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Anterior Cerebral Asymmetry and the Nature of Emotion

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This article presents an overview of the author's recent electrophysiological studies of anterior cerebral asymmetries related to emotion and affective style. A theoretical account is provided of the role of the two hemispheres in emotional processing. This account assigns a major role in approach- and withdrawal-related behavior to the left and right frontal and anterior temporal regions of two hemispheres, respectively. Individual differences in approach- and withdrawal-related emotional reactivity and temperament are associated with stable differences in baseline measures of activation asymmetry in these anterior regions. Phasic state changes in emotion result in shifts in anterior activation asymmetry which are superimposed upon these stable baseline differences. Future directions for research in this area are discussed. © 1992 Academic Press, Inc.

I. INTRODUCTION

Emotion is a class of behavior which has invited the consideration of its underlying biological substrates since the time it was first studied. Probably more than any other class of behavior, emotion often involves frank biological changes which are frequently perceptible to the individual in whom the emotion arises and occasionally even to an observer. For much of its relatively short history in scientific psychology, the focus of research on the biological substrates of emotion was mostly on autonomic changes which accompany emotion in humans or subcortical limbic system circuits which mediate specific emotional behaviors in animals. Both of these research endeavors have yielded important insights about the nature of emotion. However, it is clear that in more complex animals, and especially in humans, the cerebral cortex plays an important role in aspects of emotional behavior and experience. In particular, anterior cortical regions which have extensive anatomical reciprocity both with subcortical

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centers and with posterior cortical circuits are critically implicated in emotional behavior. These anterior cortical zones are the brain regions which have shown more dramatic growth in relative size over the course of phylogeny than the other brain regions (see Luria, 1973; Jerison, 1973, for reviews).

The focus of this article is on asymmetries in anterior cortical function, which have been implicated in different forms of emotional behavior. Among the earliest suggestions regarding the importance of hemispheric asymmetries for emotional behavior were observations on patients with unilateral cortical lesions (e.g., Jackson, 1878). The majority of these reports indicated that damage to the left hemisphere was more likely to lead to what has been termed a catastrophic–depressive reaction than comparable damage to the right hemisphere (e.g., Goldstein, 1939). More recent studies have confirmed this basic observation (e.g., Gainotti, 1972; Sackeim, Greenberg, Weiman, Gur, Hungerbuhler, & Geschwind, 1982). Of particular importance to the research reviewed in this article are studies by Robinson and his colleagues (e.g., Robinson, Kubos, Starr, Rao, & Price, 1984). They have reported that it is damage specifically to the left frontal lobe which results in depressive symptomatology. They found that among left-brain-damaged patients, the closer the lesion was to the frontal pole, the more severe the depressive symptomatology. Patients who developed mania subsequent to brain injury were much more likely to have sustained damage to the right hemisphere, sparing the left. These and other observations have provided the basis for our studies of anterior activation asymmetries associated with emotion and affective style. In the next part of this article, I sketch the major elements of the theoretical model which motivates the research that is presented. A description of the methods which are common to our studies and the unique methodological requirements of this research follows. Research on anterior asymmetries associated with the phasic arousal of emotion is presented, followed by a summary of our findings on relations between individual differences in baseline asymmetry and affective reactivity. The paper ends with a discussion of some unanswered questions which are posed by this work.

II. THE ROLE OF THE CEREBRAL HEMISPHERES IN EMOTIONAL PROCESSING: A THEORETICAL ACCOUNT

That a fundamental asymmetry in the control of functions related to emotion is present is not surprising in light of speculations concerning the evolutionary advantages of cerebral asymmetry (e.g., Levy, 1972). In searching for the basis of the asymmetry underlying emotion, it is instructive to recall that investigators in comparative psychology (Schnierla, 1959), behavioral neuroscience (Stellar & Stellar, 1985), and child development (Kagan, Reznik, & Snidman, 1988) all agree that approach and withdrawal are fundamental motivational dimensions which may be found at any level of phylogeny where behavior itself is present.

