CHAPTER TWO

HUMAN ELECTROENCEPHALOGRAPHY

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Introduction

The measurement of brain electrical activity using the electroencephalograph (EEG) provides a noninvasive and inexpensive method to directly measure brain function and make inferences about regional brain activity. It has many virtues as a direct measure of brain function that can be used in myriad applications in the biobehavioral sciences, ranging from studies of basic cognitive processes to emotional function, dysfunction, and development. It also has a number of limitations that the user must keep in mind as decisions about when and how to use such methods are made. The purpose of this chapter is to provide an overview of the major concepts and methods associated with use of EEG in biobehavioral research. In addition, some of the promising contemporary research efforts using EEG will be featured. Event-related potentials are not covered in this chapter, since they are addressed elsewhere in this volume.

HISTORICAL BACKGROUND

The measurement of human brain electrical activity is a recent development in the history of science. It was only about 70 years ago that the first demonstration of recording human brain electrical activity was published (Berger 1929). This first report was greeted with considerable skepticism in the scientific community. It wasn't until a live demonstration of scalp-recorded brain activity from the neuroscientist Adrian's head (at the 1935 meeting of the Physiological Society in London) that electroencephalographic measures became more widely accepted in the biomedical research community. In the ensuing years, rapid developments in data collection, data reduction, and data analysis have resulted in important progress in this area (Shagass 1972).

In his initial report, Berger used two large pad electrodes soaked in saline, one placed over the forehead and the other placed at the back of the head. Berger observed that there were regular rhythmic waves at about 10 Hz in relaxed adults and noticed that these waves were best seen when subjects had their eyes closed in the absence of stimulation or other mental activity such as imagining or problem solving. These waves subsequently became known as "alpha" waves. In later work, Berger had the opportunity to record directly from the cortical surface during neurosurgery and confirmed the important fact that scalp and direct recordings were essentially identical in form except that the amplitude at the scalp was attenuated.

A major event in the history of research on the EEG was the launching of the journal *Electroencephalography and Clinical Neurophysiology* in 1949. In the first volume of this journal, an article by Moruzzi and Magoun (1949) appeared that established the consequences of reticular stimulation on cortical EEG. Following stimulation of the brainstem reticular formation in cats, widespread increases in cortical arousal as reflected in EEG desynchronization were observed. This helped to launch the study of brain electrical activity as an integrated neurophysiological phenomenon and to establish a role for EEG measures in the assessment of arousal. While this and other similar experiments undoubtedly played an important role in highlighting the utility of these measures as indices of activation, the finding of global cortical activation as a consequence of brainstem stimulation also had the unwitting effect of reinforcing the view that EEG could not provide very useful information on cortical specificity (Davidson 1978). This notion was championed by some and led to the development of general arousal theory (e.g. Duffy 1962; see Thayer 1989 for modern version) in which the EEG is considered to be useful only for making inferences about global states of sleep and wakefulness.

John T. Cacioppo, Louis G. Tassinary, and Gary G. Berntson (Eds.), *Handbook of Psychophysiology*, 2nd ed. © Cambridge University Press 2000.
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SPACE AND TIME IN MEASURES OF REGIONAL BRAIN FUNCTION

The use of EEG to make inferences about neural activation and other brain processes has a number of distinct advantages and disadvantages. In general, there is some trade-off between temporal and spatial resolution in measures of regional brain function. Measures derived from brain electrical activity have very good intrinsic temporal resolution. These indices are typically recorded in a way that permits resolution in the millisecond domain, which makes these measures ideal for linking with behavior that dynamically changes over short periods of time. Moreover, changes in neuronal activation can be instantaneously reflected in changes in EEG, whereas with hemodynamic measures such as functional magnetic resonance imaging (fMRI) there is always a delay between the time a neuronal change occurs and the onset of a detectable hemodynamic change (Cohen 1996). Measures derived from brain electrical activity are thus ideally suited for tracking the neural changes coincident with rapid phasic changes in behavioral state.

A particularly appropriate role for these measures is in examining the neural correlates of irregular, spontaneously occurring behavior. For example, EEG measures have been effectively utilized in the study of the neural substrates of emotion. By collecting continuous EEG and video-recorded facial behavior, brain electrical activity that was coincident with specific, objectively coded facial signs of emotion could be extracted off-line (Davidson et al. 1990b). The onset and offset times of the extracted activity are based upon the times at which the specific facial expressions occurred. Even very brief, fleeting expressions (shorter than one second in duration) could be studied using these techniques, owing to the method's time resolution. If the EEG is sampled 200 times per second then the resolution would be 5 msec, considerably better than the resolution of video. The video frame in which the onset of the expression was judged to begin can be used to identify the sample in the EEG that coincides with this time. In a subsequent section, we will consider issues concerning the reliability of brief epochs of EEG and the minimum duration of EEG needed to establish a reliable index of a particular behavioral state.

Whereas the temporal resolution of the EEG is clearly a major advantage of the method, the relatively poor spatial resolution is a major disadvantage. Even with high-density electrode arrays, the spatial resolution of this method will always be inferior to those based upon metabolic or hemodynamic imaging. There are several reasons for this state of affairs. The methodological issues associated with high-density EEG recording will be considered in more detail shortly. However, it is important to note here that, even with electrode arrays that include 128 channels, the average interelectrode distance on a typical adult head is approximately 2.25–2.50 cm, a full order of magnitude coarser than the spatial resolution achievable with modern functional MRI. Second, the spatial distribution of neuronal potentials is distorted by the highly resistive properties of the skull. The skull acts as a spatial low-pass filter and smears the electrical activity over a relatively large region of scalp. Third, there is no unique solution to the inverse problem. A particular distribution of scalp potentials can be produced by many different combinations of intracerebral generator sources. Thus, inferring the sources of observed voltage changes on the head is fraught with methodological complications and will rarely, if ever, be definitive. We therefore cannot assume that a particular scalp distribution isomorphically reflects an underlying neuroanatomical localization.

Despite these complexities, temporal and spatial changes in scalp-recorded brain electrical activity can provide useful information on brain–behavior relations, can help to confirm specific hypotheses about functional neuroanatomy when interpreted in light of the constraints and cautions just described, and can provide unique information on the time course of neural events associated with dynamically changing behavior. Moreover, these measures are relatively inexpensive to obtain and are completely noninvasive. This makes them ideally suited for use in studies with infants and children and in large studies where the use of hemodynamic neuroimaging methods would be prohibitively expensive. Examples of each of these will be provided in this chapter.

The Physiological Substrates of EEG

Most researchers now agree that the ongoing EEG is not a direct product of summated action potentials but rather derives from summated postsynaptic potentials. Because both neural tissue and the overlying skull act as low-pass filters, the fields created by the high-frequency transients associated with action potentials diminish sharply with distance from the source. Thus, it is very unlikely that action potentials – even summated action potentials – are represented at the scalp surface in the ongoing EEG. It is also generally agreed that while glial cells may contribute to slow, DC changes in brain electrical activity, they do not account for significant variance in the scalp-recorded EEG. Thus, the primary contributor appears to be summated postsynaptic potentials. In animal studies where intracellular recordings are compared with scalp-recorded EEG, there is a close correspondence between the overall shape of these waveforms (Elul 1968; Thatcher & John 1977) that is suggestive of the contributions of summated postsynaptic potentials to EEG generation. See Figure 1.

Although summated postsynaptic potentials are thought to be the proximal substrate of most of what we record as EEG on the scalp surface, uncertainty still remains regarding the mechanisms responsible for the pacing of the EEG.

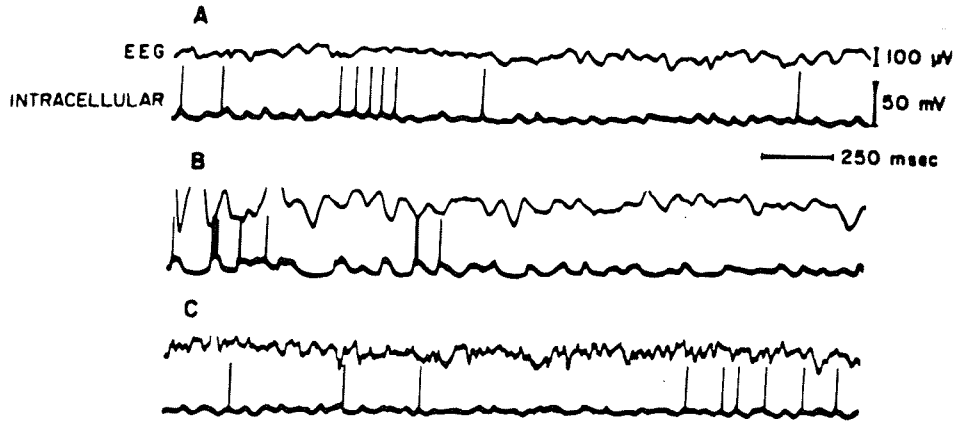

Figure 1. Neuronal activity recorded from the same cell in the posterior suprasylvian cortex, 750-μ depth; EEG taken from anterior suprasylvian cortex. Animal awake (A), sleeping (B), and intensely aroused (C), with EEG patterns characteristic of these states. Note corresponding changes in form of the neuronal waves. Reprinted with permission from Thatcher & John, *Foundations of Cognitive Processes.* Copyright 1977 Lawrence Erlbaum Associates, Inc.

Evidence from a variety of sources points toward the thalamus as a critical site for regulating the rhythmic activity of cortex.

In the early 1930s, a thalamocortical reverberating theory of rhythmicity was proposed. According to this model, rhythmic activity was not due to a particular pacemaker but rather arose as a consequence of the circular movement of impulses in a loop between cortical tissue and the thalamus. Several observations in animal studies performed within the next decade irreparably damaged the thalamocortical loop theory. First, Adrian (1941) recorded from thalamus and cortex directly and found that thalamic rhythmicity was not dependent upon an intact cortex. Morison and Bassett (1945) found that decortication did not prevent rhythmic activity in the thalamus. If rhythmic activity were dependent upon thalamocortical loops then these cortical manipulations should interfere with the expression of thalamic activity. These observations were, however, compatible with the view that the thalamus is a major pacemaker for rhythmic activity in the cortex.

The view that the thalamus is a major contributor to cortical rhythmic activity was championed in work by Andersen and colleagues (Andersen & Andersson 1968) in studies with anesthetized animals. They demonstrated that, in anesthetized cats, spontaneous barbiturate-induced cortical spindle activity was highly correlated with spindle activity in thalamus. The causal influence of thalamic activity on cortex was established in experiments that used selective cooling to produce reversible lesions. These studies demonstrated that if cortex is cooled, the amplitude of the cortical rhythms are attenuated but there is no change in frequency. However, if thalamus is cooled, dramatic changes in the frequency of cortical rhythmic activity are produced. Andersen and colleagues postulated that there were multiple thalamic pacemakers. According to this view, any thalamic nucleus was capable of exhibiting rhythmic oscillations that could then be imposed on relatively localized regions of cortex via thalamocortical cells.

More recently, Steriade and colleagues proposed an updated model of thalamic contributions to cortical rhythmic activity. In contrast to Andersen and Andersson's (1968) model, which suggests that any of the thalamic nuclei is capable of exhibiting rhythmic oscillations and imposing this rhythm on other nuclei, Steriade proposed that the nucleus reticularis in the thalamus is the true "pacemaker" (Steriade et al. 1985). Selective damage to this nucleus abolished rhythmic activity of the thalamus and cortex in rats (Buzsaki et al. 1988) and cats (Steriade et al. 1985). In addition, there are very few connections among most thalamic nuclei (Jones 1985). Only the nucleus reticularis projects to virtually all other thalamic nuclei (Scheibel & Scheibel 1966). Therefore, it was suggested that nucleus reticularis serves as the pacemaker and imposes its rhythmic oscillation on other thalamic nuclei and thalamocortical cells.

