Brain Development over the First Year of Life
Relations between Electroencephalographic Frequency and Coherence and Cognitive and Affective Behaviors

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INTRODUCTION

The dynamic organization of brain electrical activity has intrigued researchers since Berger (1929) first reported his ability to record electrical activity off the scalp. Publications describing the frequency components of the electroencephalogram, or EEG (as Berger named this rhythmic electrical activity), have been abundant since Berger’s initial report. There has been a good deal of research on the sources for the generation of electrical activity and on the origins of rhythmic activity such as the alpha waves. It is now assumed that different rhythmic periodicities in electrical activity originate from different anatomical/physiological structures (Lairy, 1975), although there is little consensus as to the specific structures (e.g., Andersen & Andersson, 1968; Elul, 1972; Hogan & Fitzpatrick, 1987; Lippold, 1973; Nunez, 1981; Steriade, Jones, & Llinas, 1989; Thatcher & John, 1977).

A number of investigators have focused on thalamic centers as the source for the generation of rhythmicities in the EEG (e.g., Thatcher & John, 1977), although here too the evidence remains inconsistent. More recently, Nunez (1981) has presented a model that characterizes the electrical activity recorded off the scalp in terms of its spatial properties. Patterns of EEG activity reflect both corticocortical links and cortical–subcortical connections. Although data on frequency and amplitude provide information on the excitability of neural networks, the interconnections between sites—the coherence and phase relations in the EEG at a given frequency—are of most interest to Nunez (1981).

Thatcher (Thatcher, 1991; Thatcher, Krause, & Hrybyk, 1986; Thatcher, Walker, & Giudice, 1987) has presented empirical support for Nunez’s postulations. Thatcher utilizes measures of the coherence of the EEG at specific frequencies between electrode sites. These measures of coherence reflect, in part, the action of both long and short axonal connections. Thatcher has predicted that with development, coherence should decrease between sites that are topographically close. This decrease should reflect greater differentiation within a particular area. On the other hand, with development, coherence should increase between sites that are topographically distant. According to the model, this change should reflect increasing connectivity between anterior and posterior sites within and between hemispheres.

In their earlier work, Thatcher and John (1977) explained the dynamic electrical activity of the brain in terms of "loop processes." The authors described the dynamics of brain organization as involving a balance between inhibitory and excitatory processes. These processes function at a control system level involving inhibitory and excitatory feedback, as well as at an information-processing level involving lateral and recurrent inhibition. Interestingly, Thatcher and John speculated that one could examine the development of these dynamic processes in the EEG as these two loop processes (one excitatory, the other inhibitory) converge.

Although Thatcher and John (1977) wrote about the possible maturation of inhibitory and excitatory processes as being reflected in the EEG over 15 years ago, the empirical work to test their hypotheses has not been completed. We still know little about the maturation of certain parameters of the EEG, particularly the coherence of rhythmic activity between certain scalp locations. The most recent attempt at examining these relations was a study by Thatcher et al. (1987), which mapped changes in coherence from birth through adolescence. There were, however, few specific data on the first year of life. This is unfortunate, given the advances in knowledge about brain development during the first year from other areas of neuroscience. The same dearth of studies may be found with regard to maturation of frequency components of the EEG during the first year of life. Although some studies have mapped the development of rhythmic electrical activity in some brain regions during the first year, few have presented data on EEG recorded from the frontal region. And while researchers have assumed a relation between brain activity and behavior, only two studies have attempted to relate developmental changes in the EEG to changes in cognitive (Hagne, 1972) or affective (Emde, Gaensbauer, & Harmon, 1976) development.

The purpose of this chapter is to report on the results of our longitudinal research (Bell & Fox, 1992; Fox & Bell, 1990) that attempts to relate maturational changes in brain electrical activity to cognitive and affective changes during the second half of the first year of life. Before discussing
our data, we first present the existing literature on the development of waking EEG during infancy. We discuss longitudinal and cross-sectional studies on the development of EEG frequency and on the development of intrahemispheric EEG coherence. We also describe in some detail the Hagne (1972) longitudinal study relating EEG development to cognitive behaviors, and the Emde et al. (1976) study that attempted to relate specific EEG parameters to the development of affective behaviors.

EEG DEVELOPMENT DURING INFANCY

Berger (1932a, 1932b) was the first to publish data on the relation between age and EEG. He found little brain electrical activity present at about 1 month of age, with increasing frequency and amplitude from occipital regions thereafter. After Berger’s initial description of the ongoing EEG, researchers set out to document the maturation of the EEG during infancy. The EEG of the full-term newborn was first recorded by Loomis, Newton, & Garrett (1938) and Smith (1938a, 1938b, 1938c). Much of the early research focused on the differentiation of states of alertness and sleep in the neonate (e.g., Dreyfus-Brissac, 1964, 1979; Samson-Dollfus, Forhomme, & Capron, 1964). These studies were primarily descriptive and relied upon the use of adult parameters of state to measure the development of brain activity in the infant.

EEG from premature infants was extensively described by Ellingson (Ellingson & Lindley, 1949; Ellingson, 1958; Ellingson & Peters, 1980) and Dreyfus-Brissac (Dreyfus-Brissac, 1964, 1979; Dreyfus-Brissac & Monod, 1975). These studies, again primarily descriptive, found that brain electrical activity of the prematurely born infant followed the same rate of maturation as if the infant were in utero (Dreyfus-Brissac, 1964). These studies, done many years ago, focused on a population of relatively large and healthy premature infants. More recent studies with very-low-birthweight infants have not found the same benign course of extraterine development (Tharp, 1986).

