed of their performance can only be interpreted as indicating that they do have some memory for an event which they say they do not remember (Squire et al. 1993). Similar dissociations between memory measured "directly" and "indirectly" have been observed for non-brain-damaged individuals as well. ERPs have been used to examine the issue of whether, and if so how, performance in implicit and explicit memory tests are subserved by different neural systems operating on the same or different representations, and the time-courses of these processes.

A good example is a study by Paller (1990) on "directed forgetting". In this experiment individuals were exposed to words printed in red or green ink and asked to remember the "red" ones and forget the "green" ones. After the study phase, half the participants were asked to use three-letter stems as cues to recall words they had just studied while the other half were asked to write down the first word that came to mind in response to each stem. Thus both groups were exposed to the same stimuli, but differed in what they had to do. Both groups also were asked to recall as many of the words (green or red) as they could in any order (free recall).

As expected, everyone recalled more of the words that they had been directed to remember than those they had been directed to forget. But directed forgetting had no differential effect on stem completion; the stems were completed with equivalent numbers of "red" and "green" words. Thus, Paller obtained the expected pattern of dissociation of the effect of directed forgetting on recall versus priming. Moreover, Paller found that the ERPs recorded during encoding (study phase) were sensitive to subsequent recall but not to priming; that is, items that would be recalled had larger late positivities than those that would not be recalled, but there were no signs in the ERP of subsequent performance in the stem completion priming task. This pattern supports a difference between the encoding factors that are important for explicit versus implicit memory performance.

In a subsequent series of studies, Paller et al. (1995) combined behavioural and electrophysiological measures to examine the processes underlying implicit (priming) and explicit (recollection) memory performance. Across a series of studies, ERPs were recorded during an implicit test of memory (either threshold identification or lexical decision) following study manipulations that either influenced behavioural priming measures but not recognition performance, or vice versa. For example, people were asked to image a word and compare its size with that of the cathode ray tube in front of them in order to process the item deeply, or instead to count the number of syllables in the word in order to process it to a shallow level; this study manipulation had the effect of varying recognition but not priming performance. In other experiments, priming but not recognition performance was manipulated by varying the physical features of the studied items from the study to the test phase. The results thus far indicate that: (a) ERPs and behavioural measures reflect different aspects of memory-related processes; (b) at least partly different brain mechanisms support priming and recollection, with the electrophysiological signs of priming occurring earlier than those of recollection (after 300ms); and (c) recollection processes may come into play even under nominally implicit tests of memory that have no immediate consequence on behavioural measures of priming.

Another contemporary line of research uses very slow potentials to examine retrieval processes from long-term memory. In one typical approach exemplified by the work of Roesler and his colleagues (e.g. Roesler et al. 1995), young adults were asked to learn various lists of facts by heart on one day and to make decisions about them on another. The materials were constructed so as to take advantage of the so-called "fan effect". This refers to the observation that the time taken to verify a proposition about a concept depends on the number of links which that concept has with other concepts in memory; more links translate into slower decision times. Thus, it is possible to vary the difficulty of retrieving an item by increasing the number of links between it and other items. In practice, this means teaching a person many facts about some items, a moderate number of facts about other items, and only a single fact about yet other items.

The relevant electrophysiological data are the slow potentials recorded for several hundreds of milliseconds during the act of retrieval. The results of these studies suggest a close relationship between different neocortical structures and different retrieval processes. For example, there appears to be a pronounced DC-like negative potential over left frontal sites during retrieval of almost any semantically encoded item (Fig. 7.12) where amplitude varies with the size of the fan. This effect was seen together with other more task-specific slow potentials the amplitude, timing and distribution of which varied with the nature of the information retrieved (general versus specific concepts, verbal

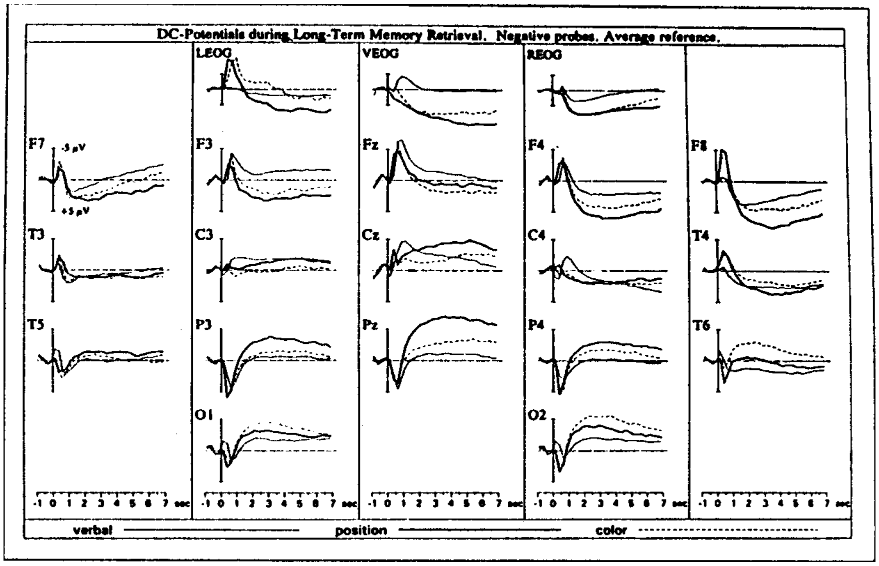

FIG. 7.12. Very slow potentials related to memory retrieval in three experimental conditions. Recordings are relative to an average reference and across subjects and different levels of fan. From Roesler et al. (1995) with permission of the authors and publisher.