Few studies have examined the relation between thalamic activity and cortical EEG in humans. In a recent study (Larson et al. 1998), we measured regional glucose metabolism using positron emission tomography (PET) and EEG simultaneously. We extracted alpha-band activity from the EEG using standard spectral analysis methods (to be described shortly) and then averaged the EEG across sites to form a whole-head composite of alpha power. We then entered this whole-head average into a correlational analysis using statistical parametric mapping (see Friston 1994 for general overview) to determine the brain regions where metabolic activity was most strongly related to average whole-head alpha power. We found that the thalamus emerged as the site that was most strongly inversely correlated with alpha power. That is, those subjects who showed greater metabolic activity in the thalamus also showed less whole-head alpha power, indicative of greater cortical activity. In other words, activation of the thalamus

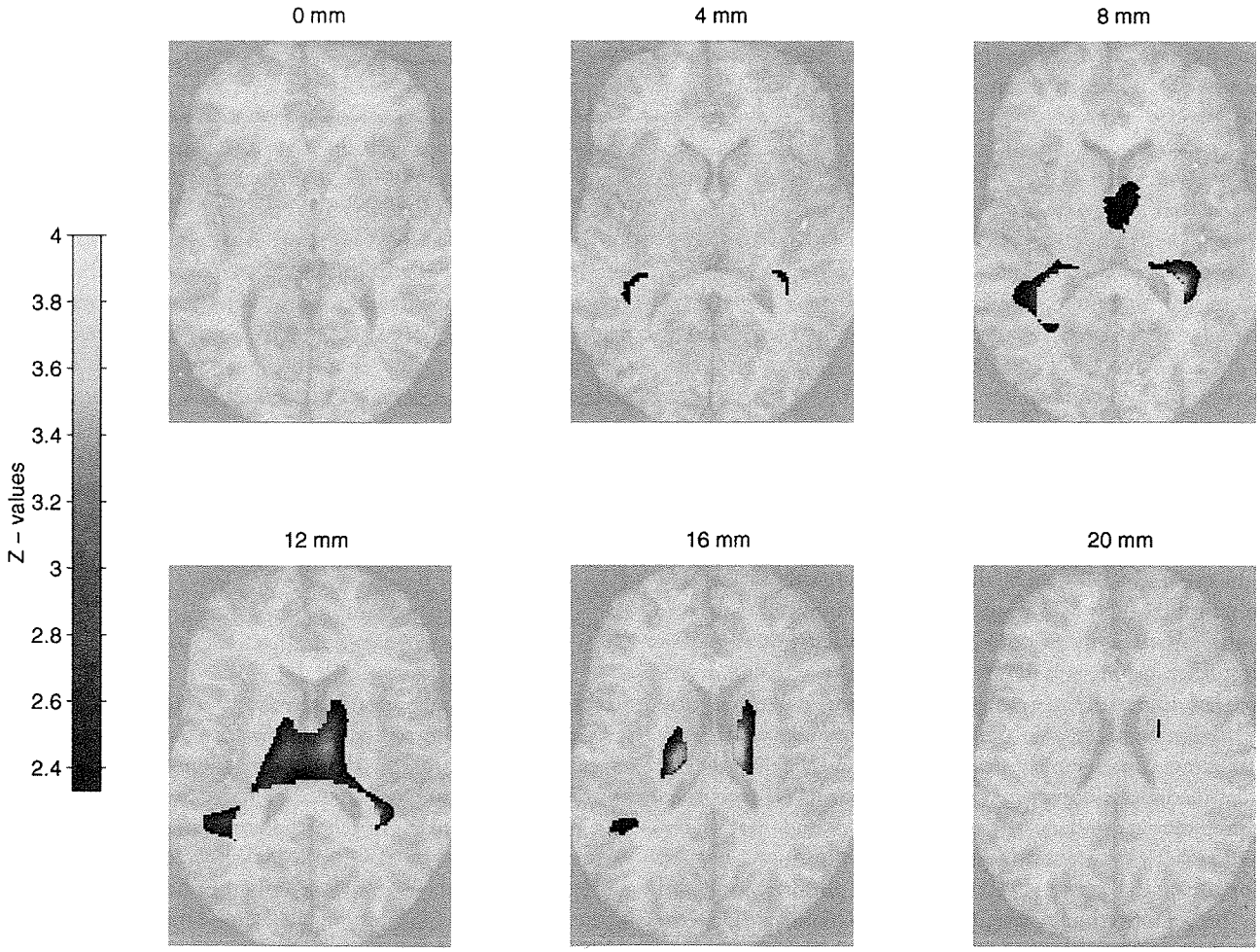

Figure 2. Negative correlation between regional glucose metabolism derived from PET from the entire brain volume and eyes-open 8–13-Hz alpha power averaged across 28 electrodes. The PET data display regions of significant negative correlations mapped onto axial MRI planes spanning the thalamus. The scale is in *z*-values. The lowest *z*-value displayed is 2.33, which is equivalent to an *r*-threshold of 0.43. Adapted from Larson et al. (1998).

was associated with desynchronization of the EEG (see Figures 2 and 3). Recently, using regions of interest drawn on co-registered structural MRI scans to specifically extract a thalamic region of interest (Lindgren et al. 1999), we replicated our previous finding and demonstrated that the association was present only in healthy control subjects, not in acutely depressed patients. Depressed and control subjects did not differ in absolute thalamic metabolism, nor did they differ in whole-head alpha power. Moreover, the variance of these measures within the depressed group was comparable to the control group. The fact that the depressed group failed to show a strong inverse relation between thalamic metabolism and alpha power – in the presence of normal EEG and thalamic metabolic means and variability – suggests an abnormality in thalamocortical interaction in the depressed patients. The mechanisms that might account for such an abnormality are not currently known and must be studied in future research.

In two major, largely theoretical books, the physicist Paul Nunez (1981, 1995) challenged the view of the thalamus as primary contributor to the regulation of cortical rhythmicity. It is beyond the scope of this chapter to present his theory in detail, but Nunez underscored intrinsic properties of intracortical interaction in the production of cortical rhythmicity. Pyramidal cells account for between two thirds and three quarters of all cortical neurons. These cells occupy cylindrical columns and are situated so that their axons and dendrites are aligned perpendicular to the cortical surface. The two major forms of interconnection among cortical neurons are short-range (< 1 mm in humans) and cortico-cortical, extending up to several centimeters. In humans, the number of cortico-cortical connections is considerably larger than afferent connections to or efferent connections from cortex. The thalamus, which is the most extensive subcortical input to cortex of any structure, does not provide more than approximately 1% of the fibers entering any given region of cortex. Nunez (1981) argued that EEG frequencies are

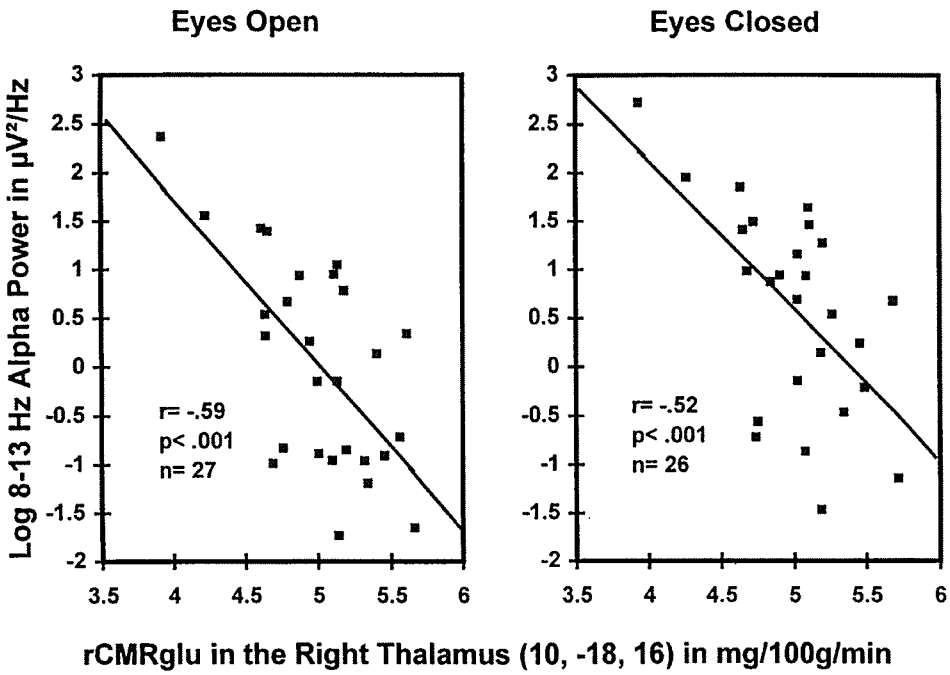

Figure 3. Scatter plot of the correlation between regional glucose metabolism ($rCMR_{glu}$) from one coordinate in the right thalamus and eyes-open and eyes-closed 8–13-Hz alpha power averaged across 28 electrodes. Adapted from Larson et al. (1998).

particularly sensitive to long-range cortico-cortical connections. He and his colleagues developed a model to predict EEG frequency based upon the following major variables: the circumference of the cortex, a long-range connection parameter (based upon cortico-cortical connections), the average velocity of action potential propagation in these long-range association fibers, and a threshold parameter that reflects the threshold for firing of pyramidal neurons. In support of this model, Nunez presented data illustrating that lesions made exclusively to white matter in cats altered EEG frequency. For now, however, scant data exist in support of this model. It is also possible that intrinsic cortical processes of the sort described by Nunez – as well as afferent influences from thalamus – both exert influence over cortical EEG frequency.

In his more recent book, Nunez (1995) speculated that the neocortex determines the resonant oscillatory activity of the brain while the thalamus adjusts its oscillatory frequencies to be synchronous with the neocortical resonant frequency. Nunez relied upon the experimental work of Steriade and colleagues (Steriade, Oakson, & Diallo 1976) to support his argument. In this latter study, Steriade et al. (1976) stimulated motor cortex electrically with a 10-Hz pulse delivered every 2 sec. After 28 passes, the thalamic nuclei began spontaneously to produce bursts of rhythmic activity near this 10-Hz driving frequency. Nunez (1995) also noted that thalamic oscillations coincident with neocortical rhythms will produce a larger cortical response than a thalamic rhythm that is unrelated to the neocortical resonant frequency. Nunez suggested that the combination of the larger neocortical response and the frequency plasticity of the thalamus causes the thalamic rhythms to become coincident with the neocortical rhythms.

Descriptive Characteristics of the EEG

In this section we describe the normal characteristics of the EEG that have been inferred from visual inspection and routine frequency analysis, and we delineate some of the major developmental changes that occur in these parameters. Normal EEG can be characterized with respect to many different parameters. However, the most common parameters used to characterize the EEG are frequency and amplitude. Methods used to extract these parameters will be described in the next section. It is primarily on the basis of frequency and amplitude that EEG differences among several major behavioral states have been described. In normal adults, deep sleep or slow-wave sleep is associated with large and very slow waves in the delta frequency range (1–4 Hz). Lighter sleep is associated with spindle bursts and some slow-wave activity. During drowsiness, amplitude is reduced to the low-amplitude theta range (5–7 Hz) and delta activity is common. "Relaxed wakefulness" is the term often used to characterize the state during which alpha activity is predominant (8–13 Hz). During alert attentiveness, the EEG is mainly characterized by low-amplitude fast activity (> 13 Hz) (see Pilgreen 1995). A commonly used strategy in EEG research is to quantify "activation" in alert waking subjects by examining the reduction in alpha power in a specific scalp location during an experimental condition compared with a control condition (see e.g. Pfurtscheller 1992; Steriade 1989). Inferences

about activation asymmetry are often made by comparing the power in the alpha band from left and right homologous electrodes (Davidson 1988).

There are major developmental changes in the EEG that evolve from a disorganized, discontinuous pattern to one that is more organized and coherent (see Niedermeyer 1993 and Pilgreen 1995 for reviews). Very premature infants (less than 28 weeks conceptual age) have a burst-suppression EEG pattern that does not vary between wakefulness and sleep. The burst-suppression pattern consists of very low-amplitude periods lasting from one to several seconds interrupted by high-amplitude complex activity. Neonates (28 to 31 weeks conceptual age) continue to show no differentiation between states of wakefulness and sleep, but they do begin to show a pattern of fast activity superimposed upon a slow delta rhythm (less than 0.5 Hz). This pattern, referred to as a "delta brush" (Lombroso 1993), is one of the hallmarks of a normally developing EEG and usually persists until the fortieth week. Differentiation among states of wakefulness, active (REM) sleep, and quiet (non-REM) sleep begins between 32 and 35 weeks from conception. The EEG during wakefulness and active sleep is very similar, with waves consisting of diffuse delta activity and occasional bursts of faster frequencies that are superimposed on the delta. Eye movements during REM at this age are similar to those found in adults. Full-term neonates spend about 60% of their time in REM sleep. The percentage of REM sleep declines throughout life. The neonatal EEG patterns typically disappear by six weeks from birth in a full-term infant. Within the first three months of life, a posterior rhythm of about 4 Hz develops. This rhythm is believed to be the precursor of the adult posterior alpha rhythm, since it is accentuated with eye closure. Delta activity in the waking EEG gradually disappears as the child develops, and the frequency of the dominant rhythm increases until it reaches its maximum value of approximately 10 Hz at about 10 years of age. Activity at about 8 Hz is usually present by 2 years of age; this activity gradually declines until approximately 25–30 years of age, when the normal adult EEG pattern is established. Some authors have noted an association between the age at which the adult EEG pattern is fully established and the age at which the final state of myelination is complete (Pilgreen 1995). At the other end of the lifespan, episodic theta and delta activity is sometimes observed at particular (e.g. temporal) scalp regions, though the functional significance of these changes has not been systematically studied.

An electroencephalogram is often decomposed into bands defined on the basis of lower and upper frequency boundaries. The classic bands for the adult EEG include delta (0–4 Hz), theta (5–7 Hz), alpha (8–12 Hz), beta (13–20 or 30 Hz) and gamma (36–44 Hz) ranges. An important issue in research is the extent to which the band boundaries are arbitrary – whether they in fact cohere if examined in a rigorous statistical fashion. Moreover, the extent to which they differ by scalp region is also of importance for making meaningful comparisons of band power among different scalp sites. In an effort to examine this question, we performed a principal component analysis of absolute power spectra from 26 scalp sites in a sample of 115 subjects (Goncharova & Davidson 1995). This analysis yielded five factors, with three corresponding to the traditional bands of delta, theta, and beta. We found support for two separate alpha bands: one at 9–10 Hz and the other at 11–13 Hz. Further analysis indicated that it was specifically the 10-Hz component that was most highly correlated with other, independent indices theoretically predicted to be associated with asymmetric anterior EEG.

There are many other important features of the EEG that have been extracted and described. These will be described after we consider the various analytic strategies that have been used for data reduction and analysis.

Recording and Measurement

INTRODUCTION

Despite the worldwide proliferation of EEG research laboratories, there are surprisingly varied data acquisition and reduction procedures used in the different labs. Few researchers agree on such basic methodological issues as choice of reference electrode, minimum number of electrodes needed, proper analysis techniques, and so forth. As turnkey high-density array EEG systems become commercially available (and increasingly more affordable), the need for a basic understanding of these issues becomes increasingly important. The following section presents a brief overview of EEG methodology, with a focus on state-of-the-art high-density recording technology. Its inclusion will help the interested researcher begin to answer this question: What is the most convenient and efficient way to collect, process, and analyze EEG data that will lead to the most useful inferences concerning underlying brain activity?