Longitudinal Studies on EEG Frequency Development

There have been a number of studies describing the ontogeny of the EEG in normal, full-term infants. Table 10.1 presents the longitudinal studies published on the maturation of waking EEG during infancy. Most of these studies report the onset of occipital rhythms during the first quarter of the first year of life at frequencies between 3 and 5 Hz. The frequency of these rhythms increases over the next 9 months, so that by 1 year of age the “dominant frequency” is about 7-9 Hz.

<table>
<thead>
<tr>
<th>Authors</th>
<th>No. of subjects</th>
<th>Ages</th>
<th>Leads</th>
<th>Focus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Smith (1938a, 1938b, 1938c, 1939, 1941)</td>
<td>14</td>
<td>1 day; biweekly, first 3 weeks; weekly, 4-28 weeks; bi-monthly, 7-18 months</td>
<td>Occipital, frontal, motor, central</td>
<td>“Alpha” in occipital</td>
</tr>
<tr>
<td>Lindsley (1939)</td>
<td>10</td>
<td>3, 6, 9, 12 months</td>
<td>Occipital</td>
<td>“Alpha” in occipital</td>
</tr>
<tr>
<td>Henry (1944)</td>
<td>6</td>
<td>3, 6, 9, 12 months</td>
<td>Occipital, central, frontal</td>
<td>“Alpha” in occipital</td>
</tr>
<tr>
<td>Hagne (1968, 1972); Hagne et al. (1973)</td>
<td>20</td>
<td>3 weeks; 2, 4, 6, 8; 10, 12 months</td>
<td>T3-T5 and T3-T6, Pz-O1 and Pz-O2, C3-C4 and Cz-C4</td>
<td>Left hemisphere; peak frequency; delta/theta quotient; cognitive development</td>
</tr>
<tr>
<td>Mizuno et al. (1970)</td>
<td>10</td>
<td>1-12 months; monthly</td>
<td>O2</td>
<td>Percentage of power</td>
</tr>
</tbody>
</table>

Many of these longitudinal studies were undertaken before the invention of frequency analyzers or computers; therefore, the EEG measures were computed by hand (Lindsley & Wicke, 1974). The principal measures derived were specific waveforms, frequency, amplitude, and the percentage of time a particular rhythmic activity existed in the EEG (Lindsley & Wicke, 1974; Ray, 1990). Lindsley and Wicke (1974) gave an example of how the alpha waveform might have been defined as “three or more waves of equal duration (corresponding to the alpha range) occurring in an uninterrupted sequence” (p. 24). Frequency and amplitude (microvolt) measures were made by ruler on the paper tracing of the EEG record.

Smith was the first to publish extensive data on the development of EEG rhythms during the first year of life. In a series of publications, he reported on the ontogeny of rhythms from the occipital and central scalp locations of the right hemisphere (Smith, 1938a, 1938b, 1938c, 1939, 1941). Smith’s major contribution to our knowledge of EEG development during infancy was his detailed description of the emergence of the occipital “alpha” rhythm, so named because its pattern of oscillation is similar to the adult 8- to 13-Hz alpha rhythm. He found no electrical ac-
a Swedish group led by Hagne (1968, 1972; Hagne, Persson, Magnusson, & Petersen, 1973) reported on a longitudinal sample of 20 infants. Bipolar recordings were made from the left and right temporal, parietal, occipital, and central regions (T3-T5, P3-O1, C3-C4, T4-T6, P4-O2, and C4-C3). Hagne also recorded EEG from the frontal region, but chose not to analyze the frontal data for two reasons. First, she predicted that there would be little frontal EEG activity in the first year of life (Hagne, 1968). Second, she reasoned that the frontal EEG would be contaminated with eye blink artifacts (Hagne, 1968; Hagne et al., 1973).

Hagne's findings were among the first longitudinal data to be analyzed by methods other than by hand. Hagne made use of a fast Fourier transform, a time series technique that decomposes a signal into frequency components. Her main interests were in relative power (specifically the delta/theta frequency quotient, 1.5-3.5 Hz/3.5-7.5 Hz) and in peak frequency. Hagne noted that results from the two hemispheres were similar, so she always reported only the data from the left hemisphere (Hagne, 1968, 1972; Hagne et al., 1973).

Hagne reported that the delta frequency band (1.5-3.5 Hz) was the dominant frequency during the entire first year of life (Hagne, 1968), and that most of the EEG activity was concentrated in either the delta band or the theta band (3.5-7.5 Hz) (Hagne et al., 1973). Like Smith, she found a great change in frequency between 2 and 4 months of age that resulted in the appearance of a 3- to 4-Hz signal (Hagne, 1968). Hagne also reported that the delta/theta quotient changed between 8 and 12 months of age, such that increases in theta activity corresponded with increases in delta activity (Hagne, 1968, 1972). The pattern of change varied with electrode location. The amount of theta (3.5-7.5 Hz) activity between P3 and O1 increased between 8 and 10 months of age and then increased between 10 and 12 months. Hagne also noted that theta activity between C3 and C4 steadily increased between 8 and 12 months of age. Finally, Hagne (1968) reported that infants displayed stable dominant frequencies across the first year of life. “Dominant frequency” was defined as the frequency at which an infant displayed the most EEG power. The greatest variability among subjects in peak frequency occurred at 8 months of age (Hagne et al., 1973). As seen in Figure 10.1, Hagne et al. (1973) reported that peak frequency at C3-C4 increased from 5.5 Hz to 6.9 Hz between 2 and 12 months of age.

