FRONTAL FUNCTION IN COGNITIVE AND EMOTIONAL BEHAVIORS DURING INFANCY: EFFECTS OF MATURATION AND EXPERIENCE

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ABSTRACT. Frontal lobe activity in human infants during the second half of the first year of life was examined using the ongoing electroencephalogram. Changes in frontal EEG activity were linked to both cognitive and emotional changes that occur during that developmental period. In one series of studies we found that the pattern of asymmetrical activation in the frontal EEG was related to an infant's temperamental disposition. Infants exhibiting greater relative right frontal activation were more likely to cry to maternal separation and to exhibit anxiety and fear in the laboratory. In a second series of studies we found that changes in performance on certain cognitive tasks was a function of frontal EEG maturation. These maturational changes in frontal activity and cognitive performance were a function of infant locomotor experience.

1. Introduction

There has been a dramatic increase in interest over the past few years in describing the neural basis of psychological behaviors. Most of this research effort has been in the area of behavioral neuroscience and has focused on the cognitive neural processes involved in learning, memory and perception. Less work has been forthcoming on the neural processes underlying emotion or emotional processes. Behaviors reflecting emotion have traditionally been viewed through arousal theory (Duffy, 1941) or as an end product of cognitive processes (Schachter & Singer, 1962). For example, Schachter & Singer (1962) argued that differences in emotion were the end result of cognitive processes or cognitive evaluation of contextual change and physiological arousal.

Due in large part to the work of Ekman (1972, 1984) and Izard (1971, 1977) the study of emotion has reemerged within the scientific psychological literature and has assumed an important part in psychological research. Two factors were involved in this reemergence. First, Ekman and Izard provided a theoretical frame of emotion, tied to the tradition of Darwin, in which emotions assumed important social communicative functions between individuals. Emotions also were seen as reflections of individual psychological state. Second, Ekman (Ekman & Friesen, 1978) and Izard (1979) provided the research community with the tools or methods for measuring emotion so that it could be coded objectively. The appeal of both theory and method for the study of emotion has been strong and has led to a good deal of research. In some instances, however, the work suffered
from the same narrow frame as that of past cognitive research in that it excluded cognitive interpretations of emotion behaviors.

More recently, there has been a rapprochement between those advocating strict emotion or cognitive based approaches. Research in emotion seems to be shifting away from a discrete emotions perspective to a more functionalist approach in which context, mood state, and temperament/personality are seen as key concepts in understanding emotional processes. There is also greater interest among cognitive scientists in integrating knowledge about attention, memory, and inhibitory capabilities with emotional state in order to understand these behaviors (Mandler, 1984).

2. Conceptual Interpretation of EEG Power and Coherence

Our own research has attempted to examine the neural correlates of both affective and cognitive behaviors during the first year of life. Our approach to examining relations among cognitive, affective, and central nervous system development has been to record the ongoing electroencephalogram (EEG) in alert infants during specific conditions designed to elicit different affects or during different types of attention tasks. In addition to quantifying the EEG by traditional means (power in different frequency bands), we have also adopted an approach first articulated by Paul Nunez and later adapted by Robert Thatcher (Nunez, 1981; Thatcher, 1991). They have argued that power in the EEG signal can be interpreted via wave theory (Nunez, 1981; Thatcher, Krause & Hrybyk, 1986). They have presented evidence that the coherence of EEG signals from different spatially distinct sites may reflect functional cortico-cortical connections in the cortex.

Coherence, conceptually, is the degree to which two periodic signals are correlated. Two signals may vary in phase over particular lag consistently, in which case the coherence of the two signals would approach unity. Likewise, the two signals may be in and out of phase with each other at a random lag, in which case the coherence would approach zero. Nunez and Thatcher have argued that the degree to which two spatially distinct EEG signals are in or out of phase reflects the degree of axonal connectivity between the two sites. They base this argument on both animal neuroanatomical data and on specific modelling of the EEG signals within the medium of the cortex and skull. Thatcher has gone on to posit that changes in coherence over developmental time reflect the degree to which different regions of cortex either link up, are linked in concert, or decouple from each other. Increases in coherence over time reflect the emergence of cortico-cortical circuits while decreases reflect regional differentiation (Thatcher, Walker & Giudice, 1987). Conceptually, one might use this model to examine the synchrony of changes in cognitive milestones with changes in linkages among different brain regions.

Power in the EEG spectrum at a particular frequency band has also been utilized as a measure of activation of cortical neurons (Davidson, 1988). The pattern of brain wave activity, first discovered by Berger (1929), involves an electrical pattern which may be described in terms of frequency and amplitude. Berger originally observed that the amplitude of what he called the alpha wave (the dominant frequency for awake adults in the posterior leads) changed as a function of the subject's level of alertness. When subjects closed their eyes the amplitude of alpha increased. With eyes open, alpha amplitude decreased.