ELECTRODE LOCATIONS AND REFERENCE ISSUES; HIGH-DENSITY ARRAYS

Electrodes and Electrode Locations

Typical commercially available electrodes consist of hollow discs or cups (composed of chlorided silver, gold, or tin), which are filled with a conductive gel before application. It is essential that the metal used to construct the electrodes be the same for all electrodes that will be applied for EEG and that different metals not be mixed. This is particularly so when commercial caps are used for scalp recording yet different electrodes are applied for mastoids or ears. For example, the default metal for the Electro-Cap (Eaton, Ohio) system is tin. Investigators using this cap

should use tin electrodes also for ear or mastoid placement, since the use of different metals will lead to electrical drift and slow DC artifact.

Electrodes may be applied singly using an adhesive material or as a group using a cap or net system. The primary goal of any electrode placement scheme should be to evenly sample the surface of the scalp. The original 10–20 system has been the traditional choice for most EEG researchers (Jasper 1958). Using the 10–20 system, electrodes may be placed in a pattern constrained by the position of several surface landmarks, including the nasion, inion, and left and right prearicular points. Electrodes are applied based upon the percentage of the distance between these various coordinates. For example, the vertex electrode is 50% of the distance between the inion and nasion on the midline. Individual electrodes are designated by a convenient nomenclature indicating brain hemisphere (odd numbers = left, even numbers = right) and general cortical zone (F = frontal, C = central, T = temporal, P = parietal, O = occipital). For example, T3 refers to the electrodes over the anterior temporal lobe on the left side of the head. It is the norm to report EEG findings by referencing standard 10–20 sites, enabling researchers to easily compare findings across studies and laboratories. It is thus crucial that electrode location be consistent across subjects and across studies. Although electrode placement is often the first task learned by EEG technicians and researchers, placement should be carefully checked across technicians to ensure compatible results across subjects. High-density arrays typically use different notation schemes to accommodate an increasing number of electrodes, but "translation" maps should be provided to enable quick interpretation of the data in terms of standard 10–20 sites.

Choice of Reference

Perhaps the most divisive issue among current EEG researchers is the choice of reference electrode. Happily, the popular fiction of a "monopolar" recording seems to be waning. All voltage recordings are in fact bipolar: they represent the difference in potential between the active site and the reference site (for a classic discussion of these issues, see Katznelson 1981). The choice of reference site has often been guided by a search for the most "inactive" available site (i.e., the site with the least EEG activity present). However, because of volume conduction, there is no site on the body that is electrically neutral with respect to brain activity; thus, the notion of an inactive site is a convenient myth. This is a particularly important issue for EEG studies that examine topographic differences, since the spatial distribution of the observed scalp voltage will depend upon the choice of reference electrode location. Many studies examine asymmetries in brain electrical activity to make inferences about hemispheric specialization and asymmetric hemispheric activation (e.g. Davidson et al. 1990a). In such studies, the choice of reference is crucial because different reference locations may provide a different pattern of results, depending upon the types of tasks that are used and the hypothesized underlying region of cortical activation involved. One strategy we have often used has been to present findings using multiple reference montages in order to establish the similarity of the basic pattern of results across reference (e.g. Davidson et al. 1990a; Henriques & Davidson 1991).

Despite the existence of theoretical and empirical justifications for the use of particular references, EEG researchers vary widely in their choice of reference electrode. At a recent professional meeting for psychophysiologists, endorsements were made for the average reference, linked-ears–linked-mastoids, sterno-vertebral, and nose reference, among others. Clearly there are differences of opinion as to which is the best reference location. The linked-ears and average reference are the most common, so these will be discussed in detail.

The linked-ears reference is perhaps the most commonly used in EEG research. The use of commercially available clip leads makes the use of an ears reference relatively easy to implement with no discomfort to the subject. One disadvantage of this reference scheme is that earlobe sensors have a tendency to pick up the ECG (electrocardiogram) signal. Physically linking the earlobe sensors may help solve this problem. Although some investigators unwittingly assume that the ears reference is particularly appropriate because it is relatively electrically neutral, this assumption is incorrect. Volume conducted brain activity can clearly be recorded at the ear (see Katznelson 1981). Moreover, in his influential chapter, Katznelson (1981) presented a theoretical argument asserting that physical linking of the ears could produce a low-resistive shunt between the two sides of the head, thus attenuating asymmetries that might be present in the brain electrical recordings (data from a single subject that appeared to support this assertion were presented). This claim provoked others to examine the issue more systematically, and a number of studies appeared that addressed whether physically linking the ears actually attenuated the magnitude of observed asymmetry. In Senulis and Davidson (1989) we examined this claim by electronically linking and unlinking the ears while recording EEG referenced to Cz (vertex). We then re-derived the EEG off-line, comparing the conditions of physically linked ears and computer-averaged ears (comparison data came from adjacent 1-min trials). We found no evidence for any impact of physically linking the ears on observed asymmetry. Averaged ears and physically linked ears yielded identical asymmetry estimates. This finding has been conceptually replicated in several other studies (Andino et al. 1990; Miller 1991). In retrospect, the idea that physically linking the ears might provide a low-resistive shunt capable of attenuating the magnitude of observed asymmetry was ill-conceived, since the electrode impedances, even when extremely low (e.g., 1 kΩ), would be higher than

the internal resistance within the head. Thus, a physical link between electrodes on the two ears could not possibly provide a shunt that was lower in resistance than what is present under normal physiological conditions inside the body.

The evidence overwhelmingly demonstrates that physically linking the ears does not in any way influence the magnitude of observed asymmetry as a consequence of providing a low-resistive shunt between the two sides of the head. Still, it is prudent *not* to physically link the ears for a different reason. Generally, variations in electrode impedance among electrodes (and specifically between homologous electrodes) do not have any bearing on the observed voltage measurement. In fact, one can calculate the change in observed voltage measurement as a consequence of variations in electrode impedance. Because modern amplifiers have very high input impedance (typically in the range of 100 kΩ), variations in electrode impedance on the order of several thousand ohms will have a negligible effect on the observed voltage measurement.

When linking the ears or mastoids prior to input to the amplifier, different issues arise. Here, variations in the impedance of the left and right electrodes will change the effective spatial location of the reference and could potentially alter the magnitude and direction of observed asymmetry. For this reason, when physical linking of the ears or mastoids is performed, it is important to equate the impedances of the two ear or mastoid electrodes as closely as possible, particularly if questions regarding asymmetry are important. If the assessment of asymmetry is an important component of an EEG study that uses linked-ears or -mastoids reference, the investigators should ideally record their measurements of the impedance of each separate ear or mastoid. These values could then be used to examine the relation between impedance asymmetry and EEG asymmetry and so establish that any small variation in the former is not accounting for variance in the latter. This issue is particularly pertinent in studies that focus on individual differences in asymmetric activation, since such studies make comparisons of asymmetry across subjects. Complete within-subject studies would not be affected, since differences among tasks would be superimposed upon whatever bias might be introduced by variations in impedance asymmetry.

If an investigator wishes to use a linked-ears reference, for most purposes it is preferable to re-derive the data off-line using an averaged-ears reference. This is done by recording the data with an original reference of either a single ear or mastoid or some other location (e.g. vertex). If a single ear or mastoid is used for the original recording, the other ear or mastoid would be recorded as an active site. Off-line, the data can then be re-referenced to an average of the two ears (or mastoids). This referencing strategy avoids the pitfalls of using a physically linked ears or mastoids reference because variations in electrode impedance of the two ears would in this case have no effect on the data since they are each recorded as separate channels.

There are probably only two instances in which a linked-ears (-mastoids) reference might be preferred over an averaged-ears (-mastoids) reference. First, the linked reference can help to reduce artifact. For example, electrocardiogram artifact is typically reduced when using a linked-ears or -mastoids reference compared with a single ear or mastoid. In addition, there are special recording conditions during which specific types of artifact are prominent that might benefit from linked-ears recording. One such case is the simultaneous recording of EEG and impedance cardiography (ZCG); the latter involves the imposition of a high-frequency signal across the torso and often leads to prominent EEG artifact (Dalton & Davidson 1997). We have found that a physically linked ears reference, in conjunction with specific types of amplifiers, helps to attenuate the artifact and allows such simultaneous recordings to be made. The second instance in which an investigator might prefer a linked-ear or -mastoid reference is when there are a limited number of channels available. The averaged-ears or -mastoids reference requires one additional channel compared to the physically linked reference.

Some investigators (e.g. Tucker 1993) have argued that the average reference, although computationally intensive, is probably the best solution to the reference problem. The logic underlying the average reference solution is based on the following assumption: If a sufficient number of electrodes are sampled, then – given the variations in voltage and phase across the head – the average voltage across the entire braincase at any given moment should be zero. Of course, this assumption is predicated on the view that a sufficient number of electrodes are sampled and that these sampled electrodes are distributed fairly evenly across the entire head. Because of the geometry of the head, the ventral surface of the braincase is not adequately sampled, even in very high-density sensor applications. However, with a sufficiently large number of electrodes, this problem is minimized. Just how large a number of electrodes is acceptable for the computation of an average reference is not definitively known, but most investigators agree that a minimum of 20 electrodes (assuming they are evenly spaced on the scalp surface) is about the fewest number possible for an average reference computation. Of course, the more electrodes that comprise the average, the better. It is essential when using an average reference to ensure that the sampled electrodes are distributed relatively evenly across the scalp. With fewer than about 32 electrodes, the investigator must exercise caution in the construction of the average reference if significant artifact is present on several channels, necessitating that these channels not be included in the average. This scenario would result in different reference montages across subjects.

The average reference can be computed off-line and subsequently used as the reference for each "active" electrode. The on-line reference used makes no difference; the average reference can be re-derived using a recording made with any original reference (for a detailed explanation, see Lehman & Skrandies 1984; for a solution that takes into account the distance between electrodes, see Hjorth 1982).

It is worth reiterating that every recording is essentially a bipolar recording. Data should not be interpreted as reflecting scalp activity at the "active" site; rather, the voltage obtained reflects the potential difference between the target site and the reference site. This knowledge should lead to more cautious interpretation of topographic features of data derived from using any of the references described here. Oftentimes, the best solution is to report each data set using two or more reference schemes and so ascertain the extent to which similar findings emerge for each (see e.g. Davidson et al. 1990a; Henriques & Davidson 1991). Consistencies across reference in topographic patterning increase confidence in topographic interpretations.

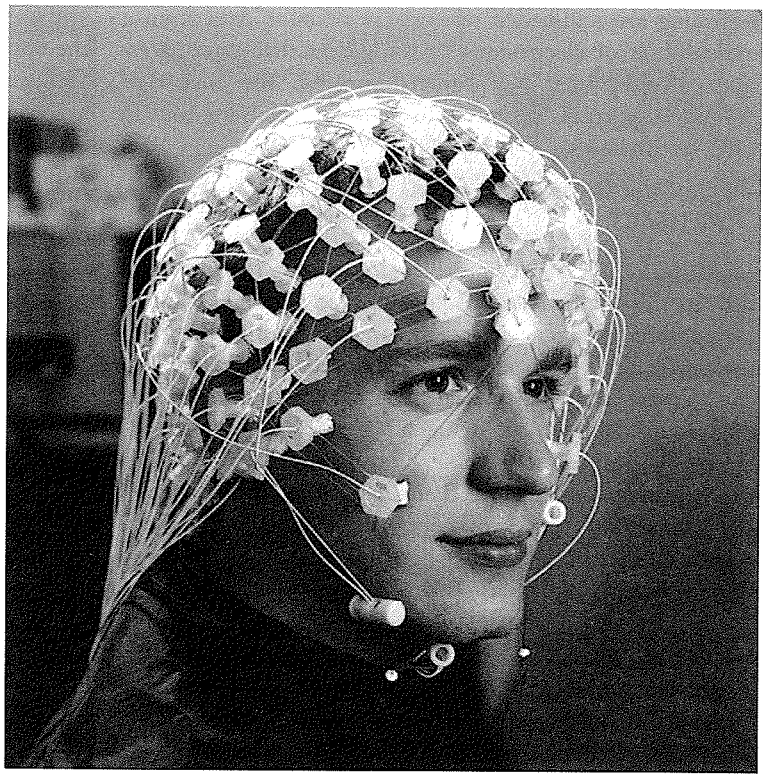

Figure 4. Photograph of the sensor net with 128 electrodes, manufactured by Electrical Geodesics, Inc. (EGI; www.egi.com). Photography by Greg Sutter.

High-Density Electrode Arrays

Recent advances in EEG technology have made high-density (up to 256-channel) recording systems commercially available. Such arrays provide more even coverage of the scalp than traditional 16- and 32-channel electrode arrays, with an average interelectrode distance of less than 3 cm (see Figure 4). Average reference derivations should be more accurate with an increasing number of electrodes (the average voltage across all electrodes should be closer to zero at any given time point). As EEG researchers use more sophisticated experimental designs, increase their knowledge of neural generators, and develop new analysis techniques, the use of high-density arrays will be important in identifying highly localized patterns of EEG activity. Using a paradigm of iterative subsampling of phantom ERP data, Srinivasan, Tucker, and Murias (1998) showed how focal "hot spots" can be washed out by 19- and 32-channel recording montages as a result of spatial aliasing.

However, important questions remain concerning the use of high-density recording arrays. The most important issue is a conceptual one and concerns the additional yield provided by these arrays. As we have noted, the skull acts as a spatial filter and smears brain electrical activity. The intercorrelations among closely spaced electrodes tend to be very high, typically in the range of 0.8 to 0.9. And most importantly, for certain types of questions, the likely size of the underlying aggregate generator might be quite large. For studies of simple sensory and motor function, where small discrete brain locations are likely, the increase in resolution afforded by high-density arrays is quite apparent (Srinivasan et al. 1998). However, with more complex cognitive and affective processes, it is not entirely clear at present how much additional information will be gained from these methods (using EEG frequency analysis methods and not event-related activity). It is critical, however, that studies be conducted with quantitative EEG using high-density sampling in order to examine the extent to which spatial aliasing is present in the lower-density recordings.