At about the same time, a Japanese group led by Mizuno (Mizuno et al., 1970) described maturation of the EEG in the right occipital area. A frequency analyzer divided the EEG into 10 preselected bands. Results were reported in terms of relative power, specifically the 7.17-10.3 Hz/2.4-3.46 Hz quotient. The investigators reported that this alpha/delta quotient increased between 1 and 12 months of age (see Figure 10.2),

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tivity in the occipital recordings of the neonate (Smith, 1938a). However, Smith documented that at about 3 to 4 months of age, an alpha-like rhythm appeared in occipital EEG recordings. This rhythm first appeared around 3-5 Hz and was apparent in the awake infant (Smith, 1938b). This occipital activity increased by 6-7 Hz by 12 months of age (Smith, 1938b, 1939, 1941). Smith (1938b) speculated that the onset of this occipital activity at 3 to 4 months of age is correlated with the onset of cortical visual mechanisms. He cited reaching behavior as an emergent skill of the infant at this age. This work is noteworthy for its attempt to relate behavioral development to the ontogeny of the EEG.

Smith (1939, 1941) also reported on a 7-Hz alpha-like rhythm in the central region that was observable in the neonate during sleep. He noted that this central rhythm could begin to be recorded in the awake infant by the 3- to 5-Hz occipital rhythmic emerges, about 3 to 4 months of age (Smith, 1941). He linked the emergence of this central activity during awake states with the loss of infant primitive reflexes, such as the Babinski and the Moro, and the emergence of reaching behaviors. He postulated that this central rhythm signifies the onset of voluntary control of neuromuscular behaviors (Smith, 1941). Smith (1941) reported that this 7-Hz central rhythm did not begin to increase in frequency until 10 months of age. Smith also recorded EEG from the frontal region (Smith, 1938a), however, he presented no data from these recordings in any of his published reports.

Another longitudinal study from the same period was that by Lindsley (1939). Like Smith, Lindsley emphasized the emergence of the 3- to 5-Hz alpha-like occipital rhythm at 3 to 4 months of age, although Lindsley had no recordings from infants younger than 3 months of age. Lindsley reported that this rhythm increased to 6 Hz by 12 months of age. He speculated that the emergence of this rhythm at 3 to 4 months is associated with the functional capacities of the visual area (Lindsley, 1939).

A final longitudinal study from this era was done by Henry (1944). In his publication, Henry also noted a 3- to 4-Hz occipital frequency at 3 months of age that increased to 7 Hz by 12 months. This information was given in tables reporting longitudinal changes in occipital alpha for boys and girls, where Henry showed that the girls had a higher occipital rhythm (i.e., greater frequency) at each age than did the boys. Although Henry discussed correlations among EEG measures, skeletal maturity, and IQ for older children, he never discussed the infant data. Nor did he comment on the central and frontal EEG recordings made from the infants in the study.

The next longitudinal studies over the first year of life did not appear in the literature until some 25 years later. In a series of publications,
Cross-Sectional Studies on EEG Frequency Development

Cross-sectional samples of infants have confirmed findings on the maturation of EEG rhythms reported from longitudinal samples. One of the first cross-sectional studies was conducted by Gibbs and Knott (1949) and included 37 infants. Although EEG recordings were made from scalp locations over both hemispheres of the frontal, parietal, temporal, and occipital regions, only EEG data from the right occipital recordings were reported. Gibbs and Knott (1949) were the first to report use of a frequency analyzer on newborn EEG. They reported that EEG power was concentrated below 5 Hz during infancy, but that some infants showed power at 9 Hz or greater by 12 months of age. The infants in the sample displayed a pattern of decreased 1- to 6-Hz power with age, increasing and decreasing 7- to 8-Hz power over time, and increasing 9+ Hz power with age.

Ohtahara (1964, 1981) reported on a data set of 585 infants and children in an EEG study that recorded both waking and sleeping EEG from the parietal and occipital areas of the right hemisphere. The EEG power values were divided into frequency bands, and findings are reported as changes in relative power. Ohtahara (1981) reported that relative delta (1.5-3.5 Hz/1.5-40 Hz) decreased rapidly until 12 months of age, whereas relative alpha (8-12 Hz/1.5-40 Hz) increased gradually during the same time period. He also reported that theta 1 (3.5-6 Hz/1.5-40 Hz) and theta 2 (6-8 Hz/1.5-40 Hz) (see Figure 10.3) both increased between 1 and 12 months of age (Ohtahara, 1964).

FIGURE 10.1. Relative presence of peaks, mean peak height, and mean peak frequency at C3-C4 as functions of age. The mean peak frequencies in Hz are indicated above circles, whose diameters are proportional to the frequency. From Haghe et al. (1973). Copyright 1973 by Raven Press, Ltd. Reprinted by permission.

FIGURE 10.2. Maximum, average, and minimum occipital EEG activity at each age, expressed as R (ratio of 7.17-10.3 Hz to 2.4-3.46 Hz). From Mizuno et al. (1970). Copyright 1970 by the Tohoku University Medical Press. Reprinted by permission.
Studies of EEG Coherence

Fourier analysis provides the power-spectral density at each electrode site. The EEG coherence measure gives the covariance of spectral energies between any pair of electrode sites at a specific frequency band (Ray, 1990). Nunez (1981) has speculated that the coherence of the EEG recorded between electrode sites at different locations reflects the degree to which there are axonal connections between these regions. Thatcher has proposed that coherence values are related to the density of white matter axons and the short- and long-fiber networks of these axons (Thatcher et al., 1986, 1987). The strength and number of these axonal connections are reflected by coherence values. Coherence is equivalent to the absolute value of the cross-correlation function in the frequency domain. Coherence values range between 0 and 1, with a value of 1 indicating a complete linear relationship between two electrode sites (Kuks, Vos, & O'Brien, 1988).