In several previous articles (e.g., Davidson, 1984, 1987, 1988; Davidson, Ekman, Saron, Senulis, & Friesen, 1990b; Davidson & Tomarken, 1989), I have suggested that the anterior regions of the left and right hemispheres are specialized for approach and withdrawal processes, respectively. The basis upon which this suggestion is made are several. First, the left frontal region has been described as an important center for intention, self-regulation, and planning (Luria, 1973). The functions which have been ascribed to this area are those which have historically have been assigned to the *will,* a hypothetical structure of central import to approach-related behavior. Second, over the course of ontogeny, the infant and toddler will approach and reach out to objects of interest using its right hand much more often than its left (e.g., Young, Segalowitz, Misek, Alp, & Boulet, 1983). It would be of interest to examine whether episodes of right-handed reaching and grasping are in fact associated with expressive signs of positive affect (e.g., smiling). Right-handed reaching and positive affect are taken to be the collective manifestation of an approach system centered in the left frontal region. Third, as I have noted above, damage to the left frontal region results in behavior and experience which might best be characterized as a deficit in approach. Patients with damage to this brain region are apathetic, experience loss of interest and pleasure in objects and people, and have difficulty initiating voluntary action (i.e., psychomotor retardation). Thus, hypoactivation in this region should be associated with a lowered threshold for the experience of sadness and depression.

The claim that the right anterior region is specialized for withdrawal is based upon a less extensive, but growing corpus of evidence. The most compelling evidence is the data on normal humans involving electrophysiological measures of regional hemispheric activation. These findings, which are reviewed in detail in later sections, indicate that during the experimental arousal of withdrawal-related emotional states (e.g., fear and disgust), the right frontal and anterior temporal regions are selectively activated. In addition, subjects with baseline tonic activation in these regions show a propensity to respond with accentuated withdrawal-related negative affect to appropriate emotion elicitors. Such individuals also report greater dispositional negative affect.

Recently, Morris and colleagues (Morris, Bradley, Bowers, Lang, & Heilman, 1991) have studied a patient with a right temporal lobectomy using psychophysiological measures of affective reactivity in response to standardized laboratory elicitors of positive and negative emotion. The resection was performed to remove an arteriovenous malformation in the right temporal lobe and included the anterior portion of the temporal lobe and the whole right amygdala. The stimuli presented to the patient were slides which differed in valence, but which were matched on overall salience. They recorded the skin conductance response to these slide stimuli. They found that the skin conductance response to the positive stimuli was equivalent in magnitude to that observed in normals. However, skin conductance responses to the negative slides were markedly attenuated. Using measures of regional cerebral blood flow derived from positron emission tomography (PET), Reiman and his colleagues (Reiman, Raichle, Butler, Hercovitch, & Robins, 1984) have reported accentuated activation during a resting baseline in a right hemisphere subcortical site which projects to the amygdala in panic-prone patients. Taken together, these observations suggest a specialization for certain anterior cortical and subcortical right hemisphere regions in the mediation of withdrawal-related negative affect. Precisely what the differential role of the anterior temporal and frontal regions is in the mediation of the negative affective responding is not clear from the available evidence.

Some of the evidence referred to above is derived from the study of patients with unilateral lesions. Other findings come from the assessment of regional brain activation in neurologically intact subjects. In light of the assumption that lesions result in selective deficits in activation in the lesioned area (e.g., Burke, Younkin, Kushner, Gordon, Pistone, Shapiro, & Reivich, 1982), the findings described above support the following hypotheses regarding the anterior hemispheric substrates of emotion and emotion-related processes. Activation in the left anterior region is associated with approach-related emotions; deficient activation in this region is associated with emotion-related phenomena that might be best described as reflecting approach-related deficits such as sadness and depression; and activation in the right anterior region is associated with withdrawal-related emotions such as fear and disgust and withdrawal-related psychopathology such as anxiety.