versus spatial materials, etc.) and the decision (yes or no) required (for a review see Heil et al. 1994). Most importantly, all these studies revealed a pronounced negative slow wave that was temporally related to retrieval, the spatial topography of which reflected the type of material that was being retrieved and the amplitude of which varied with the difficulty of the retrieval. These results fit with the notion that the brain areas involved in explicit memory are the same ones that are needed for encoding and perception; there is no single memory store for all memories. In addition, the ERP data offer a real-time view of the time-course and relative location of retrieval processes.

7.3.5 Electrophysiological studies of neural plasticity

Nature or nurture? It's almost outdated to pose the question, for when it comes to brain development (and the associated perceptual, cognitive and motor functions), the answer is most certainly "Both to some degree". So, the better questions are what is the impact of each and with what time-course? For example, how do the brain and behaviours of someone who has hearing differ from those of someone who is born deaf? Exactly what is the auditory cortex of a deaf individual doing? These are the sorts of question that are being asked and answered using ERP/ERF recordings. Insofar as a deaf individual's brain responses to visual and somatosensory stimuli differ, we can infer that different brain systems are involved in their processing.

Neville and her colleagues (for a review see Neville 1995) addressed these questions by comparing the scalp-recorded visual EPs of hearing adults, congenitally deaf adults (individuals who have been deprived of auditory input since birth), and hearing adults whose first language was American Sign Language by virtue of having been born to deaf parents. In a number of studies, they found that the visual EPs of deaf individuals were in fact different from those of hearing individuals, especially for stimuli occurring in the periphery. Specifically, early sensory compoments (N150 and P230) were larger in amplitude for the deaf. The larger N150 over frontal and temporal regions was taken as consistent with the hypothesis that auditory areas deprived of their normal input were processing visual information instead, while the larger amplitude P230s over occipital sites were hypothesized to reflect structural changes in the intact visual areas.

Neville & Lawson (1987a-c) also pursued this question within a selective attention task that required detection of motion in different regions of visual space. While there were some similarities in the overall pattern of attention-related effects in the deaf and hearing subjects, there were also some notable distribution differences, especially for stimuli in the periphery. For example, deaf individuals had larger attention effects on both the N1 component and a subsequent latency positivity (PD) and showed these effects at the occipital sites - locations where the hearing group had no such effects. Deaf individuals also had larger N1 effects over the left hemisphere than hearing individuals, regardless of the visual field of presentation. These ERP results indicate that the neural systems which mediate attention to visual space and perception of motion are different in part in hearing and congenitally deaf individuals.

The interpretation of these differences is clarified in part by comparing them with the ERPs of hearing individuals born to deaf parents and whose first language is American Sign Language. With this comparison we can determine the extent to which each of these group differences in attention is attributable to sensory deprivation versus the acquisition of a visuospatial language. Relative to the hearing and congenitally deaf individuals, these hearing-of-deaf adults show very similar ERP waveform morphologies; differences occur primarily in the size and distribution of the attention effects (Fig. 7.13). On the one hand, the hearing-of-deaf look more like the hearing in that they do not show the large N1 or PD effects at the occipital sites. On the other hand, the hearing-of-deaf are more similar to the deaf in the lateral distribution of their attention effects; that is, they show large effects over the left hemisphere in response to left visual field stimuli. As the larger ERP (N1 and PD) effects over the occipital region are specific to individuals who are deaf, they are probably a consequence of auditory deprivation since birth. In contrast, the apparently greater involvement of the left hemisphere in attentional selection based on motion for both the deaf and the hearing-of-deaf (relative to normal hearing) individuals is most consistent with an explanation based on the early acquisition of sign language.

Mapping via magnetic recording techniques has also been used to investigate the reorganization of the somatosensory system in humans. For instance Mogilner, et al. (1993) used magnetic recordings to