In a sample of 577 infants and children ranging in age from 2 months to 18 years, Thatcher et al. (1987) assessed the development of the cerebral hemispheres by using EEG coherence measures. Thatcher et al. (1986) used coherence values to speculate that the frontal region is strongly coupled to the posterior regions via long-distance axonal connections. The investigators noted that there is evidence that the periods of change in the magnitude of coherence between electrode sites across the first 12 years of life may correspond to the ages of major cognitive change (Thatcher et al., 1987).

Thatcher et al. (1987) further reported that from birth to age 3 the coherence in each pair of leads showed differential patterns of development. Some pairs displayed increasing coherence between birth and age 3, while at the same time other pairs showed decreasing coherence. These irregular patterns changed to more synchronous ones after age 3, with all the pairs of leads simultaneously increasing or decreasing in coherence across age. However, the investigators appear to have grouped together all infants less than 12 months of age into one category (Thatcher et al., 1987). Thus, specifics about the developmental pattern of coherence during infancy cannot be determined from these data.

Studies Examining Relations between EEG and Behavior

From Berger's first recordings, human EEG has been associated with behavioral states (Woodruff, 1978). Since Lindsley (1952) suggested a link between EEG frequency, state of awareness, and behavior, researchers have continued to use EEG frequency as a measure of state.

Recent studies of EEG development of full-term infants have attempted to correlate normal EEG development with the development of specific behavioral responses during infancy. Proposing correlations between parameters of sleep EEG and affective behaviors, Emde et al. (1976) recorded EEG from 12 sleeping infants at 2 weeks of age and then monthly between 1 and 12 months of age. EEG was recorded from frontal (F₃, F₄), temporal (T₉, T₁₀), and central (C₃) leads in the right hemisphere, and referenced to both vertex (Cz) and the right ear (A₂). Emde and associates reported periods of rapid change in sleep EEG between birth and 2.5 months of age and between 5 and 9 months of age, each followed by a plateau. Notably, sleep spindles and non-rapid-eye-movement (non-REM) sleep were noted between 1 and 4 months, while hypersynchronous drowsy activity (consisting of high-amplitude 4- to 8-Hz activity) and K-complexes (negative sharp wave followed by a posi-


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tive wave seen at the vertex and characteristic of non-REM sleep) were common between 4 and 9 months of age (Emde et al., 1976). All EEG parameters examined in the study were specific to sleep. No frequency data were reported.

Emde and associates also measured each infant's affective behaviors in the laboratory. There were no relations between sleep EEG parameters and smiling or fussiness. Likewise, there were no links between sleep EEG parameters and onset of separation distress or stranger fear (Emde et al., 1976).

There is in the literature only one other longitudinal study with infants that systematically related EEG parameters to behavior throughout the first year of life. The work by Hagne (1968, 1972; Hagne et al., 1973) focused on EEG frequency development and its relation to normal mental development during the first year of life. Hagne recorded EEG in 20 infants at 3 weeks of age, and then at 2, 4, 6, 8, 10, and 12 months. At each EEG recording, Hagne also did neurological and developmental assessments (Hagne, 1972). The neurological assessments were conducted for the purpose of detecting deviations; however, Hagne reported that any deviations from the norm were slight and transient, and showed no correlation with EEG parameters.

The developmental assessment used by Hagne (1972) was the Griffiths Scale of Mental Development, and there were significant correlations between the total score on this scale and EEG parameters. Specifically, at 4 months of age, infants with a lower delta/theta quotient (higher relative theta and lower relative delta) at T₃-T₅ and at C₃-C₄ scored higher on the Griffiths, as did infants with a higher peak frequency at C₃-C₄. At 10 months of age, infants with a higher peak frequency at P₃-O₁ had a higher Griffiths score. Correlations between the various Griffiths subscales and EEG parameters resulted in sporadic significant coefficients (Hagne, 1972).

Summary

Most of the longitudinal work on EEG in infants has been descriptive in nature. Although we have learned much about the development of certain EEG frequencies during the first year of life, there has been little work or speculation on the meaning of these frequency changes. Does the increase in the "dominant frequency" correspond to certain neurophysiological changes in the brain or in the dynamics of organization? At the moment, we do not know. However, it is clear (as presented in the next section) that changes in frequency are associated with significant developmental/behavioral events during the first year of life. As we shall see, there is solid neuroanatomical evidence linking changes in brain structure to these behaviors. Although at the moment the data are correlational, the EEG measures do provide a window into the maturation of brain systems associated with important behavioral changes over the first year of life.

10. Brain Development over the First Year of Life

A LONGITUDINAL STUDY OF THE RELATIONS BETWEEN EEG AND COGNITIVE-AFFECTIVE DEVELOPMENT DURING INFANCY

The longitudinal research program we undertook was based upon four different and, until now, unrelated areas of work. These were (1) the literature on maturation of the EEG during infancy, and studies that have examined EEG-behavior relations; (2) current models of coherence, which relate anatomical and physiological data regarding the cerebral cortex and the genesis of the EEG; (3) behavioral neuroscience work on a specific area of prefrontal cortex and its maturation and functional significance in the performance of specific cognitive behaviors; and (4) work on the relation between EEG activation asymmetries in infants and affect.

The purpose of the study was to document the maturation of EEG rhythmic activity and coherence in infants over the second half of the first year of life in both the left and right hemispheres and in multiple sites, including frontal leads. We examined specific EEG-behavior relations in an attempt to test hypotheses regarding the possible functional meaning of specific EEG parameters. A group of infants was followed monthly from 7 until 12 months of age. At each assessment point, EEG was recorded and performance was observed on a cognitive task known to involve maturation of dorsolateral frontal cortex. This task, first described by Piaget (1937/1954), is known as the AB task. Collaborative research by Diamond and Goldman-Rakic (1983, 1986, 1989) had previously demonstrated in nonhuman primates that maturation and integrity of dorsolateral frontal cortex was essential for successful performance on the AB task. We reasoned that individual differences in maturation of frontal cortex should be reflected in the EEG and should be related to performance on the AB task.