There are a number of important practical considerations in the use of high-density arrays. Application of electrodes must be fairly quick to avoid subject fatigue. Scalp abrasion must be kept to a minimum to avoid subject discomfort. Care must be taken to avoid any shunts between neighboring electrodes due to electrolyte leaking. (See Tucker 1993 for a practical discussion of these issues in high-density recording.) Price is obviously an important consideration for most researchers. A long-standing benefit of EEG recording has been its low cost as compared with other functional neuroimaging methodologies. High-density arrays must likewise be competitively priced if they are to become a realistic option for mainstream EEG researchers. Finally, analysis techniques must be developed that allow for the integration of the huge amount of data these arrays produce. The benefits of high-density

recording are nullified if researchers examine data from a mere subset of electrodes. To the extent that these questions are answered and caveats resolved, the advent of high-density arrays promises to be a valuable new tool in EEG research.

ARTIFACT

Artifact can be a formidable problem for the investigator. In this context, it should be noted that EEG allows for considerable subject motion compared with other neuroimaging procedures. It is the only method available that can tolerate fairly substantial head movement, and it does not require the subject to be lying prone during experiments. If desired, the ambient noise in the environment can be almost completely eliminated. These features make the use of EEG particularly attractive in pediatric samples and other populations where it is not likely that head movement could be eliminated.

Biological Artifact

Muscle Artifact. "Noise" in the EEG data – including but not limited to electromyographic (EMG) activity near the recording sites, gross head/body movement, and eye movements or blinks – is one of the foremost problems facing EEG researchers. Standard procedures for recognizing and addressing various types of biological artifact (arising from cephalic or noncephalic sources) are an important component of preanalysis data processing. Reduction of artifact in the data is best dealt with in a prophylactic manner; subjects can be instructed to try to remain as still as possible during the recording trials, to try not to blink excessively, to try to relax as much as possible, and so forth. However, it is important to recognize that following these instructions becomes a de facto task that may divert attention away from the experiment itself. Moreover, certain types of experiments, such as those involving emotion induction, could be adversely affected by instructing subjects to remain still. In those experiments where the tasks under study do enable the experimenter to instruct subjects to keep motion to a minimum, muscle activity can often be reduced by careful observation during the recording session; subjects who appear tense should be encouraged to relax and possibly take a break from the experiment. If possible, trials can be re-presented if the experimenter judges the level of artifact to be excessive during a particular trial. However, in experiments where such flexibility is not possible or where it would be inappropriate to instruct the subject to refrain from movement, it is necessary to consider procedures other than simple instruction to reduce or eliminate artifact. Dealing with artifact on a post hoc basis is time-consuming but necessary to ensure the integrity of the data. Although some laboratories employ computer algorithms to detect and score out artifact (e.g., eliminating data epochs in which a predetermined amplitude criterion is surpassed), only visual scanning of the data will detect all artifact.

Electromyographic contamination by muscle activity is a common occurrence in EEG recording. High-frequency activity, particularly in the temporal and lateral-frontal sites, may represent tension or jaw movement and is commonly observed in certain task situations (see Figure 5). The EMG is a broadband signal that is most prominent in frequencies above the EEG frequencies (i.e., above 50 Hz). However, a simple low-pass filter cannot be used to remove all of the EMG contributions to the observed signal, since the EMG signal is typically very broad and includes frequencies all the way into the alpha-band range (10 Hz). In fact, the use of such a filter can be quite misleading, because it removes the visible muscle artifact but retains that component that is in the same frequency range as the EEG. Assuming that the amplifier filter settings are set to allow observation of the high-frequency EMG (the low-pass filter must be set to permit passage of signals up to about 100 Hz), the researcher may elect to score out such data epochs completely. If a sufficient quantity of data is available for a given condition, this strategy may be appropriate. However, it will bias the data toward the inclusion of epochs during which muscle activity is minimal and thus may skew the findings. For example, if an experiment compares the EEG during two emotion induction conditions, one of which results in more muscle activity than the other, and if the investigator excludes all epochs during which muscle artifact was present, then the comparison between the conditions may be biased because of the differential sampling of epochs in each of the two conditions. If such a bias is likely or if an insufficient amount of data exists to exclude data confounded by muscle activity, then other data analytic strategies are required.

An alternative strategy that we have advocated is to derive a measure of power in an EMG band from each of the EEG leads; then regress this value on power in the traditional EEG bands to derive measures of EEG power with the component accounted for by EMG removed. (See Pivik et al. 1993 for description of this technique and Ekman & Davidson 1993 for an example of its application.) This strategy is predicated on the assumption that power in different frequencies within the broad EMG band is linearly related, so that increases in power in higher-frequency EMG components are accompanied by increases in power in lower-frequency components (Pivik et al. 1993). In order to perform this analysis, brain electrical activity must be sampled at a sufficiently high sampling rate to derive a metric of power in an EMG band. We typically sample the EEG at 250 Hz; this puts the Nyquist frequency at 125 Hz, and one may then extract power in the 70–100-Hz band. To obtain a more reliable estimate of EMG band power, sampling of the EEG can be performed at a higher rate so that a broader EMG band can be extracted. Measures of EMG power are derived separately for each electrode site.

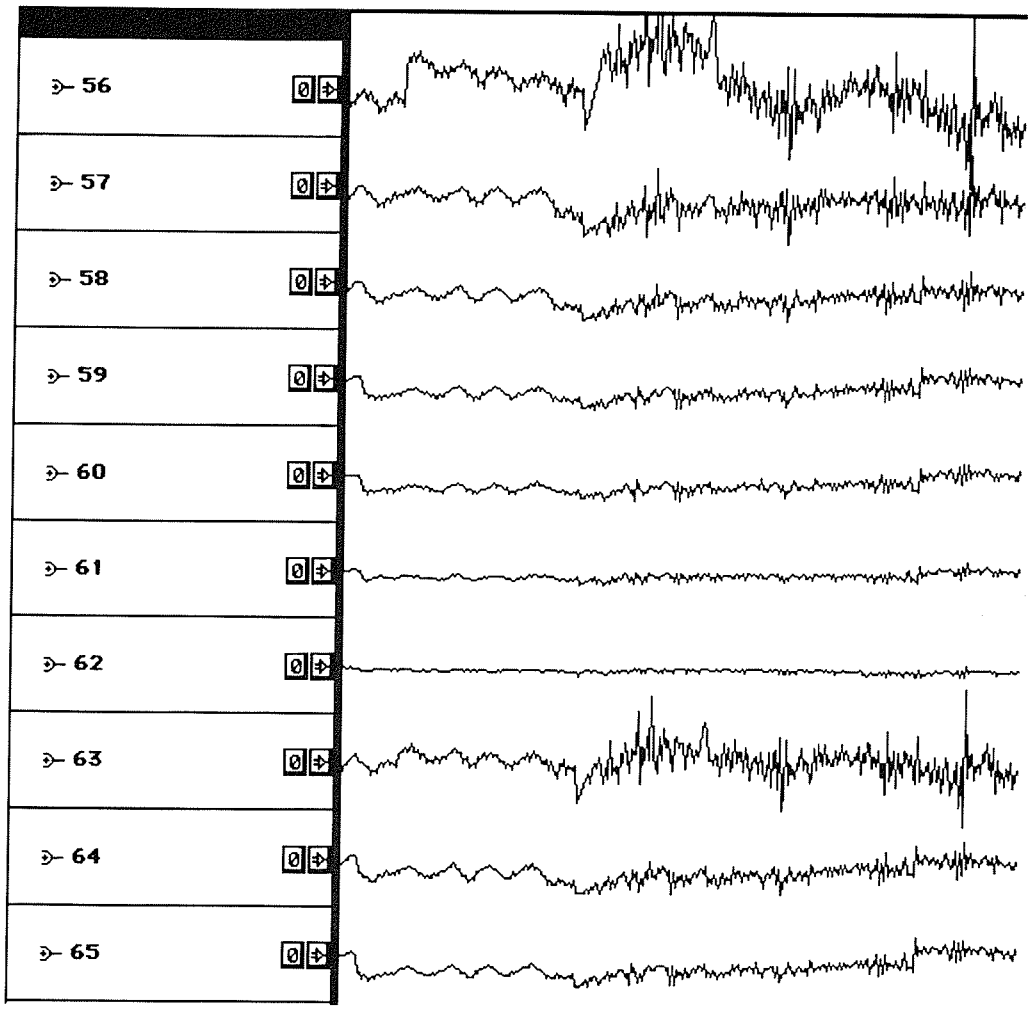

Figure 5. Example of muscle artifact in the EEG produced by jaw clenching. Note the high-frequency activity in channels 56, 57, and 63. These are the leftmost lateral temporal electrode sites on the EGI 128-channel net.

Assuming that a sufficient amount of data is available for each subject, the regression of the EMG on EEG power can be performed within subjects.

Special care must be taken to ensure the absence of EMG contamination when measuring power in the gamma band, typically defined as the 36–44-Hz range. Interest in the measurement of gamma activity has been generated by the observations in animals of gamma activity associated with the "binding" of perceptual features (Singer 1995). Although such observations have been from recordings directly in cortex, some investigators have suggested that scalp-recorded activity in the gamma frequency range may be observed and is associated with focused attention and perceptual binding (see e.g. Spydell & Sheer 1982). Unless adequate procedures are used to regress out EMG from the gamma band, measures of activity in this band should be suspected of being confounded with muscle activity.

Eye Movement Artifact. Eye movements and eye blinks are a problem in virtually all experimental paradigms. Large eye artifact can contaminate the EEG, especially in the frontal sites. Careful instructions to the subject to minimize these behaviors will help, but they seldom eradicate the problem. One strategy in dealing with eye artifact is to score out any contaminated EEG data, although this may lead to a dramatic loss of data in some paradigms. Another strategy is to use one of several computer algorithms designed to remove the effect of eye artifact from the EEG signal (Gasser, Ziegler, & Gattaz 1992; Gratton, Coles, & Donchin 1983). These programs generally rely on regression techniques to determine the magnitude of correlation between eye electrodes (vertical and horizontal leads) and each EEG signal. "Eye-corrected" EEG data may then be processed and analyzed as would any other data.

Nonbiological Artifact

Given the hardware involved in EEG research, it is inevitable that nonbiological sources of artifact will influence the data. For example, 60-Hz noise from nearby electrical

devices is easy to identify but not so easy to eliminate. Initial suspects may be computer monitors, overhead lighting, power cables, and power strips. If the noise source cannot be located, 60-Hz notch filters may be used either off-line or during data collection in order to reduce the effect of the noise source on the data. High electrode impedances or a faulty ground connection can exacerbate 60-Hz noise problems. Another source of artifact comes from the recording electrodes themselves. Care must be taken to see that the electrodes are carefully washed after each use to prevent corrosion and the build-up of electrical potentials across the surface of the electrode.

RECORDING

The gain by which the EEG signal is amplified is generally chosen from a number of predetermined settings (generally from 5k to upwards of 30k). When choosing the gain, it is best to find the optimal setting: sufficiently high that the amplifier is sensitive enough to pick up small deflections in the signal, yet sufficiently low that saturation or "clipping" does not occur. In systems that allow differential selection of gain values for different EEG sensors, it is useful to set the gain for frontal and temporal channels at a lower level than that for central, posterior, and occipital channels, since contamination from eye artifact is more likely to affect the sites closer to the front of the head. Avoiding clipping in the eye channels and frontal-temporal EEG sites becomes especially important when eye artifact correction procedures are to be used, because clipped data points cannot be used when determining the EEG–eye lead correlations. It should be standard procedure to collect calibration values (gain and zero offset) by passing signals of known frequency and amplitude through each amplifier channel. Collection of calibration data both before and after each recording session provides a means to correct variable gain and offset in individual amplifier channels, and careful inspection of calibration data can often expose amplifier malfunction. In particular, if the recorded calibration data at the end of a session differ from that collected at the beginning of the session, there is some indication that a change of gain occurred during the session. This might signify amplifier malfunction or some other problem that would render the data questionable. Once the analog EEG signal has been digitized, amplitude is expressed as A-D (analog-to-digital) units. It is crucial that EEG data be reported in terms of microvolts; the calibration data are used to convert the raw A-D counts into real units.

Filters are used to selectively attenuate signals that are unwanted or not of interest. Filtering of the EEG signal may be accomplished by using analog filters during the recording or by using digital filters during or after the recording. Filter settings depend largely on the frequency bands of interest in the data. For example, if the experimenter is interested in examining alpha-band (8–13-Hz) activity, a bandpass filter – with a high-pass setting well below the lower boundary and a low-pass setting well above the upper boundary of the alpha band – is required, given the roll-off characteristics of analog filters. These characteristics (expressed in decibels per octave) will partially determine the appropriate filter setting. Care must be taken to attenuate as little as possible the frequency bands of interest, and investigators should be encouraged to examine a graph of the filter roll-off to ensure that the frequencies of interest are not attenuated.

Another methodological issue that depends largely on the frequency bands of interest is selection of sampling rate. When the EEG signal is sampled discretely, the Nyquist theorem states that the highest frequency that can be accurately resolved is half the sampling rate. If the experimenter were interested in examining frequencies of up to 90 Hz, a sampling rate of 200 Hz would prevent temporal aliasing in the digitized signal. In practice, however, the sampling rate is usually set at a level somewhat above twice the highest frequency of interest; in the preceding example, a sampling rate of 250 Hz would suffice. If high-frequency EMG is of interest, sampling rates of 500 Hz or even 1,000 Hz are sometimes used. However, the capacity for data storage increases along with sampling rate. Twice the disk space is required for data collected using a sampling rate of 1,000 Hz as for data sampled at 500 Hz.