Two additional conceptual issues deserve emphasis. The first concerns the subcomponents of emotion which I address in this paper and in the research which is described. The focus here is on the experience and expression of emotion. The hemispheric substrates of perceiving emotional information are likely to be different from those involved in actual emotional experience. Similarly, the underlying neural controls for the communication of information *about* emotion are likely to be different from those implicated in the experience and expression of *actual* emotion. In this regard it is instructive to note that some investigators have argued for a more general role for the right hemisphere in all emotion (e.g., Borad, Koff, Perlman, & Nicholas, 1986; Etcoff, 1986). However, it is imperative to emphasize that data upon which this claim is based are largely studies of the perception of emotional information (e.g., facial expressions) in which the weight of the evidence does indeed suggest that the right *posterior* region is specialized for the perception of emotional information irrespective of valence. This fact underscores the importance of differentiating among different components of emotional functioning, most importantly between the perception of emotion and the experience/expression of emotion. In addition to my own writing on this issue (e.g., Davidson, 1984, 1988), a number of other commentators who have reviewed this literature have reached similar conclusions (e.g., Leventhal & Tomarken, 1986; Silberman & Weingartner, 1986).

The second issue concerns the importance of specifying the hypothesized logical status of the relation between asymmetrical anterior activation and emotion-related processes. Failure to consider this problem has been a source of considerable confusion in previous reviews of this topic. Although a large number of reports indicate that damage to the left hemisphere, particularly in the anterior regions, results in depressive symptomatology far more frequently than damage to corresponding regions of the right hemisphere, some investigators have underscored the fact that a number of reports have appeared which have shown no clear difference in the incidence or severity of depressive symptomatology in left- versus right-brain-damaged patients (see review by Gainotti, 1989). In addition to the obvious fact that many of the studies cited by Gainotti (1989) combined patients with both anterior and posterior damage, there is another crucial point in the interpretation of such data which has not been explicit in most of the reviews on this subject. We have proposed that anterior activation asymmetry functions as a diathesis which predisposes an individual to respond with predominantly positive or negative affect, *given an appropriate emotion elicitor*. In the absence of a specific elicitor, differences in affective symptomatology among individuals with different patterns of anterior activation asymmetry or asymmetry of anterior brain lesions would not be expected. Consistent with this prediction is our observation in normals that while baseline anterior asymmetry predicts reactivity to an affective challenge, it is unrelated to measures of the individual's current, unprovoked emotional state (e.g., Davidson & Fox, 1989; Tomarken, Davidson, & Henriques, 1990).[1] Thus, in a patient with left anterior damage, depressive symptomatology would be expected only if that patient were exposed to the requisite environmental stresses. Left anterior damage is not in itself *sufficient* for the production of depressive symptomatology. We would therefore *not* expect *all* patients with left frontal damage to show depressive symptomatology. Only those exposed to an appropriate set of environmental stresses would be expected to show the hypothesized final state.[2]

[1] While baseline anterior asymmetries are unrelated to measures of unprovoked emotional *state*, they are related to individual differences in dispositional mood or emotional *traits* (Tomarken, Davidson, Wheeler, & Doss, 1992).

[2] One important variable in evaluating the literature on the effects of unilateral lesions

III. CEREBRAL PSYCHOPHYSIOLOGICAL METHODS IN THE STUDY OF HEMISPHERIC ASYMMETRY RELATED TO EMOTION AND AFFECTIVE STYLE

Several important considerations apply in the choice of methods to study regional brain activity which underlies emotion. Many of the core phenomena of emotion are brief and therefore require measures which have a very fast time resolution. Moreover, periods of peak emotional intensity are unpredictable. They can occur at different points in time for different subjects in response to the same emotional stimulus. For example, some facial expressions of emotion are present for as little as 1–2 sec. An ideal method would be one which could resolve activity as brief as the behavioral manifestations of emotion. It is also important to be able to record physiological activity over much longer time intervals. This is needed when subjects are presented with affect elicitors that last several minutes, requiring physiology to be integrated over the entire period of the eliciting stimulus. In addition, as I describe in detail below, one of the most exciting new areas in psychophysiological research on emotion is the study of the biological bases of individual differences in emotional reactivity. Such studies often require baseline physiology to be integrated over several minutes in order to obtain a reliable estimate of an individual's characteristic pattern. Thus, with respect to time resolution, the ideal measure would range from subsecond intervals to several minutes.