We were, in addition, interested in the maturation of infants' affective responses and their relation to changes in EEG activity. Previous research from our laboratory (Fox & Davidson, 1986, 1987, 1988) had documented relations between EEG asymmetry in the frontal region and expression of different emotions. Consequently, at each age mothers were asked at the end of the cognitive assessment to leave the room for a brief period. Infants' latency to cry was recorded so that we could examine the development of latency to cry at maternal separation.
In the remainder of this section we describe the EEG recording procedures and analyses for our longitudinal study and the results of the coherence analyses. We then report our findings on the relations between frontal EEG and cognitive development, and between frontal EEG and affective development.

EEG Recording and Analysis

Thirteen full-term infants (seven girls, six boys) were the subjects. Infants were born within 2 weeks of their calculated due dates, weighed at least 6 pounds at birth, and required no oxygen after delivery. In addition, the infants had no neurological difficulties, and none had ever sustained a head injury. Nine of the infants were born to two right-handed parents, three to one left-handed and one right-handed parent, and one to an ambidextrous and a right-handed parent. Infants were seen monthly from 7 until 12 months of age, for a total of 6 sessions. Infants were seen within 5 days of their monthly "birthdays." Each of the 13 infants participated throughout the 6-month time period of the study.

At each laboratory visit, EEG was recorded from six sites: left and right frontal (F1 and F2), parietal (P1 and P2), and occipital (O1 and O2) regions referenced to Cz. EEG was recorded while each infant sat quietly on the mother’s lap for a period of 2 minutes. During the EEG recording a research assistant seated 5 feet away from the infant blew soap bubbles into the air. This procedure quieted the infant and allowed him or her to tolerate the EEG cap for the EEG recording.

Electrode impedances were measured and were accepted if they were below 6000 ohms. The electrical activity from each lead was amplified and digitized at a sampling rate of 512 Hz to prevent aliasing. The digitized EEG were later scored for eye movement and motor artifact. For the subjects in this study, 24% of each 2-minute EEG recording was rejected because of artifact.

After artifact scoring, the EEG was re-referenced via software, and the data were analyzed using an average reference configuration. This reference is considered optimal when coherence is being computed between spatially distinct electrodes (Fein, Raz, Brown, & Merrin, 1988; Lehmann, Ozaki, & Fal, 1986). The average reference data were analyzed with a discrete Fourier transform, using a Hanning window of 1-second width and 50% overlap. Prior to computation of the transform, the mean voltage was subtracted from each data point to eliminate any power results due to direct current offset. Power in single-hertz bands was computed for frequencies between 1 and 18 Hz. The power was expressed as mean microvolts squared. Only the average reference data were used in subsequent statistical analyses.

Subsequently, spectral power for individual leads was plotted for each session for each individual subject. Examination of these plots revealed two dominant frequencies in all leads at each age—one between 1 and 4 Hz, and the other between 6 and 9 Hz. Little power was evident beyond 12 Hz. Power values were positively skewed; therefore, subsequent analyses utilized a natural log transformation (ln) of the raw power values or relative power (i.e., 6-9 Hz/1-4 Hz).

Measures of coherence for the 6- to 9-Hz band were computed with an algorithm published by Salzberg, Burton, Burch, Fletcher, and Michaels (1986). Coherence for anterior-to-posterior electrode sites was computed separately for the left (F3-O1 and F1-P3) and right (F4-O2 and P4-P4) hemispheres. Following Thatcher et al. (1986), we interpreted increases in coherence between electrode sites as reflecting increased axonal connectivity between two topographically distinct brain regions.

EEG Development

To compare our EEG data with previous longitudinal findings, we plotted relative power for each region. Of particular interest was relative power in the frontal EEG leads. Figure 10.4 presents the mean ratio of 6-9 Hz to 1-4 Hz for the frontal leads at each age. As can be seen, there was a trend toward an increase in the ratio of 6-9 Hz to 1-4 Hz across the 7- to 12-month age period. Thus, the changes in relative power for fron-
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tal leads in our longitudinal data set followed the same pattern shown by other studies in posterior EEG leads (see Figures 10.1 through 10.3). However, it was not evident whether the increase in the ratio was attributable to an increase in 6-9 Hz or a decrease in 1-4 Hz, or both. To investigate this issue, all subsequent analyses utilized in power of the 6- to 9-Hz band. The higher-frequency band was selected for analysis because the other longitudinal studies reviewed here have confirmed that power in the lower frequencies becomes less dominant as an infant reaches 12 months of age.

The month-to-month correlations of the EEG in power (6-9 Hz) values for the 13 infants in the longitudinal sample are reported in Table 10.2. Because of technical problems with the electrophysiological record-

<p>| TABLE 10.2. Month-to-Month Correlations of EEG in Power (6-9 Hz) |
|---------------------|-----|-----|-----|-----|-----|-----|</p>
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<td>.37</td>
<td>-.17</td>
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Note: Lower-triangle correlations for each region represent left-hemisphere leads (e.g., F3, P3, O1), and upper-triangle correlations for each region represent right-hemisphere leads (e.g., F4, P4, O2).

* p ≤ .10, ** p ≤ .05, *** p ≤ .01.