ANALYTIC STRATEGIES AND ISSUES

Windowing, FFT, and FHT

The raw EEG signal may be thought of as being primarily composed of rhythmic sinusoidal patterns of activity. After the raw EEG signal has been recorded, saved to disk, and scored for artifact, the next step is to select epochs for the computation of the power spectrum. Epochs should be sufficiently short so that they meet the stationarity assumption, which holds that the data during the epoch do not change in their frequency composition. The frequency resolution of the analysis will be affected by the length of the epoch selected for analysis, with better frequency resolution associated with longer epochs. Epochs should be selected with a Hanning or Hamming window, essentially a cosine taper function. This type of window attenuates the contributions of the data from the ends of the epoch, thus minimizing spurious frequencies in the analysis that might arise from the abrupt transition to the analysis epoch. Most investigators use windows that overlap by 50% so that the data from the tails of each window are reflected in the adjacent window, thus providing maximal data yield.

The power spectrum provides information on the contributions of each frequency to the entire EEG spectrum. The fast Fourier transform (FFT) decomposes the complex EEG signal into its underlying sine wave constituents. (The fast Hartley transform, or FHT, is conceptually identical

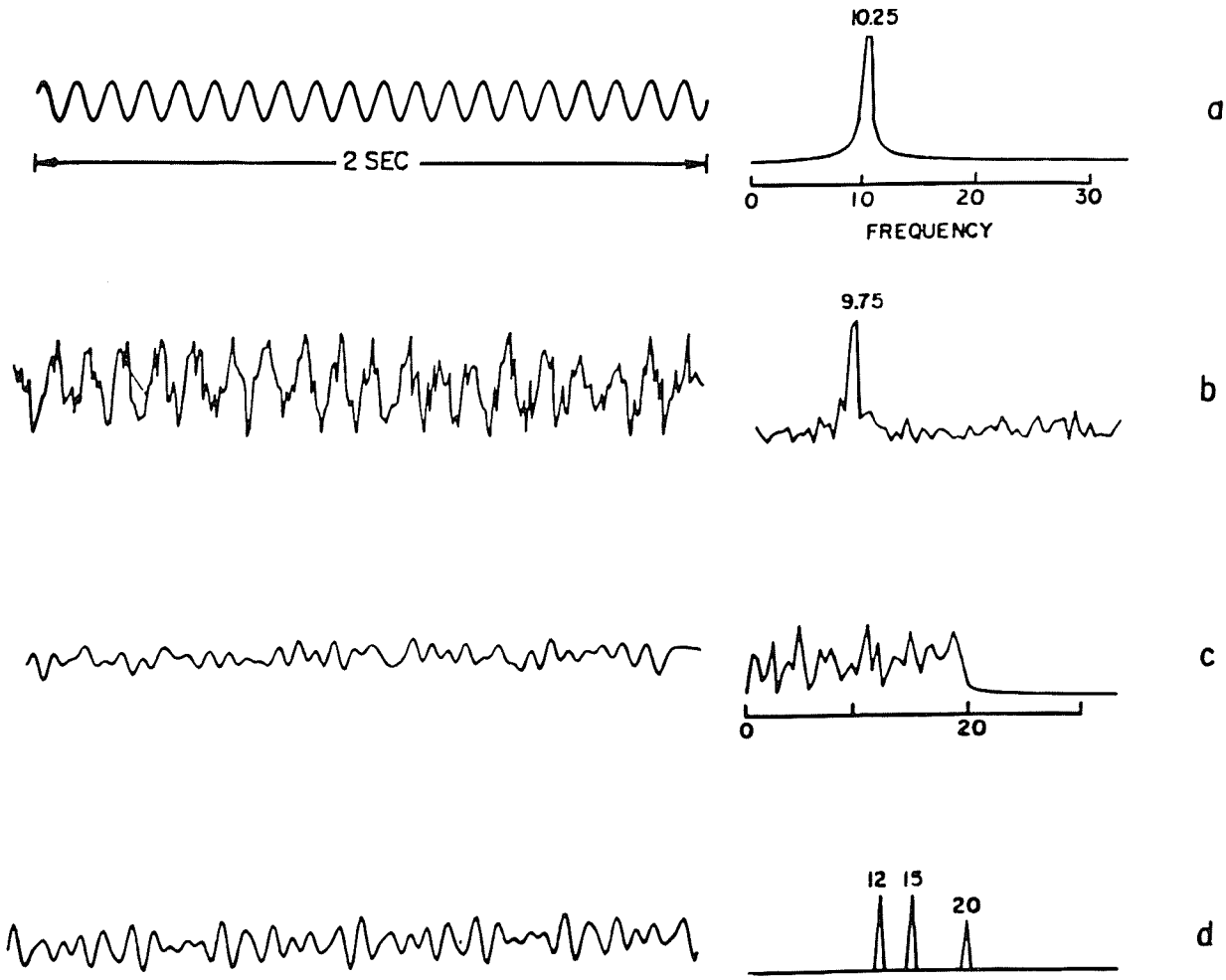

Figure 6. Raw signals (right) and corresponding power spectra (left) for various mathematical functions. (a) Sinusoidal oscillation of frequency 10.25 cps, sampled over an epoch length of 2 sec. (b) Oscillation at 9.75 cps with noise of equal power added. (c) Noise only, bandlimited to contain frequency components only below 20 cps. (d) Mixture of three sinusoidal oscillations having frequencies of 12, 15, and 20 cps. From *Electrical Fields of the Brain: The Neurophysics of EEG* by Paul Nunez. Copyright © 1981 by Oxford University Press, Inc. Used by permission of Oxford University Press, Inc.

but computationally less intensive; Bracewell 1984.) The results of the spectral decomposition are used to compute the amount of power at different frequencies. Figure 6 presents artificially generated EEG signals and their corresponding power spectra. The top portion of the figure displays the power spectra for a pure sine wave of 10.25 Hz. The second line of the figure displays the raw signal and power spectra for a 9.75-Hz signal, plus random noise of equal power added. In the third line of the figure, the power spectrum for random noise below 20 Hz is presented. Note the absence of any discernable peak in the power spectrum. In the bottom line of the figure, a mixture of three sinusoidal oscillations is depicted. Note how the spectral analysis neatly separates each of the frequencies in the complex raw signal.

Power is typically expressed in units of μV^2. Because distributions of power tend to be skewed, most investigators transform the data in order to normalize its distribution. The most common transform used is the natural log transformation (see Davidson et al. 1990a for a comparison of different transformations). Power is usually aggregated across frequency bins to form measures of band power. Also, different epochs of the same condition are averaged to provide more reliable estimates of spectral power for a given condition. The effects of such averaging can be clearly seen in Figure 7. As the figure shows, noise that is random will become attenuated with additional epochs included in the average, so that the signal-to-noise ratio increases. We strongly advocate that all studies using spectral analysis of EEG report the average and minimum amounts of artifact-free data used to compute a within-subject average for each condition of an experiment.

Another decision faced by the EEG researcher is whether to express power in absolute or relative units. Typically, if power is expressed in relative units, then power in a particular band is expressed as a proportion of power in

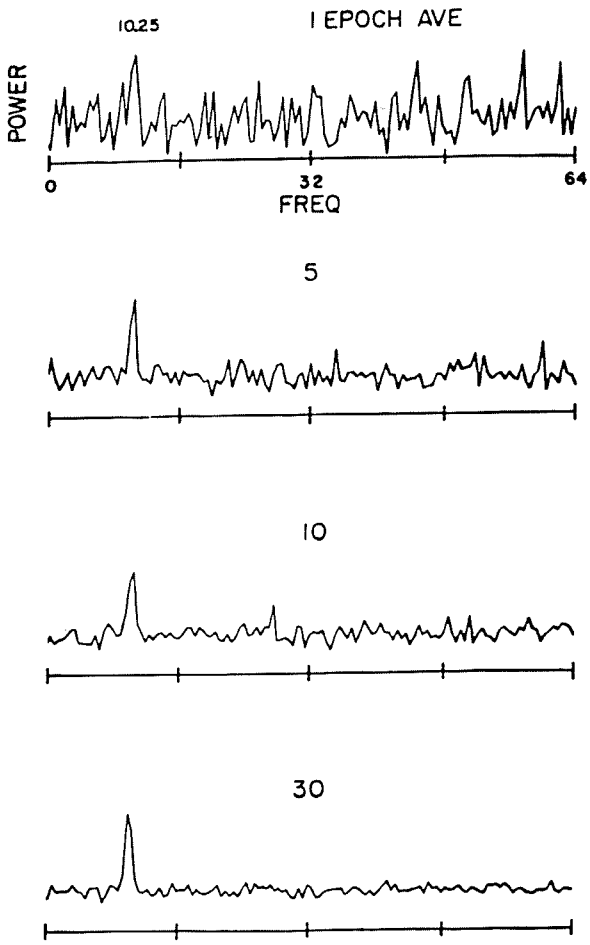

Figure 7. Average power spectra for a sinusoidal function (10.25 cps) plus noise having twice the power of the sine function. Plots are obtained by averaging the power spectra of various numbers of individual 2-sec epochs, as shown. From *Electrical Fields of the Brain: The Neurophysics of EEG* by Paul Nunez. Copyright © 1981 by Oxford University Press, Inc. Used by permission of Oxford University Press, Inc.

the entire spectrum. This computational strategy helps to minimize individual differences across subjects in absolute power magnitude. However, it has the disadvantage of obscuring just where in the power spectrum the differences among conditions or groups might reside. Other strategies are preferable for removing the influence of individual differences in absolute power, as we describe next. Also, the general issue of psychometric considerations in computing different EEG parameters will be addressed in a separate section.

Coherence Analysis

Examination of relations between pairs of EEG channels may be achieved using coherence analysis. The coherence between signals is a squared correlation coefficient expressed as a function of frequency that measures the phase consistency between two signals. Coherence measures will therefore always range between 0 and 1. Coherence is independent of amplitude, so it is possible to obtain high coherence over parts of the spectrum with low amplitude and low coherence in parts of the spectrum with high amplitudes. If two noise-free signals have a constant phase relation between them (regardless of what the actual phase is) at some frequency, then the coherence between them is always 1. Many factors can produce spuriously high coherence estimates; these are detailed in Nunez (1995, pp. 164–5). Some of the more important factors include statistical unreliability, volume conduction, and reference electrode effects. The first problem can be addressed by including a sufficient number of epochs and then averaging across epochs, just as was recommended for spectral analysis. If the phase is close to 0 degrees, it is likely that volume conduction and/or reference electrode effects are affecting the data. These effects can be reduced by either recording from closely spaced bipolar electrodes or by using the Laplacian. The Laplacian of the electrical potential results in a quantity that is proportional to either the source intensity or sink intensity, depending upon the sign. The Laplacian will highlight local sources and higher spatial frequencies in topographic data. Nunez (1981, p. 198–9) provided a computational method for deriving the Laplacian. It is computed as the second derivative in space of the potential field at each electrode. In practice, the computation of the Laplacian uses an array of closely spaced electrodes to derive a value for an electrode at the center of an array (see e.g. Hjorth 1975). A more accurate estimate is based upon three-dimensional (3D) spline interpolations for computing the Laplacian over the actual shape of the head (Le et al. 1994). Because the Laplacian amplifies high–spatial frequency noise, a spatial filter should be applied after the computation of the Laplacian (Le, Menon, & Gevins 1994). One drawback of all Laplacian methods is that it is not possible to estimate the Laplacian at peripheral electrodes, since there is an incomplete set of surrounding electrodes for these sites.

Coherence analysis has been suggested to reflect connections among different cortical generators (see e.g. Thatcher, Krause, & Hrybyk 1986). Thatcher and his colleagues (Thatcher, Walker, & Guidice 1987; Thatcher 1992) used such data to make inferences about developmental changes in the cortical connectivity. A particularly dramatic demonstration of the reflection of cortical connectivity in coherency can be found in data on interhemispheric coherence in normal subjects compared with split-brain individuals (i.e., patients who have undergone a surgical severing of the corpus callosum as a treatment for intractable epilepsy). Nunez (1981) reported on three split-brain subjects and three matched normal controls for resting eyes-closed data recorded from the left and parietal electrodes (P3 and P4) referenced to the ipsilateral mastoid. Among normal controls, average interhemispheric coherence for the peak in the alpha band was approximately 0.7. Among the split-brain patients, two individuals failed

to show interhemispheric coherence above 0.4, while the third patient showed a maximum coherence between these sites of approximately 0.6. Thus, it appears that surgical severing of the corpus callosum resulted in a lowering of interhemispheric coherence, implying that the cortico-cortical connections provided by the corpus callosum are essential in the maintenance of normal coherence.

ASYMMETRY METRICS

One common use of EEG in psychophysiology is to make inferences about differential activation of regions of the two hemispheres. Various indices have been proposed to provide a convenient metric in which to express the magnitude and direction of asymmetry. Most commonly, the investigator will use power in the alpha band from two homologous electrodes in the derivation of the asymmetry index. For example, one of the most common asymmetry metrics is the log right minus log left ($\log R - \log L$) alpha power asymmetry index. In light of the fact that alpha tends to be inversely associated with activation in the waking EEG, positive numbers on this index denote left greater than right activation, whereas negative numbers denote right greater than left activation. As we shall explain in more detail, the $\log R - \log L$ alpha asymmetry index has been demonstrated to show moderate test–retest stability and excellent internal consistency reliability (Tomarken et al. 1992b). The validity of different asymmetry metrics can be established only by correlating values on the metric with independent variables that are predicted to be associated with the asymmetrical process in question. It is important when using an asymmetry metric to examine also the separate contributions of the two hemispheres to the effect in question. For example, in an experiment in which two conditions are compared on an asymmetry metric and condition A is found to have a significantly larger asymmetry index compared with condition B, we can only conclude that condition A produced greater *relative* left-sided activation compared with condition B. However, this difference could be a function of one of three different patterns:

1. condition A has greater left-sided activation than condition B and no difference in the right hemisphere;
2. condition A has less right-sided activation than condition B and no difference in the left hemisphere; and
3. condition A has *both* greater left-sided and less right-sided activation than condition B.