Subsequently, researchers used this relation between amplitude and state to argue that decreases in amplitude (or spectral power) reflected increased cortical activation while increases in power (analogous to the adult with eyes closed) reflected decreased cortical activation (Lindsley & Wicke, 1974). Thus, one might measure alpha activity from the left and right hemispheres and gain a measure of the relative activation of one hemisphere to another. In our work, we have recorded power from the frontal, parietal and occipital regions of human infants and have computed power at each site. We have also examined the patterns of power between left and right hemisphere homologous leads. This approach is one that has been used with some success in examining hemispheric asymmetry in adults.

3. EEG Asymmetry and Affect

3.1 SUMMARY OF STUDIES

In a series of studies we have found that individual differences in the degree to which either the left or right frontal lobes are activated are strongly associated with the infant's predisposition to respond with negative or positive affect to mild stress (Davidson & Fox, 1989; Fox, Bell & Jones, 1992). The stressor we have used in our laboratory most frequently has been brief separation from mother. Across studies the data reveal that infants who exhibit greater relative right frontal activation are more likely to cry. Infants who exhibit greater relative left frontal activation are less likely to cry. Differences in frontal activation are recorded prior to any separation episode and are generally not associated with differential affect during the recording. Rather, we believe that these differences in frontal activation reflect an important moderator variable. We have suggested (Davidson & Fox, 1989; Fox, 1991; Fox & Davidson, 1991) that there are temperamental differences in infant's emotional response to stress.

For example, Davidson & Fox (1989) found greater relative right frontal asymmetry among a group of 10-month old infants who subsequently cried to maternal separation. And, Fox, Bell & Jones (1992) found stable patterns of frontal asymmetry among infants who consistently cried to separation across the second half of the first year of life. Calkins, Fox and Marshall (1992) reported that the pattern of frontal asymmetry is associated with four-month infant temperament and predictive of anxious, fearful, inhibited behavior in early childhood. Specifically, infants selected for high motor activity and irritability at four months displayed greater relative right frontal activation at nine months of age. These same infants were observed to be more fearful and anxious at 18 and 24 months of age than infants who exhibited either greater relative left frontal activation or whose pattern of EEG asymmetry was not right frontal and stable across the first year of life. Of particular interest across these studies is the fact that differences between infants who expressed negative affect versus those who did not only emerged specifcally to the right frontal region. The irritable infants displayed less right frontal power or greater right frontal activation. Importantly, across these studies, the locus of the effect was found in the frontal scalp leads.
3.2 INTERPRETATIONS OF DIFFERENCES IN FRONTAL ASYMMETRY

What is it about the frontal lobes that involves them in the predisposition toward positive or negative affect? The frontal lobes have direct connections with limbic areas known to be involved in the conditioning and expression of certain emotions - specifically fear (Fuster, 1980). In particular, there are well-mapped out connections between the frontal region and certain nuclei in the amygdala involved in fear conditioning. Our EEG findings may reflect the differential excitability of these amygdaloid structures. There may be, in addition, important neurochemical asymmetries that are associated with differences in emotional response. Work by Glick and colleagues (1974) has suggested that there are different distributions of serotonergic and dopaminergic receptors in the rat neocortex and that these differences in the neurotransmitters and neurochemistry of the two hemispheres and their associated subcortical regions underlie the electrophysiological asymmetries that we have found.

A second possibility is that these asymmetries represent functional differences in the two hemispheres for the response to threat. The right hemisphere has been implicated in processes associated with immediate attention and orienting (Tucker & Williamson, 1984). The increased activity in the right hemisphere may reflect arousal of and sensitivity to novelty and stress. Right hemispheric specialization for behaviors associated with withdrawal may be actively involved in the expression of responses to this hyper arousal/orienting behavior. Conversely, the left hemisphere has been implicated as involved in sequential fine motor behavior, more attuned to exploratory and approach patterns. Thus, situations that elicit approach rather than withdrawal might activate programs in the left hemisphere as opposed to right hemisphere.

A third possibility is that the role of the frontal lobes have as a center for integrating information from diverse brain regions (Fuster, 1980). Emotion and emotion regulation change over the years of life as motor and cognitive behaviors become finely integrated to produce new responses to the environment. The infant's ability to regulate distress changes dramatically over the first two years of life (Kopp, 1989). In particular, infants depend upon external aids in their attempt to regulate distress during the first year of life (hand or finger sucking) or gaze aversion. During the second year there is the beginning of a change to more internal coping strategies in the regulation of negative affect. These changes are a result, in part, of greater coordination and integration of motor and cognitive programs which allow the infant to deal successfully with novelty.