10. Brain Development over the First Year of Life

ings at the onset of data collection, there were complete occipital EEG data on only 9 of the 13 subjects. As can be seen, EEG power values for each lead were intercorrelated, with the EEG data from adjacent months showing relative stability.

Figure 10.5 presents the mean EEG in power (6-9 Hz) for both frontal leads (F3 and F4), both parietal leads (P3 and P4), and both occipital leads (O1 and O2) at each age. There were changes (i.e., monthly increases and decreases) in in power (6-9 Hz) across age in the left- and right-hemisphere leads of each region.

These data indicate that there are changes in frequency from 7 to 12 months of age in frontal EEG recordings. Longitudinal research on the development of EEG during infancy has traditionally involved posterior scalp locations (e.g., Henry, 1944; Lindsley, 1939; Mizuno et al., 1970; Smith, 1938a, 1938b, 1938c, 1939, 1941), the assumption being that the underdevelopment of the frontal lobes during infancy would yield no important EEG data. However, Chugani and Phelps (1986) recently reported an increase in glucose metabolism in the frontal cortex of human infants between 8 and 12 months of age. Thus there is evidence of maturation of frontal cortex, as measured by glucose metabolism, during the second half of the first year of life.

Likewise, these scalp-recorded EEG data from the frontal area of the infants in this study might reflect maturation of the frontal brain region. Nunez (1981) has interpreted changes in EEG frequency as reflecting the excitability of neural networks or the degree to which the networks may be aroused. These data suggest that there is frontal EEG activity from 7 to 12 months of age.

Coherence Development

Figure 10.6 presents the coherence data for the infants in the study. There was greater coherence between the frontal and occipital sites across age than between the frontal and parietal sites. The frontoparietal connections displayed a U-shaped function in coherence across age, while the fronto-occipital connections remained stable.

Thatcher et al. (1986) have reported that the frontal region is strongly coupled to the posterior regions via long-distance axonal connections. Our data support this notion. Anterior-to-posterior connections may be critical for successful performance of complex behaviors during infancy. For example, the sequencing of goal-directed behavior during a means-end task such as the AB task may involve the alignment of processes regulated by posterior regions of the cortex (Pribram, 1973).
Frontal EEG and Cognitive Development

Recent work by Diamond (1985, 1988, 1990a, 1990b; Diamond, Zola-Morgan, & Squire, 1989) and Goldman-Rakic (1987a, 1987b; Goldman-Rakic, Isseroff, Schwartz, & Bugbee, 1983), as well as their collaborative work (Diamond & Goldman-Rakic, 1983, 1986, 1989), presents examples of research that illustrates the interface of neuroscience and human developmental studies. This research has been done with infant and adult lesioned and unlesioned monkeys and with full-term normal human infants. Diamond and Goldman-Rakic have demonstrated that maturation or integrity of the dorsolateral area of prefrontal cortex is essential for an infant’s increasing ability to tolerate delay and successfully search in the Piagetian AB task (Piaget, 1937/1954).

Diamond’s speculation is that the underlying abilities essential for solving the AB task involve inhibiting a motor response and holding a representation in memory over time, or recall memory (Diamond, 1985, 1988, 1990b). These are competencies attributed to frontal lobe functioning (Fuster, 1980; Pribram, 1973). Diamond (1990b) has argued that the integration of these two skills (recall memory and inhibitory control) is a primary competency of prefrontal cortex. Tasks that utilize only one of these skills can be successfully solved by monkeys with lesions of dorsolateral prefrontal cortex.

The purpose of the cognitive testing in our longitudinal study (Bell & Fox, 1992) was to examine the relations between regional changes in EEG and the development of frontal lobe skills that are manifested in
successful performance of the AB task with delay. The AB task requires
the infant to successfully retrieve an object twice at site A. The object is
then hidden in well B, with either no delay or a timed delay before the
infant is allowed to search for the object. Use of a delay during the task is
essential for observing the AB error in older infants.

Also included in the design was a task that examined response inhibi-
tion but not memory. This task involved presenting different moving
novel toys to the infants and observing latency to grasp each toy.
Rothbart (1988) and Schaffer and Parry (1969) found a developmental
change in performance of this task: Infants nearing 10 months of age in-
hibited their reach for novel objects. Because this task involved response
inhibition and not memory, we reasoned that performance should not be
associated with differences in frontal EEG activity.

We made two predictions in using this study design. First, we ex-
pected that there would be differences in frontal EEG development and
in coherence development from 7 to 12 months between infants who
displayed an increasing tolerance of delay during the AB task and infants
who displayed little tolerance of delay. Group differences in EEG devel-
opment would not be evident in the parietal or occipital regions. Second,
we expected that there would be no differences in frontal EEG develop-
ment or in coherence between those infants who displayed different pat-
terns of development in latency to grasp a novel moving toy.

AB Task
There was a clear change across age in the mean delay tolerated without
errors in reaching during the AB task. However, there was great variabil-
ity in individual infant performance. K-means cluster analysis was used
to group the infants into two AB task performance groups based on pat-
tern of delay tolerated from 7 to 12 months of age. As seen in Figure
10.7, one group (n = 6; 3 girls and 3 boys) tolerated a 13-second delay at
12 months of age, and the other group (n = 7; 4 girls and 3 boys) toler-
ated a 3-second delay at 12 months. The two groups differed on AB task
performance at 10, 11, and 12 months of age (all t’s > 3.05, p’s < .01).