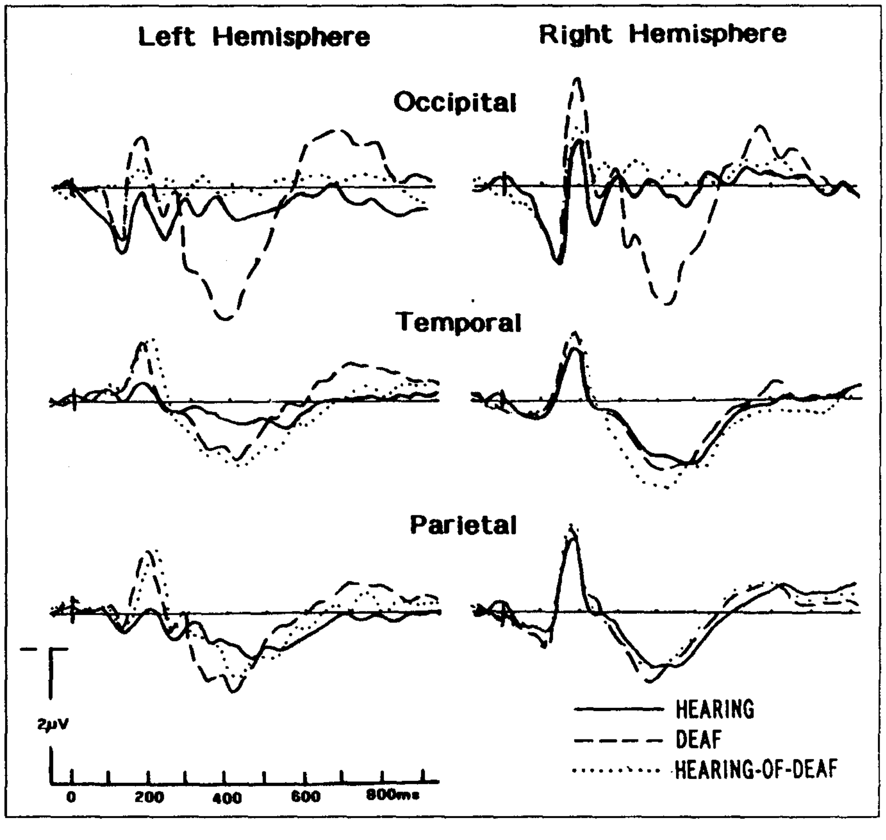

FIG. 7.13. Comparison of visual ERPS from hearing, deaf and hearing-of-deaf individuals. Note that only deaf individuals show large occipital N1 and later positivity. Both deaf and hearing-of-deaf show large N1 over left hemisphere temporal and parietal sites. Thus, the occipital effects are related to altered sensory experience, whereas as the temporal and parietal effects are more likely due to altered language experience (a visuospatial manual language). Adapted from Neville & Lawson (1987c) with permission of the authors and publisher.

compare the somatosensory map of the hand areas of a group of control people with those obtained from two adult men both before and after surgical separation of congenitally webbed fingers. The pre-surgical recordings revealed that hand areas of the abnormal hand in these two patients were quite small and unusual in their lack of a consistent topography; however, a few weeks after surgery, a normal somatotopic organization was evident. Somatosensory reorganization in humans has also been observed in MEG recordings of a patient with an amputated limb; via behavioural testing this patient felt touch as well as heat and cold in the phantom limb when a certain area on his cheek or a few inches above the amputation line were stimulated (Yang et al. 1994). The MEG patterns revealed no real "hand" area in the hemisphere contralateral to the amputated limb, but a normal topographically organized area in the other hemisphere; moreover, the presumed hand area was activated by touching either the lower face or the upper arm 10cm above the line of amputation. This is one of the strongest pieces of evidence of cortical remapping in humans following abnormal experience. All in all, these data support the emerging view that receptive fields and cortical maps are dynamic in the face of experience, rather than static and inborn.

7.4 CONCLUSIONS

The reader should now have a good idea of the many types of question that have proven amenable to the ERP methodology. Different aspects of the ERP/ERF are sensitive to stimulus parameters, response parameters, preparation, modulation and direction of attention, establishing expectancies and noticing violations thereof, discrimination, categorization, decision-making, conscious recollection and implicit processing among other factors. ERPs can be used not only to help determine which factors influence brain activity, mental state and/or an individual's behaviour but also to provide some important information about the time-course of their influences. This time-course of sensitivity to experimental and internal variables can be combined with other neural-imaging techniques of greater spatial but coarser temporal resolution to unfold the active brain areas across time.

ACKNOWLEDGEMENTS

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NOTES

1. More generally, σ denotes a tensor, to allow for anisotropic conductivity.
2. The corresponding equation for the magnetic field produced by a current dipole is

$$\vec{\mathbf{B}}_2 \approx \left(\frac{\mu_0}{4\pi}\right)\frac{s\vec{\mathbf{d}}\times\vec{\mathbf{r}}}{r^3}, r \gg d ,$$

   where μ_0 is the permeability of free space.
3. These differences are reflected in the e_{ij} and m_{ij} in Equations (11) and (12).
4. Note that the "components" derived from PCA do not necessarily correspond to the ERP components as defined above.
5. Note that, if two or more generators are strongly correlated in time, the number of principal components may be lower than the actual number of generators.
6. See e.g. Fodor (1989) for a thorough review of the issues involved in processing empty categories. More recent work has favoured models where the parser maintains parallel syntactic analyses in certain situations (e.g. Gibson 1990). Moreover, MacDonald et al. (1992) provide evidence that there are working memory-related individual differences in the computation of such multiple analyses, thereby muddying the interpretation of Garnsey et al.'s data somewhat. If subjects were maintaining multiple syntactic analyses, the N400 observed may simply have reflected the fact that the "first resort" is one of several analyses that is being pursued.

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