For certain theoretical models, the differentiation among these possibilities is crucial. In order to ascertain which of these alternatives might be accounting for a given asymmetry difference, the investigator must examine the separate activation levels from the left- and right-hemisphere electrodes. In the next section, we consider some of the methodological complications of such analyses.

WHOLE-HEAD RESIDUALIZED POWER

Some theoretical questions require an investigator to examine relations between power in a particular electrode or group of electrodes and some criterion variable. For example, we have investigated relations between asymmetric activation in anterior scalp regions and reactivity to emotional stimuli (Tomarken, Davidson, & Henriques 1990; Wheeler et al. 1993). In these studies, we used an asymmetry metric ($\log R - \log L$ alpha power) and correlated individual differences in baseline indices of this metric and measures of reactivity to short emotional film clips. In the Wheeler et al. (1993) study, once we observed a significant relation between the asymmetry metric and the affect variables, we wanted to determine which hemisphere was accounting for the effect in question. It would not be appropriate simply to take the power at a given electrode (e.g., the left medial frontal electrode, F3) and correlate alpha power at this site with the affect variable, because one of the major contributors to variations among individuals in absolute amount of alpha power is skull thickness (Leissner et al. 1970). When the asymmetry score is computed, it removes individual differences in skull thickness, since variation across subjects in skull thickness is far greater than variations among scalp locations within subjects. Thus, to determine which hemisphere was accounting for the effect in this example requires procedures other than simply using the raw (or log-transformed) power from an individual site. We have developed a straightforward procedure for this purpose.

Assuming that a sufficient number of sites are sampled, a measure of whole-head EEG power can be derived. We assume that the major contributor to individual differences in whole-head power is anatomical variability (primarily skull thickness) across individuals. By regressing the EEG from each site on whole-head power, we can then remove the contributions of this unwanted variable and determine the amount of variance in our outcome measure accounted for by the EEG measure following the removal of variance that is primarily produced by gross anatomical variability. We have suggested as a rule of thumb that at least 20 electrodes be used for the computation of the whole-head average. This will minimize the possibility of any single electrode or region dominating the whole-head average. The average whole-head power is computed by first obtaining the individual electrode site powers and then averaging these data across sites. We then use a hierarchical regression model, where our outcome measure is the variable to be predicted. First entered is the whole-head power average; next we enter the power from the site of interest and determine the percentage of variance accounted for by power at this site. We can directly compare the amount of variance accounted for by power at each of the homologous sites that constituted the original asymmetry metric.

SOURCE LOCALIZATION

It is important to emphasize that even high-density EEG, analyzed with various deblurring methods such as the Laplacian transform, do not provide direct information about the anatomical origins of the observed signals. When data from high-density EEG recordings are mapped onto a three-dimensional head surface, the data are not true 3D data but instead are 2D data displayed on a 3D surface. One of the hopes of high-density arrays is that they might be used with source localization techniques to provide information on just where in the brain the observed signals are generated. Source localization techniques involve methods to mathematically represent the location, orientation, and strength of a hypothetical dipolar point current source. This problem is a version of the inverse problem, the description from a surface distribution of the underlying sources that gave rise to such a distribution. There are differences of opinion regarding the utility of these techniques. Their major limitation is that there is no unique solution to the inverse problem. The solution to the problem must therefore be constrained by some a priori assumptions. In the case of simple sensory and motor processes, source localization techniques may be quite useful (Gevins 1996a,b). However, with more complex processes that likely involve several sources that partially overlap in time, source localization is more problematic. New developments on the horizon include testing the same subjects in the same paradigm using both fMRI and EEG methods and then using the fMRI data to constrain the source localization solution. The electrophysiological data can provide useful information on the temporal dynamics of the source that are unavailable with fMRI methods alone.

EVENT-RELATED DESYNCHRONIZATION

As we have noted, cortical activation is generally associated with an attenuation of alpha rhythms in the cortex. Phasic desynchronization of the alpha rhythm was first quantified and reported by Pfurtscheller (1977; Pfurtscheller & Aranibar 1977). Event-related desynchronization (ERD) is a measurement of the time-locked average power associated with desynchronization of alpha rhythms. This ERD is measured using an event-related potential (ERP) paradigm: an average is taken across multiple experimental events within the same condition in order to measure ERD in response to particular events. The ERD has been studied as a function of cortical activation (Van Winsum, Sergeant, & Geuze 1984) and arousal (Boiten, Sergeant, & Geuze 1992; Van Winsum et al. 1984) and has been shown to occur in paradigms using voluntary movement (Pfurtscheller & Aranibar 1979) and cognitive processing (Sergeant, Geuze, & Van Winsum 1987).

PSYCHOMETRIC ISSUES

When investigators use biological measures, they often unwittingly assume that such measures are reliable and therefore rarely bother to examine the psychometric characteristics of the data they generate. However, particularly in the EEG area, where many derived indices are obtained and where such indices are often used to reflect both instantaneous state as well as trait differences, the consideration of psychometric issues is important. There are several different parameters of reliability that can be computed. First, it is often useful to know whether the metric we extract displays *internal consistency* reliability. This form of reliability reflects the extent to which different trials or epochs of the same measure within a condition are reflecting the same process. It is typically used with paper-and-pencil measures, where individual items are entered to determine if they cohere as a unitary construct. We have applied measures of internal consistency reliability to metrics of activation asymmetry (Tomarken et al. 1992b) and have found these metrics to show excellent reliability, with reliability coefficients consistently exceeding 0.85. *Test–retest* reliability is another form of reliability. Often EEG metrics are used as traitlike indicators to differentiate among groups. When used in this way, it is imperative to establish that the metric in question shows adequate test–retest stability. The intraclass correlation is the preferred statistic to assess test–retest stability, since it is sensitive to both relative position within a group and to absolute value of the metric. Electroencephalogram measures of alpha-power asymmetry obtained during a resting state show moderate stability over a period of approximately one month, with stability estimates ranging between 0.65 and 0.75 (Tomarken et al. 1992b).

When computing measures of reliability, it is particularly important to use measures that are not strongly affected by individual differences in such anatomical variables as skull thickness. Thus, for example, the test–retest stability of absolute levels of power in the alpha band tends to be very high (above 0.85). However, it is likely that basic anatomical differences among subjects, which obviously do not change much over short periods of time, account for these high stability coefficients.

Research Applications

INTRODUCTION

In this section, we selectively highlight some applications of quantitative EEG methods to specific questions that have long occupied the attention of biobehavioral scientists. In light of space limitations, this review is meant to showcase examples of particular approaches and not to provide a comprehensive survey of the findings based on EEG methods in the study of psychological processes. The

section is divided into four parts: cognition, affect, individual differences, and psychopathology; specific examples are provided in each of these areas. It is important to emphasize that we consider here only those studies that have used measures of the spontaneous EEG and not studies that examine event-related potentials. Moreover, there are topics (e.g. sleep) that we have omitted because they are covered elsewhere in this volume.

COGNITIVE PROCESSES

In EEG studies of task-induced changes in activity, it is important that tasks be matched on several basic characteristics. Two of the most important characteristics for matching include the difficulty level of the tasks being compared and the motor requirements of the tasks. If the tasks are not matched on these dimensions, it is difficult to conclude that the specific cognitive processes that may have been engaged by the task are responsible for the observed changes. Davidson et al. (1990a) performed a study comparing EEG changes elicited during psychometrically matched verbal and spatial cognitive tasks. These tasks were specifically chosen since we predicted that posterior activation asymmetry would differentiate between them, with the greater relative left-sided activation predicted for the verbal task compared with the spatial task and greater relative right-sided posterior activation during the spatial task compared with the verbal task. The verbal task was the word-finding task modeled after the Boston Naming Test (Kaplan, Goodglass, & Weintraub 1978). Subjects were presented with sentences that defined particular words such as "a box or house for bees to live in." Items varied in difficulty level. Following presentation of the sentence and after the subjects had arrived at their response, they pressed a button that terminated EEG data collection. At this point, they were instructed to write down their response.

The spatial task was the dot localization task, adapted from a measure developed by Hannay, Varney, and Benton (1976). The subject is shown a drawing of two open rectangles, one above the other. The top rectangle contains two dots and the bottom rectangle contains an array of numbers. The bottom rectangle is slightly offset to the right or left of the top rectangle. The subject is presented with the stimulus and is asked to indicate the numbers that the two dots would cover if the two rectangles were superimposed. Task difficulty was manipulated by varying the size of the number array, with larger arrays associated with more difficulty. The subject was instructed to press the response key when he or she arrived at the two numbers corresponding to the response. As in the word-finding task, this button press terminated data collection. The subjects then wrote the two numbers corresponding to the dot locations on their answer sheet.

The tasks that were used were carefully matched on basic psychometric properties including mean accuracy, mean item difficulty, and coefficient alpha (based upon a behavioral-only study with 151 subjects). Because EEG was collected only during the presentation of the stimulus and since data collection was automatically terminated when subjects pressed their response key, there was no possibility that differential movement during each of the two tasks could have biased the results.

In this study, EEG was recorded from only a small number of anterior and posterior scalp locations – left and right medial frontal, central, and parietal electrodes. We compared two reference montages, vertex (Cz) and an averaged-ears reference. Band power was extracted in the delta, theta, alpha, and beta bands. Finally, relations between the EEG data and measures of performance were also examined. Several important findings emerged from this study. First, asymmetry of alpha power in the central and parietal regions differentiated between the verbal and spatial task, with greater relative left-sided activation associated with the verbal task. This finding was present for both the vertex and averaged-ears reference. The specific pattern of hemispheric activation in the central and parietal region differed. In the central region, greater activation in the left hemisphere (less alpha power) occurred during the verbal task compared with the spatial task. No difference was present in the right hemisphere. In the parietal region, it was the right hemisphere that differentiated between the two tasks, with greater activation (less alpha power) observed during the spatial compared with the verbal task. In the parietal region, there were no alpha power differences for the left hemisphere. This general pattern was present for both the averaged-ears and the vertex reference. That the specific individual hemispheric contributions to the overall laterality difference between tasks was different for the central and parietal regions underscores a point made earlier about the importance of decomposing asymmetry scores so that differential contributions by the left and right hemisphere can be identified.

When we examined differences in other frequency bands between the two tasks, we found that they were considerably less robust than the differences identified in the alpha band. However, when differences did occur in any of the other bands (delta, theta, and beta), they were in the same direction as those found for alpha: greater suppression of power in the hemisphere putatively activated and greater accentuation of power in the other hemisphere. Investigators sometimes assume that, when alpha power is attentuated during task performance, there is a "compensatory" increase in beta power. An alternative view holds that all synchronous activity in cortex is attenuated during states of cortical activation, and that – although most synchronous activity is in the alpha band – there is some activity in other bands and hence the power in these other bands should also decline. In this study, we examined correlations between alpha and beta power asymmetry to ascertain the extent to which these correlations would be

positive or negative. One classical view would hold that they should be inversely correlated, since beta power would increase when alpha power is suppressed. However, on the view that activation should be associated with attenuation of power in all frequency bands, measures of alpha and beta asymmetry during task performance should actually be positively correlated. Most of the correlations we reported in this study were positive, challenging the older view that, when alpha power is suppressed, it is replaced by an increase in beta power. Our findings are consistent with the alternative notion that activation is associated with suppression of power across the entire spectrum.

When we examined correlations between measures of EEG asymmetry and task performance, we found that asymmetry in alpha power was most consistently and strongly correlated with task performance. For example, the correlation between parietal alpha asymmetry and performance on the word-finding task was 0.63. Correlations between alpha asymmetry and performance for dot localization were opposite in sign, though none failed to reach significance. In general, correlations were higher for the vertex-referenced than for the averaged-ears data. This likely reflects the fact that the vertex-referenced data involved recording between two more closely spaced electrodes and thus were likely to reflect more local sources. Clearly, the resolution of this issue would benefit from recording with high-density electrode arrays.

We compared the correlations between power asymmetry and measures of absolute power from a particular site or the average of left and right power for homologous sites. We consistently found that it was the difference in power between homologous sites – the asymmetry metric – that accounted for more variance in task performance than power in any individual site or region. This finding underscores the potential importance of asymmetry and suggests that the relative difference in activation between the hemispheres may, in certain cases, be far more important for behavior than the absolute amount of activation in a region.

In a study using high-density EEG recording methods, Gevins et al. (1997) examined the patterns of cortical activation associated with verbal or spatial working memory. The task studied was a version of the *n*-back task, requiring subjects to compare the current stimulus to one presented one or more trials previously. In the version used by Gevins et al. (1997), letter stimuli were presented on each trial and appeared in one of four quadrants of the visual field. Spatial matches required subjects to press a button if the spatial location of the stimulus on the current trial was the same as the spatial location of the stimulus that appeared three trials back. The identity of the letter was irrelevant on spatial match trials. For the verbal trials, the subjects' task was to press if the current stimulus was the same letter as was presented three trials back, independent of the spatial location of the stimulus. Verbal and spatial control tasks consisted of the recognition of a particular letter or spatial position, respectively.