All EEG analyses were made using ln power (6-9 Hz) as the de-
pendent measure. Group was the between-subjects factor, and hemisphere
and age were the within-subjects factors. Results of a repeated-measures
multivariate analysis at variance (MANOVA) on the frontal EEG power
data revealed a group × hemisphere × age interaction for the frontal EEG,
multivariate F (5, 7) = 4.89, p = .03. The long-delay group exhibited
changes in frontal EEG development not seen in the short-delay group.
Examination of the means showed that the long-delay group (see Figure
10.8, top) displayed a decrease in right frontal EEG power between 7 and
8 months of age, and displayed the greatest monthly increase in frontal

EEG power between 9 and 10 months of age. This trend was apparent in
both hemispheres. The short-delay group only showed a change in right
frontal power between 10 and 11 months of age (see Figure 10.8, bot-
tom).

There were no group effects or any interactions involving group in
the parietal EEG data. For the occipital EEG data, there was a group ×
 hemisphere interaction, F (1, 7) = 8.92, p = .02. The long-delay group
had greater power in the left occipital lead relative to the right occipital
lead across age.

Coherence analyses revealed a group × age interaction for the left-
 hemisphere coherence values, multivariate F (5, 3) = 9.76, p = .05. Follow-
up analyses revealed that when we averaged across frontoparietal and
fronto-occipital data, the long-delay group showed an increase in coher-
ence from 9 to 12 months of age after an initial decrease in coherence be-
 tween 8 and 9 months. There were no changes in coherence for the
short-delay group. Likewise, there were no group effects or interactions
involving group for the right-hemisphere coherence data.

Novel Toy Task
Infants did not display a clear developmental trend in inhibition of reach
toward a moving novel toy, as demonstrated by Rothbart (1988). Rather,
infants tended to display inhibition across age. Because of the wide vari-
ation in latency, K-means cluster analysis was used to group infants into
two performance groups based on pattern of latency to grasp. One group
All EEG analyses utilized ln power (6-9 Hz) as the dependent measure. Group was the between-subjects factor, and hemisphere and age were the within-subjects factors. Results of a repeated-measures MANOVA revealed no main effects or interactions for frontal, parietal, or occipital EEG power or for coherence (all $F$'s $\leq 1.85$, $p$'s $\leq .33$).

Our data indicate the importance of changes in EEG activation in the frontal region, and also of the connections between frontal and parietal regions and frontal and occipital regions for the AB task with delay. It is particularly intriguing that the two AB task performance groups first showed differences in the length of delay tolerated at the age (10 months) when the long-delay group displayed the largest monthly increase in power in the frontal leads. This was the same age at which the long-delay group showed an increase in anterior-to-posterior coherence.

**Frontal EEG Asymmetry and Affect**

In our longitudinal study, we also investigated relations between frontal maturation and a specific affective behavior, crying at maternal separation. Research from our laboratory (Fox & Davidson, 1987, 1988; Davidson & Fox, 1982, 1989) has indicated that the frontal region is critical in the experience and expression of emotion, as well as in emotion regulation. The notion of “experience” here does not refer to perceptual features of emotion; the perception of affective information has been linked to posterior right-hemisphere regions (Bryden & Ley, 1983). Rather, the frontal region is most likely associated with three major features of emotion: the motor components, the organization of the multisystem response pattern that constitutes emotion, and the ability to inhibit or regulate emotion.

For the past several years we have been investigating the relations between the expression of emotion and cerebral asymmetry. The measure of asymmetry that we have used is EEG activation in the left and right hemispheres. We have computed a laterality difference score (ln right power - ln left power, 6-9 Hz) for the pairs of EEG leads within a region. A positive score indicates left-hemisphere activation. In a number of studies (e.g., Fox, Bell, & Jones, 1992), we have found that by the second half of the first year of life there is modest stability in the asymmetry score between individuals. This individual difference is illustrated in the month-to-month correlations for asymmetry scores of both the frontal and parietal regions (Table 10.3). As can be seen, the EEG asymmetry values for the frontal region show a stronger pattern of intercorrelation than the asymmetry values for the parietal region.

Our studies have demonstrated that there are changes in the EEG that are associated with emotion expression. For example, 10-month-old infants approached by a stranger were more likely to exhibit greater rela-
TABLE 10.3. Month-to-Month Correlations of EEG Asymmetry Scores

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**Frontal scores (n = 13)**

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**Parietal scores (n = 13)**

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*p ≤ .10. **p ≤ .05. ***p ≤ .01.

tive right frontal activation, while infants approached by their mothers exhibited the opposite pattern of frontal EEG activation (Fox & Davidson, 1987). Similarly, infants displaying facial expressions of joy exhibited greater relative left frontal activation, while those displaying sadness or distress exhibited greater relative right frontal activation. These changes in EEG during the experience of certain emotions seem to be superimposed upon a stable level of EEG arousal or activity that characterizes an infant’s affective general predisposition. We described this relation between EEG asymmetry and predisposition to respond in a study of 10-month-old infants. EEG was recorded prior to an emotion-eliciting event, and the pattern of EEG asymmetry predicted infant response to the event (Davidson & Fox, 1989). Specifically, infants with greater relative right frontal EEG activation were more likely to cry at maternal separation than infants with left frontal activation. These differences in resting asymmetry may reflect a child’s individual temperamental characteristics (a threshold to respond with either positive or negative affect), or they may represent differences in the maturation of the left and right hemispheres (Davidson & Fox, 1989).

In order to examine these two alternative hypotheses (i.e., individual differences vs. maturation), we observed infants in the longitudinal study described above in an affect-eliciting situation (Fox et al., 1992). After the cognitive testing in our longitudinal study, each mother waved to her infant, said "Bye-bye," and left the room, shutting the door. Latency to cry was coded from the time the door closed and ranged from 0 seconds (cried before the mother closed the door) to 30 seconds (never cried). We predicted differences in frontal asymmetry between those infants who cried at separation and those who did not. We also predicted that this asymmetry difference would not be evident in other regions.