Another important consideration is related to the first. Data must be stored in a form which will permit posthoc extraction of epochs of varying durations. The capacity for posthoc data extraction is required so that physiology coincident with objective measures of emotional state (e.g., emotional expression) can be extracted. In some of the research described below, brain activity which is coincident with the display of spontaneous facial expressions of emotion is extracted for analysis. Other measures of emotional state might also be utilized in a similar fashion, including vocal indices and on-line self-report. This requirement presupposes the accurate synchronization of the behavioral and physiological data streams. Modern computer and video technologies allow for this possibility.

Another essential requirement of any measure of regional brain activity used in the study of emotion is that it be relatively noninvasive. There are three major reasons for this. First, the more intrusive a method, the greater will be the interference with the elicitation of actual emotion. For example, certain types of PET scan protocols are highly intrusive and it is difficult to override the anxiety which is an inherent side effect of the

is the time from lesion to assessment. With increased time, there should be an increased likelihood of exposure to negative life events and, therefore, a higher probability that the individual would show depressive symptomatology.

procedure. It would likely be very difficult to elicit strong positive affect in many subjects undergoing a PET scan. The second important reason for limiting measures of regional brain activation to those that are relatively noninvasive is the need to study individuals over time as they undergo several different emotional states. It is crucial that psychophysiological studies of emotion compare among at least two different emotions and a baseline period (see Davidson et al., 1990b, for a complete discussion of methodological desiderata in psychophysiological studies of emotion). Such comparisons enable the investigator to determine if the physiological pattern observed during the emotion period differs from baseline and if the pattern is simply characteristic of emotion per se (in which case the pattern associated with each of the two different emotions will not differ) or is emotion-specific. The third reason for preferring relatively noninvasive procedures is the possibility of using them with infants and young children. These age groups are particularly important to study in research on the biological bases of emotion and the methods used must be appropriate for this population.

In light of the considerations noted above, we have been using scalp-recorded brain electrical activity to make inferences about regional brain activation during the experimental arousal of acute emotions and emotion-related patterns of brain activity during resting baselines. The electroencephalogram (EEG) meets all of the requirements noted above. It is noninvasive, has a fast time resolution, and can be effectively synchronized with a behavioral data stream which permits extraction of data based upon posthoc specification of periods of intense behavioral signs of emotion.

We have used recordings of brain electrical activity to make inferences about regional brain activation both during baseline periods and in response to a variety of emotion elicitors in adults, toddlers, and infants. We can examine brain activity during very brief epochs of emotion (1 sec), provided that periods of the same emotion type occur sufficiently frequently within an individual. To obtain stable estimates of spectral power from which measures of activation are derived, one needs a minimum of approximately 10–15 sec of activity. The individual epochs themselves can be as brief as 1 sec, but when aggregated together, their sum must exceed approximately 10 sec (Davidson, 1988; Tomarken, Davidson, Wheeler, & Kinney, in press). Movement and muscle activity frequently accompany the generation of emotion. We have developed procedures to statistically partial out the contributions of the muscle activity from the EEG (see Davidson, 1988, for a description of the method and Henriques & Davidson, 1990, for the application of the method in an actual experiment). Finally, we use an electrode cap for EEG recording (Blom & Anneveldt, 1982). Such a cap permits accurate and rapid placement of electrodes and is particularly useful in studies with infants and children, where rapid application of electrodes is essential.

The principal measure extracted from the EEG in the studies I present in this article is power in the alpha band, which in adults represents activity between 8 and 13 Hz.[3] A wealth of evidence indicates that power in this frequency band is inversely related to activation in adults (e.g., Shagass, 1972). In the studies I describe on infants, we have used power in a lower frequency band as our dependent measure since this represents the functional equivalent of adult alpha activity (see, e.g., Davidson & Fox, 1989; Davidson & Tomarken, 1989). Our measures of band power are computed from the output of a Fast Fourier Transform (FFT), which decomposes the brain activity into its underlying sine wave components.