Two neural changes may be involved. One is the change associated with developing dominance in and maturation of the left hemisphere. Left hemisphere competencies in the verbal, symbolic, fine motor, and sequential realms may assist infants in coping with stress. For example, we have found that individual differences in response to separation are associated with increasing language facility. Toddlers with greater expressive language are less likely to exhibit distress. The infant's growing ability to utilize verbal and symbolic means to deal with stress may enable him or her to cope successfully in potentially negative situations. A second change involves developing connections between the left and right hemispheres. There is reason to believe that regulation of emotion involves not only activation of either the left or right hemisphere but the dynamic balance between the two sides of the brain. This balance may be achieved more efficiently when the necessary fibers are in place and myelinated to allow proper interhemispheric communication. We have suggested that developmental changes in interhemispheric communication may be an important factor in the infant’s increasing ability to control its negative (as well positive) affect (Fox & Davidson, 1984). Thus, both the specific development of left hemisphere competencies and the overall general maturation of the frontal region may facilitate infant modulation of negative affect.

3.3 IMPLICATIONS FOR COGNITIVE FUNCTIONING

These neuro-developmental changes have implications for cognitive performance as well. Changes in frontal functioning during the second year of life may be involved in the toddler’s increasing ability to inhibit a prepotent motor response and in the ability to break attentional set. These speculations are based in part on studies of the neural basis of learning in animals. Work by Goldman-Rakic and colleagues (e.g., Goldman-Rakic, 1987a; 1987b; Goldman-Rakic, Isseroff, Schwartz, & Bugbee, 1983) has demonstrated that nonhuman primates can not perform behaviors necessary to solve tasks such as the delayed response with lesions of dorsolateral frontal cortex. In addition, infant monkeys displayed a developmental onset in their performance which, Goldman-Rakic argued, reflected maturation of this area over the first months of life (e.g., Goldman-Rakic, 1987a).

In collaboration with Goldman-Rakic, Diamond studied the performance of infant and adult nonhuman primates on a variant of the delayed response task, the A not B task, and found identical results to those reported by Goldman-Rakic concerning delayed response (Diamond & Goldman-Rakic, 1983, 1986, 1989). Monkeys with lesions of dorsolateral frontal cortex could not solve the A not B task with delay. Interestingly, human infants begin to solve this task around 9 months of age, a period coincident with changes in regulation of negative affect. At least three components or competencies are important for successful performance of the A not B task. The first is a memory component (Diamond, 1985, 1988, 1990b). Once the infant can successfully find an object at hiding place A and the object is hidden at B, a delay of 2 to 10 seconds is instituted. Infant performance after the delay is examined. A second component is the ability to inhibit a reinforced motor response (Diamond, 1990a). Infants are given two to three reinforced trials finding the object successfully at A prior to having the object's location switched to B. The infant must break the set of reaching to A in order to successfully search at B. A third component is the ability to retain that memory in the face of distraction (Bell & Fox, 1992). During the delay the experimenter breaks the infant's gaze from the hiding locations. The infant is temporarily distracted and the memory must withstand this initial break. In sum, it is the infant's abilities to represent the object in its absence, to remember its location, to inhibit a prior response, and to ignore a distraction that allow for successful search.
4. EEG Activity and Cognitive Development

4.1 LONGITUDINAL STUDY

The connection between changes in performance on this frontal task and changes in emotional response may be more than coincidental. The neural changes occurring in frontal cortex may underlie changes in both developmental realms. In an attempt to investigate this issue we performed two studies in which frontal EEG was recorded and performance on the A not B task was assessed. In the first (Bell & Fox, 1992), 13 healthy infants were seen monthly beginning at seven months of age through their year birthday. At each visit, EEG was recorded from frontal, parietal and occipital locations. Also at each visit the child’s performance on a task thought to involve the integrity of dorsolateral frontal cortex was observed. The task was a variant of Piaget’s A not B task (Piaget, 1954).

We found that there was an increase in successful performance on the A not B task over the second half of the first year of life, with infants tolerating longer delays as they got older. However, there was quite a bit of variability. We examined the EEG data taking into account this wide variation in performance. Infants were divided into two groups - those who by 12 months could tolerate long delays versus those who by 12 months could only solve the A not B problem with short delays. We found clear differences in the development and change in EEG power specific to the frontal leads between the two groups of infants. Those infants able to tolerate long delays showed a significant increase and change in power between 9 to 10 months (see Figure 1) while those who can tolerate only brief delays showed relatively little change over this same age period (see Figure 2). Interestingly, the period between nine to ten months is also the time with the biggest jump in performance among the long delay group.