K-means cluster analysis was used to classify the infants into two groups based on the latency-to-cry data. One group of infants (n = 8; 5 girls and 3 boys) displayed a longer latency to cry across age (i.e., the latency decreased from 26 seconds at 7 months to 20 seconds at 12 months). The other group (n = 5; 2 girls and 3 boys) displayed a shorter latency across age, in that latency decreased at an even faster rate (from 30 seconds at 7 months to 6 seconds at 12 months; see Figure 10.9). All EEG analyses utilized the laterality difference score (In right power - In left power; 6-9 Hz) as the dependent measure. Group was the between-subjects factor, and age the within-subjects factor. Results of a repeated-measures MANOVA on the frontal laterality difference scores revealed a main effect for group, F(1, 11) = 7.58, p = .02. As can be seen in Figure 10.10, the group with the longer latency to cry displayed left frontal activation across age, while the group with the shorter latency to cry displayed right frontal activation.
cry across age displayed right frontal activation. There were no group differences in asymmetry for either the parietal or occipital EEG data.

The two hypotheses we proposed to predict crying at maternal separation, maturation versus individual differences, may not be mutually exclusive. Eventually most infants learn to inhibit the distress caused by a mildly stressful situation such as maternal separation. The differences in frontal activation across time found between the longer-latency-to-cry and the shorter-latency-to-cry groups of infants may reflect a lag in left-hemisphere maturation for the shorter-latency infants. These differences may underlie an inability to inhibit right-hemisphere negative affect (e.g., crying at maternal separation). Left-hemisphere differences between these two groups of infants should become less pronounced. Most children display a decrease in distress at separation toward the end of the second year and into the third year of life. This decrease in distress co-occurs with the onset of expressive language, a left-hemisphere function. Thus, the coping strategy of internal speech may aid in the development of the ability to self-monitor responses associated with distress (Kopp, 1989). However, there may be a subgroup of infants who will continue to display distinct patterns of distress to mild stressors. These patterns of behavior may be related to underlying patterns of cerebral activation (Davidson & Fox, 1989).


There are many issues concerning the interpretation of EEG recordings. For example, it seems critical to understand the functional significance of increases in dominant frequency over the first year of life. Use of the EEG itself can tell us little about source generation of the electrical potentials. Indeed, a number of major questions regarding generator localization should be noted as caveats to interpretation of our EEG findings. First, the assumption that scalp electrodes necessarily reflect brain activity from the cortical region immediately underlying the electrode is problematic. Event-related potential (ERP) evidence indicates that under certain conditions, the ERP from the hemisphere opposite to the one that is unambiguously generating the potential displays larger-amplitude responses. This is a well-known phenomenon and occurs as a function of a particular orientation of cortical dipoles whose fields are then volume-conducted to a region distant from the one actually generating the potential. The claims we make about localization must be restricted to scalp locations rather than cortical locations. Two factors, however, increase our confidence in the possibility that the scalp potentials we are recording from the frontal region are indeed generated in this location.

The first factor is that data from our work on EEG and cognitive behavior and on EEG asymmetry and affect in infants are consistent with data derived from several other domains, using methods quite dissimilar from our own. These methods include effects of localized lesions in humans on emotion expression (Gainotti, 1972) or in animals (Diamond & Goldman-Rakic, 1989).

The second factor that increases our confidence in the localization of the EEG is the difference between studies of the type we have described in this chapter and those indicative of the effects of volume-conducted nonstandard dipole orientations. The ERP data to which we refer are based upon highly discrete stimulus and/or response conditions (e.g., foot movements). These events are likely to stimulate a relatively small region of cortex, compared with the measures that we collect of EEG activity during different states of arousal. When small regions of cortex are stimulated, there is an increased probability that the stimulated region will fall in a fissure whose geometry is such that the maximal amplitude will be detected over the hemisphere opposite to the one that generated the potential (Blumhardt, Barrett, Halliday, & Kriss, 1978). Given the more global recording conditions used in our research, it is unlikely that such discrete regions of cortex were stimulated, and thus the problems of dipole orientation were less likely to be present.

A second issue in our EEG research concerns the degree to which the EEG measures reflect cortical versus subcortical brain activity. Some
evidence from the ERP literature suggests that potentials recorded from the scalp may be generated at subcortical foci (Desmedt & Cheron, 1982; Jerger, 1982). At present, we cannot specify with any confidence the percentage of variance in the scalp measures that reflect cortical versus subcortical activity. It is certainly likely that infant EEG in particular contains some subcortical contributions. Until measures that will allow us to disentangle these different sources of activity are more readily available, we cannot differentiate these two sources of activation. However, evidence from converging sources that utilize different measures of regional brain activity may be informative. There is research that has directly compared (in adults) EEG to regional cerebral blood flow at the same points in time, and has obtained high correlations (Ingvar, Sjolund, & Ardo, 1976). There is also research on regional glucose metabolism in infants (Chugani & Phelps, 1986), which indicates increases in frontal metabolism over the first year of life; these data parallel the data we have presented on increases in EEG frequency in this region. Thus, we feel confident that our measurement of EEG will reveal important new information on the developing infant brain.

SUMMARY

The electrophysiological data we have presented here suggest that the measurement of EEG in infancy may provide meaningful information regarding the development of dynamic organization of the brain. Changes in EEG frequency and coherence are associated with major behavioral events during the second half of the first year of life. The pattern of EEG activation between the two hemispheres seems to be related to expressions of emotion and individual differences in an infant’s predisposition to express different affects.

ACKNOWLEDGMENT

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IV. Brain Development over the First Year of Life


III. Developing Brain-Behavior Relations


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