The EEG was recorded from a 115-channel array referenced to linked mastoids; EEG spatial topography was enhanced utilizing the "finite element deblurring" method (Le & Gevins 1993), which provides an estimate of the electrical fields as they would be recorded from the cortical surface. The method uses MRI-derived, anatomically realistic models of volume conduction to project the scalp-recorded signals downward onto the cortical surface. Local tissue thicknesses are derived for each subject from their individual MRI, and these data are then used to estimate the conductivity of each finite element on an individual subject basis. Fast Fourier transforms were computed on 2-sec samples of EEG, using a 50% overlapping Hanning window. Average power spectra were then averaged within condition for each subject.

Frontal midline theta power increased in magnitude with increasing memory load. Dipole modeling implicated the anterior cingulate region as the source of this signal. A low-frequency parietocentral alpha power signal (average of 9 Hz) decreased with increasing memory load. A faster occipitoparietal alpha power signal (average of 11 Hz) was relatively attenuated during the spatial version of the task, particularly over the right posterior hemisphere. The findings from this study suggest that decrements in alpha power during the difficult compared with the easy tasks indicates that this signal is inversely related to the amount of cortical resources devoted to the task. Results also demonstrated that the alpha signal increased with practice, implying that fewer cortical resources are required for task performance following skill development. The midline frontal theta signal was interpreted by these and other authors (e.g. Gundel & Wilson 1992; Inouye et al. 1994; Iramina, Ueno, & Matuoka 1996) to reflect attentive states that occur during complex task performance. Why such a process should be reflected in increases in theta activity is not clear from this or other reports.

In a complementary article based upon the same data set, Gevins et al. (1997) reported on the stimulus-locked ERP correlates associated with performance of these tasks. In discussing the different information provided by the spectral data versus the ERP data, the researchers suggested that "changes in EEG spectra are probably more closely related to changes in the state of the functional networks underlying task performance (cf. Lopes da Silva 1991), while the subsecond EP responses probably more closely index different operations being performed on internal representations (cf. Ritter et al. 1982)" (Gevins et al. 1997, p. 383). However, they do not offer any data on actual correlations between ERP and spectral measures. In a study that directly compared spectral to ERP measures, we found that the spectral measures were more sensitive to incentive variations compared with the ERP measures (Sobotka, Davidson, & Senulis 1992).

AFFECTIVE PROCESSES

One of the chief virtues of brain electrical activity measures is the excellent time resolution they afford. This is particularly advantageous when studying spontaneous emotion, since episodic bursts of emotion are often fleeting and so their occurrence cannot be predicted with certainty. We have performed a series of studies during which EEG measures were obtained while subjects were exposed to complex emotional stimuli (e.g., short film clips – see Davidson et al. 1990b; Ekman, Davidson, & Friesen 1990). In these studies, we unobtrusively videotaped subjects' facial behavior in response to the stimuli so that we could go back, objectively code facial behavior, and then extract portions of the EEG during which specific facial expressions were present. Used as such, the facial behavior provides a flag to index the occurrence of a specific emotion. In our first major article on this topic (Davidson et al. 1990b), we developed a set of methodological desiderata for the psychophysiological study of emotion:

1. adequate procedures must be used to independently verify the presence of the intended emotion;
2. epochs of different discrete emotions must be separable;
3. the physiological measures chosen for study must have a sufficiently fast time constant to reflect brief periods of emotion;
4. at least two emotions and a baseline condition must be compared;
5. the intensity of the elicited emotion must be matched across conditions; and
6. sufficient data for each condition must be collected to yield reliable estimates of the physiological parameters under study.

Comment on some of these desiderata is certainly warranted. The first desideratum refers to the use of some independent procedure – such as facial expression, emotion-modulated startle, facial EMG, or a similar measure – to verify that the intended emotional changes have been produced. Some of these procedures can also be used to isolate specific parts of the record during which a peak emotional response is present. The fourth desideratum is offered to establish that a particular profile of biological change that might be found for one emotion condition is unique to that specific emotion and is not something generically associated with emotion or states of arousal. The fifth desideratum on intensity matching is particularly important, because often two or more emotion conditions are compared that clearly differ in intensity or arousal. Any EEG difference observed in this case could be a function of intensity or arousal differences between conditions rather than differences in the specific emotional states that were produced. Lang developed a picture set specifically for this purpose from which appetitive and aversive pictures that are matched on arousal can be selected (Lang, Bradley, & Cuthbert 1995).

In the Davidson et al. (1990b) study, we compared EEG during film clips designed to elicit happiness and disgust. The intensity of amusement in response to the positive film clips and disgust in response to the negative film clips was matched. We found greater right-sided prefrontal activation (indexed by decrements in alpha power) during facial signs of disgust in response to the negative clips compared with facial signs of happiness in response to the positive clips. No differences between conditions were observed in posterior scalp regions for the same points in time. Anterior temporal alpha power asymmetry also differentiated between conditions (see Figures 8 and 9). It is important to note that these EEG differences were not present when data were aggregated over the entire film period, independent of the subjects' facial behavior. These findings highlight the utility of using the ongoing EEG in investigations of this kind, where the occurrence of discrete epochs of spontaneous emotion cannot be predicted in advance and are of short duration.

INDIVIDUAL DIFFERENCES

We have examined relations between individual differences in both anterior and posterior EEG asymmetry measures and measures of affect and cognitive function, respectively. In infants (Davidson & Fox 1989) as well as adults (Davidson & Tomarken 1989), we noticed that there were large individual differences in baseline electrophysiological measures of prefrontal activation and that such individual variation was associated with differences in aspects of affective reactivity. In infants, Davidson and Fox (1989) reported that 10-month-old babies who cried in response to maternal separation were more likely to have less left and greater right-sided prefrontal activation during a preceding resting baseline compared with those infants who did not cry in response to this challenge. In adults, we first noted that the phasic influence of positive and negative emotion elicitors (e.g., film clips) on measures of prefrontal activation asymmetry appeared to be superimposed upon more tonic individual differences in the direction and absolute magnitude of asymmetry (Davidson & Tomarken 1989).

During our initial explorations of this phenomenon, we needed to determine if baseline electrophysiological measures of prefrontal asymmetry were reliable and stable over time and thus could be used as a traitlike measure. Tomarken and colleagues (1992b) recorded baseline brain electrical activity from 90 normal subjects on two occasions separated by approximately three weeks. At each testing session, brain activity was recorded during eight 1-min trials, four eyes-open and four eyes-closed, presented in counterbalanced order. The data were visually scored to remove artifact and then Fourier transformed. Our focus was on power in the alpha band (8–13 Hz). We computed coefficient alpha as a measure of internal

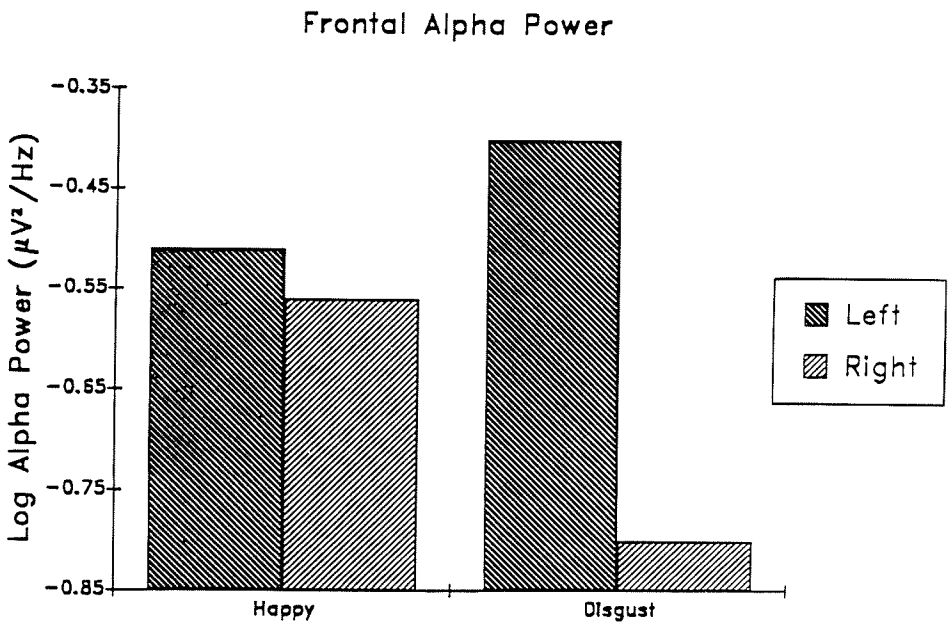

Figure 8. Mean log-transformed alpha power (in $\mu V^2/Hz$) for the left and right frontal regions (F3 and F4) during the happy and disgust facial expression conditions. Increasingly negative numbers indicate less alpha power; the negative numbers are a function of the log transformation, so lower (i.e., more negative) numbers are associated with increased activation. Reprinted with permission from Davidson, Ekman, Saron, Senulis, & Friesen, "Approach–withdrawal and cerebral asymmetry: Emotional expression and brain physiology 1," *Journal of Personality and Social Psychology,* vol. 58, pp. 330–41. Copyright © 1990 by the American Psychological Association.

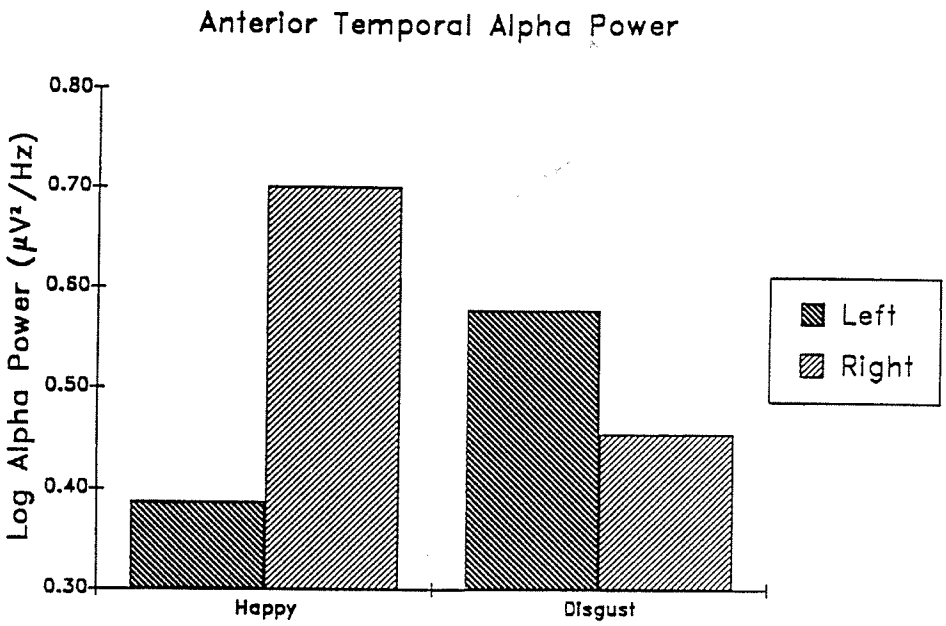

Figure 9. Mean log-transformed alpha power (in $\mu V^2/Hz$) for the left and right anterior temporal regions (T3 and T4) during the happy and disgust facial expression conditions (lower numbers are associated with increased activation). Reprinted with permission from Davidson, Ekman, Saron, Senulis, & Friesen, "Approach–withdrawal and cerebral asymmetry: Emotional expression and brain physiology 1," *Journal of Personality and Social Psychology,* vol. 58, pp. 330–41. Copyright © 1990 by the American Psychological Association.

consistency reliability from the data for each session. The coefficient alphas were quite high, with all values exceeding 0.85, indicating that the electrophysiological measures of asymmetric activation indeed showed excellent internal consistency reliability. The test–retest reliability was adequate, with intraclass correlations ranging from 0.65 to 0.75 depending upon the specific sites and methods of analysis. The major finding of import from this study was the demonstration that measures of activation asymmetry based upon power in the alpha band from prefrontal scalp

electrodes showed both sufficiently high internal consistency reliability and acceptable test–retest reliability to be considered a traitlike index.

The large sample size in this reliability study enabled us to select a small group of extreme left and extreme right frontally activated subjects for MR scans to determine if there existed any gross morphometric differences in anatomical structure between these subgroups. None of our measures of regional volumetric asymmetry revealed any difference between the groups (unpublished observations). These findings suggest that whatever differences exist between subjects with extreme left versus right prefrontal activation are likely functional and not structural.

On the basis of our prior data and theory, we reasoned that extreme left and extreme right frontally activated subjects would show systematic differences in dispositional positive and negative affect. We administered the trait version of the Positive and Negative Affect Scales (PANAS; Watson, Clark, & Tellegen 1988) to examine this question and found that the left frontally activated subjects reported more positive and less negative affect than their right frontally activated counterparts (Tomarken et al. 1992a). More recently, Sutton and Davidson (1997) showed that scores on a self-report measure designed to operationalize Gray's concepts of Behavioral Inhibition and Behavioral Activation (the BIS/BAS scales; Carver & White 1994) were even more strongly predicted by electrophysiological measures of prefrontal asymmetry than were scores on the PANAS scales (see Figures 10 and 11). Subjects with greater left-sided prefrontal activation reported more relative BAS to BIS activity compared with subjects exhibiting more right-sided prefrontal activation.

We also hypothesized that our measures of prefrontal asymmetry would predict reactivity to experimental elicitors of emotion. The model that we have developed over the past several years (see Davidson 1992, 1994, 1995) features individual differences in prefrontal activation asymmetry as a reflection of a diathesis that modulates reactivity to emotionally significant events. According to this model, individuals who differ in prefrontal asymmetry should respond differently to an elicitor of positive or negative emotion, even when baseline mood is accounted for.