![Figure 1. Frontal EEG activity from 7 to 12 months of age for the group tolerating long delays on the A not B task at 12 months of age. From Bell & Fox, 1992.](image)

Examination of the EEG coherence for both long and short distance connections found significant changes between these two groups in frontal-parietal but not frontal-occipital coherence. Infants tolerating long delays displayed a significant decline in frontal-parietal coherence between 7 and 10 months of age, suggesting increased regional differentiation in frontal-parietal connections among this group.

We confirmed these data with a cross-sectional group of infants, seen at the same ages as the longitudinal group. The data from the cross-sectional group essentially replicated the findings for the longitudinal study.

![Figure 2. Frontal EEG activity from 7 to 12 months of age for the group tolerating short delays on the A not B task at 12 months of age. From Bell & Fox, 1992.](image)

4.2 EFFECTS OF EXPERIENCE ON PERFORMANCE AND BRAIN DEVELOPMENT

In a next study (Bell, 1992), we attempted to examine the effects of experience on behavioral performance and brain maturation. From the psychological literature there was reason to believe that experience with self-produced locomotion, crawling on hands and knees, would affect performance on object permanence tasks. Kermoian and Campos (1988), for example, had found that infants with longterm crawling experience were more successful on the A not B task as compared to infants with no locomotor experience. From a neurophysiological perspective, Greenough (Greenough & Black, 1992) has argued that there may be experience expectant changes in synaptic connections that should occur during development. For experience expected changes, Greenough had predicted the over production of connections at the time of the experience with pruning or decreases in that experience afterwards.
The sample in the second study consisted of 80 infants all of whom were eight months old. The infants were selected based upon their history of self-produced locomotion. Four groups of infants were involved: eight-month-old infants with no locomotor experience; those with 1-4 weeks of hands and knees crawling experience (mean of 2.4 weeks); those with 5-8 weeks experience (mean of 6.5 weeks); and those with 9 or more weeks experience (mean of 10.5 weeks). Infant EEG was assessed as we have in the past from frontal, parietal, and occipital regions. In addition, each infant was assessed on the A not B task and on two spatial tasks.

The behavioral data for this study suggested that onset of locomotor experience does in fact influence performance on the A not B task. Infants with no locomotor experience performed most poorly of all groups. Infants in the other three groups were similar in their performance, although there was a trend for longer experience at crawling to be associated with tolerating longer delay on the A not B task.

There were clear changes in brain activity and connectivity as a function of experience with self-produced locomotion. First, there was an increase in the amount of power, the degree of mass neuronal excitability, as a function of experience. This increase was largest just after locomotion began (i.e., between the group with no locomotor experience and the one with 1-4 weeks of experience). Second, there seemed to be asymmetrical changes in power distribution between the groups with infants who failed A not B (i.e., the nonlocomotor group) displaying greater relative right frontal activation as compared to all three locomotor groups, where dominant activity was in the left hemisphere.

Finally, there were significant changes in cortico-cortical connections, measured via coherence, as a function of crawling experience, as would be predicted from Greenough's model of synaptic overproduction and pruning. The pattern of over-production and pruning was different for different sets of connections based upon the length of the connection and whether it consisted of anterior or posterior sites. Frontal-parietal connections (see Figure 3, top) showed the steepest increase with onset of locomotion and the sharpest decline, suggesting the immediate effects of linkage between these two brain regions with the onset of locomotion and their subsequent decoupling with experience. Parietal-occipital connections (see Figure 3, middle) also showed steep increases with locomotor onset, but a more gradual decline with length of experience. Finally, the long distance frontal-Occipital connections (see Figure 3, bottom) showed the most gradual increase and persistence with experience, and gradual decline. Figure 3 also shows the differences between connections within the left and right hemispheres. These changes in connectivity/coherence are most obvious within the right hemisphere.

These findings suggest that onset of locomotion produces profound changes in regional neuronal excitation and in cortical connectivity. It appears as if there is an overproduction of cortico-cortical connections with the immediate onset of this experience and these connections either decrease rapidly or slowly depending on the type of connection. In general, there is a decrease or pruning of these connections as the behavior becomes automatized and solidified. Here we have a strong demonstration of Greenough's experience expectant changes in connectivity during the first year of life.

Figure 3. Coherence for frontal-parietal connections (top), parietal-occipital connections (middle), and frontal-occipital connections (bottom) as a function of hands and knees crawling experience.
5. Summary

These studies demonstrate the role of the frontal lobes in the experience/expression of emotional behaviors and argue perhaps that the distinctions that have been arbitrarily set between affect and cognition even in infancy are unjustified. The functions of the frontal lobes in the ability to hold a memory representation in the face of distraction and perhaps also to inhibit a prepotent motor response may all be involved in the active regulation and expression of both positive and negative affects. The data indicate that there is active sculpting and changing of cortex occurring during the second half of the first year. These changes involve long distance connections which may, in fact, model coupled linear oscillators. They also implicate decoupling processes both within and between hemispheres.

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References


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