In order to examine this question, we performed the following experiment (Wheeler et al. 1993). We presented short film clips designed to elicit positive or negative emotion. Brain electrical activity was recorded prior to the presentation of the film clips. Just after the clips were presented, subjects were asked to rate their emotional experience during the preceding film clip. In addition, subjects completed scales that were designed to reflect their mood at baseline. We found that individual differences in prefrontal asymmetry predicted the emotional response to the films, even after measures of baseline mood were statistically removed. Those individuals with more left-sided prefrontal activation at baseline reported

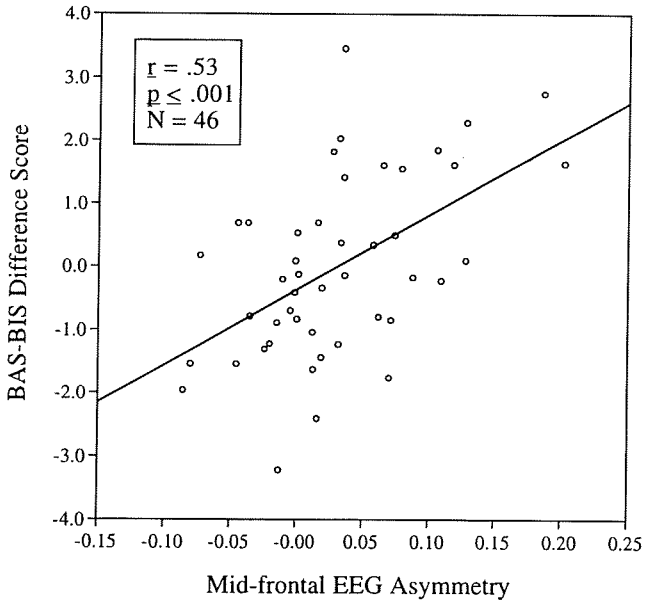

Figure 10. Scatter plot of the correlation between mid-frontal (F3 and F4) EEG asymmetry and BAS – BIS difference scores (score for Behavioral Approach System minus score for Behavioral Inhibition System). Higher EEG asymmetry scores reflect greater relative left-frontal activation. Higher BAS – BIS difference scores reflect greater relative BAS activity. Adapted from Sutton and Davidson (1997).

more positive affect to the positive film clips, and those with more right-sided prefrontal activation reported more negative affect to the negative film clips. These findings support the idea that individual differences in electrophysiological measures of prefrontal activation asymmetry mark some aspect of vulnerability to positive and negative emotion elicitors. That such relations were obtained following the statistical removal of baseline mood indicates that any differences in baseline mood between left and right frontally activated subjects cannot account for the prediction of film-elicited emotion effects that were observed.

In addition to studies using self-report and psychophysiological measures of emotion, we have also examined relations between individual differences in electrophysiological measures of prefrontal asymmetry and other biological indices, which in turn have been related to differential reactivity to stressful events. Two recent examples from our laboratory include measures of immune function and cortisol. In the case of the former, we examined differences between left and right prefrontally activated subjects in natural killer (NK) cell activity, since declines in NK activity have been reported in response to stressful, negative events (Kiecolt-Glaser & Glaser 1991). We predicted that subjects with right prefrontal activation would exhibit lower NK activity compared with their left-activated counterparts because the former type of subject has been found to report more dispositional negative affect, to show higher relative BIS activity, and to respond more intensely to negative emotional stimuli. We found that right frontally activated

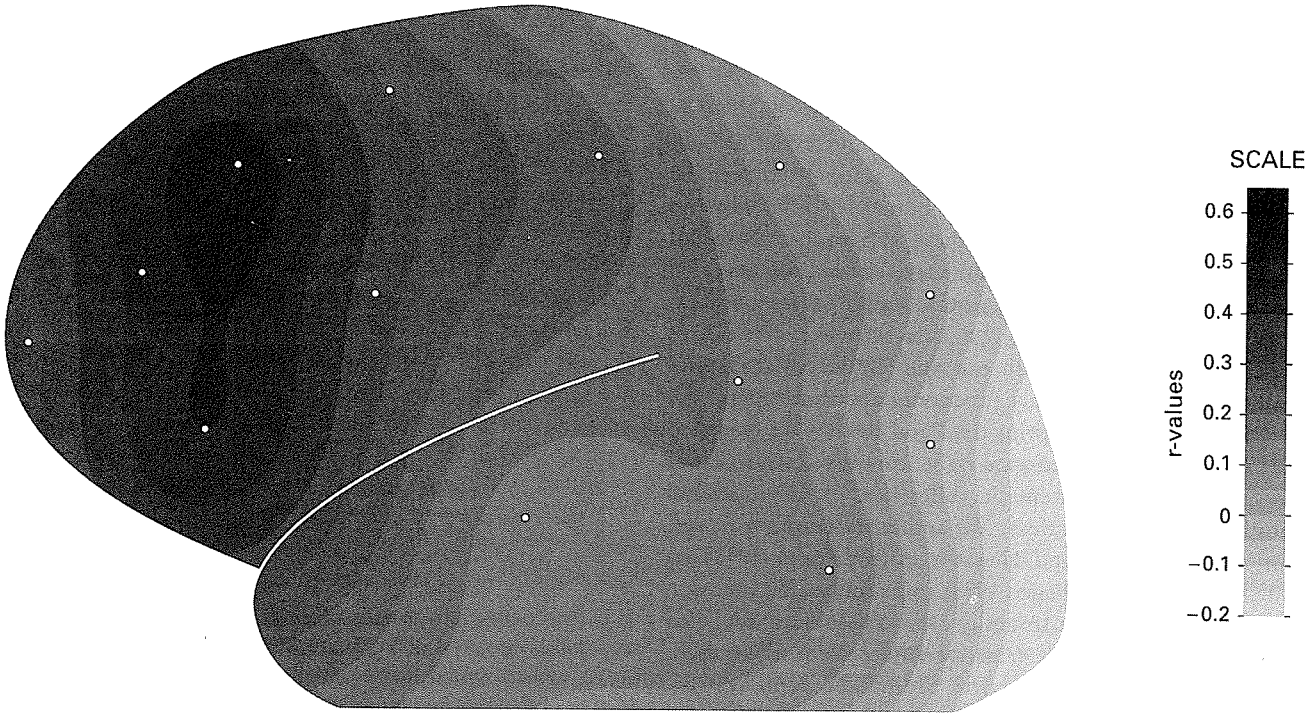

Figure 11. Topographic map of the relation (Pearson correlation coefficient) between resting EEG asymmetry (log right minus log left alpha-band power density) and the BAS − BIS difference score (*z*-transformed score for BAS minus *z*-transformed score for BIS). The asymmetry score for each homologous electrode pair (represented by small circles) was correlated with the BAS − BIS difference score. These correlations were used to generate a spline-interpolated map across a lateral view of the head. This map is used for display purposes only; all inferential statistics are based on actual measured values at specific scalp electrode sites. Adapted from Sutton and Davidson (1997).

subjects indeed had lower levels of NK activity compared to their left frontally activated counterparts (Kang et al. 1991).

In collaboration with Kalin, our laboratory has studied similar individual differences in scalp-recorded measures of prefrontal activation asymmetry in rhesus monkeys (Davidson, Kalin, & Shelton 1992, 1993). In Kalin et al. (1998) we acquired measures of brain electrical activity from a large group of rhesus monkeys ($N = 50$); EEG measures were obtained during periods of manual restraint. A subsample of 15 of these monkeys was tested on two occasions, four months apart. We found that the test–retest correlation for measures of prefrontal asymmetry was 0.62, suggesting similar stability of this metric in monkey and man. In the group of 50 animals, we also obtained measures of plasma cortisol during the early morning. We hypothesized that if individual differences in prefrontal asymmetry were associated with dispositional affective style then such differences should be correlated with cortisol, since individual differences in baseline cortisol have been related to various aspects of trait-related stressful behavior and psychopathology (see e.g. Gold, Goodwin, & Chrousos 1988). We found that animals with right-sided prefrontal activation had higher levels of baseline cortisol than their left frontally activated counterparts. Moreover, when blood samples were collected two years following our initial testing, animals classified as showing extreme right-sided prefrontal activation at age 1 had significantly higher baseline cortisol levels when they were 3 compared with animals who were classified at age 1 as displaying extreme left-sided prefrontal activation. These findings indicate that individual differences in prefrontal asymmetry are present in nonhuman primates and that such differences predict biological measures that are related to affective style.

PSYCHOPATHOLOGY

Electroencephalography has been extensively used to study brain dysfunction in psychopathology. Several reviews have appeared on EEG changes in schizophrenia (Kemali, Galderisi, & Maj 1988; Nunez 1995, pp. 616–19); these data will not be reviewed here. Brief mention will be made of the use of EEG to examine asymmetric activation hypothesized to characterize both affective and anxiety disorders. Readers interested in a review of EEG studies in depression may consult Davidson and Henriques (in press).

We have conducted several studies examining regional brain electrical activity in depression. We hypothesized that most depression is fundamentally associated with a deficit in the approach/appetitive motivation system and should therefore be specifically accompanied by decreased

activation in the left prefrontal region as measured by scalp electrophysiology; see Davidson (1998) for a general review. Henriques and Davidson (1991) obtained support for this hypothesis. Moreover, in another study, these authors demonstrated that the decrease in left prefrontal activation found among depressives was also present in recovered depressives who were currently euthymic, compared with never-depressed controls who were screened for lifetime history of psychopathology in themselves and in their first-degree relatives (Henriques & Davidson 1990). The findings from patients with localized unilateral brain damage, together with neuroimaging and electrophysiology studies in psychiatric patients without frank lesions, converge on the notion that depression is associated with a deficit in at least the prefrontal component of the approach system. We view this pattern of left prefrontal hypoactivation as a neural reflection of the decreased capacity for pleasure, loss of interest, and generalized decline in goal-related motivation and behavior.

Based upon other evidence (Davidson 1998), it has been hypothesized that – in contrast to depression – anxiety disorders should be associated with an increase in right-sided rather than a decrease in left-sided prefrontal activation, particularly during an acute episode of anxiety. To test this hypothesis, we exposed social phobics who were particularly fearful of making public speeches to the threat of having to make a public speech (Davidson et al. in press). Brain electrical activity was recorded during an anticipation phase as subjects were presented with an audiotaped countdown that noted how much time remained before their speech. The tape-recorded message was presented every 30 sec for a total of 3 min. We found that the phobics showed a large and highly significant increase over baseline in right-sided prefrontal activation. During this anticipation period, the control subjects showed a very different pattern of regional changes. The only change to reach significance was in the left posterior temporal region. We interpret this latter change as likely a consequence of verbal rehearsal in anticipation of making the public speech. No region in the right hemisphere exceeded an even liberal statistical threshold for increased activation relative to a baseline condition. The change in prefrontal activation among the phobics is consistent with our hypothesis of increased right-sided activation associated with an increase in anxiety. A modest increase was also found in right parietal activation and is consistent with the hypothesis of increased right-sided activation associated with the arousal component of anxiety (Heller & Nitschke 1998). Indeed, simultaneous measures of heart rate in this study indicated that the phobics had higher heart rate compared with the controls, particularly during the anticipation phase.

Research using self-report measures of positive and negative affect as well as experienced increases in autonomic arousal indicate that decreased positive affect is uniquely associated with depression, whereas increased autonomic arousal is uniquely associated with anxiety. However, reported negative affect is something that has been found to be common to both anxiety and depression (Watson et al. 1995). We have hypothesized that the decrease in left prefrontal activation may be specific to depression and that the increase in right-sided prefrontal activation (as well as right parietal activation) may be specific to certain components of anxiety. Considerably more research is required to understand the contribution being made by the activated right prefrontal region to negative affect. Other work (see Posner & Petersen 1990 for a review) indicates that portions of the right prefrontal region are activated during certain types of vigilance and attention (Knight 1991). Anxiety-related negative affect is accompanied by heightened vigilance (McNally 1998), which may be reflected in the right prefrontal increase.

Conclusions

Although the human EEG provides a highly indirect measure of brain function, it has been used in a remarkably diverse array of applications and research paradigms. New developments in EEG recording and analysis methodology enable modern investigators to record from a large number of electrodes relatively inexpensively. Such measures provide an economical, noninvasive, and potentially informative window on certain aspects of brain function. The low cost of these measures, particularly in comparison with hemodynamic neuroimaging procedures, makes them ideally suited for studies requiring the testing of large samples of subjects. Among their other virtues (besides being noninvasive) is their fast time resolution. This makes these measures particularly well-suited for studying behavioral phenomena that occur with short duration. However, as noted in this chapter, the chief disadvantage of these methods is their relatively poor spatial resolution and the impossibility of making definitive conclusions about the sources that give rise to the scalp voltage distributions.

In the future, the combination of electrophysiological and hemodynamic measures may provide optimal complementary views of brain function. Recent research indicates that vascular and electrophysiological activity may be uncoupled (Cannestra et al. 1996) as a result of vascular "overspill," a phenomenon associated with the spreading of a vascular response outside the spatial boundaries of neuronal activity. Thus, although hemodynamic methods may provide better intrinsic spatial resolution, inaccuracies can arise owing to overspill. In addition, there is a hemodynamic delay following a local neuronal response, so that the time resolution of hemodynamic methods will always be inferior to those based upon electrophysiology.

It is our expectation that – when used with the appropriate methods and cautions – scalp-recorded EEG spectral activity will continue to provide noninvasive, useful information on integrative brain function for many years to come.

NOTE

The research reported in this chapter was supported by NIMH grants MH43454, MH40747, Research Scientist Award K05-MH00875 and P50-MH52354 to the Wisconsin Center for Affective Science (R. J. Davidson, Director), by a NARSAD Established Investigator Award, and by a grant from the John D. and Catherine T. MacArthur Foundation.

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