Below I briefly review the findings from several recent studies performed in our laboratory in which we examined brain activity during the experience/expression of experimentally aroused positive and negative emotion.

IV. ANTERIOR ASYMMETRIES DURING THE EXPERIMENTAL AROUSAL OF APPROACH- AND WITHDRAWAL-RELATED EMOTION

A. Studies in Adults

We recently completed a collaborative study with Ekman and Friesen (Davidson et al., 1990b) in which adult subjects were exposed to short film clips designed to induce approach-related positive emotion and withdrawal-related negative emotion. Happiness and amusement were the positive, approach-related emotions and disgust was the negative, withdrawal-related emotion. Subjects were presented with two positive and two negative film clips in a darkened room while we videotaped their facial behavior unobtrusively. We also recorded brain electrical activity from the left and right frontal, central, anterior temporal, and parietal regions.

An important consideration in research on emotion is that when two or more emotions are compared for their effects on either physiological or behavioral dependent variables, the intensities of the elicited emotion must be comparable. If the emotions differ in intensity, then any differences found between them could be attributed to intensity per se, rather than to the qualitative nature of the emotion aroused. Accordingly, our positive and negative films were carefully matched on the intensities of

[3] We typically examine power in all frequency bands. However, the majority of variance in task-related and baseline EEG is in the alpha band. Moreover, we have demonstrated that asymmetries in alpha power are more consistently related to both cognitive (e.g., Davidson, Chapman, Chapman, & Henriques, 1990) and affective (e.g., Davidson et al., 1990b) processes than asymmetries in power in other frequency bands. Therefore, in this article, data from the alpha band only will be presented.

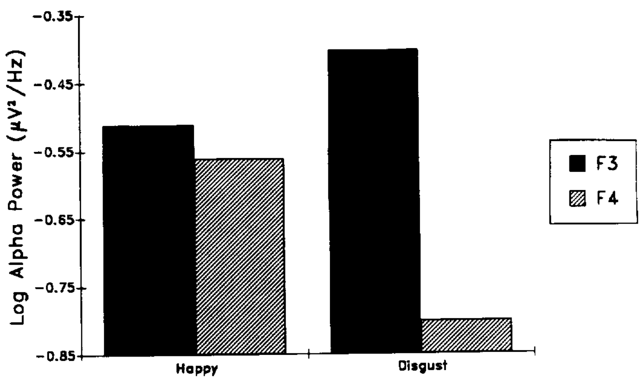

FIG. 1. Mean log-transformed alpha power (in $\mu V^2/Hz$) for the left and right midfrontal regions (F3 and F4) during happy and disgust facial expression conditions. (More negative numbers indicate less alpha power. The negative numbers are a function of the log transformation. Lower numbers (i.e., more negative) are associated with increased activation). From Davidson, Ekman, Saron, Senulis and Friesen (1990).

the primary emotion elicited by each (amusement for the positive films and disgust for the negative films) as determined by self-report.

The video record of each subject was coded with Ekman and Friesen's (1978) *Facial Action Coding System* (FACS). FACS distinguishes 44 action units, the minimal units that are anatomically separable and visually distinctive. Any facial movement can be described in terms of the particular action unit, or units, that produced it. The scorer identifies the action units, such as the one which lowers the brow or pulls the lips corners up, rather than making inferences about underlying emotional states such as anger or happiness. FACS scoring of the facial data from this experiment revealed that the two types of expression which occurred with the most frequency were happy expressions in response to the positive film clips and disgust expressions in response to the negative film clips. For each subject, the onset and offset of each happy and disgust expression were identified with FACS. These times were then entered into the computer so that EEG coincident with these expressions could be extracted.

Following removal of eye movement, muscle and gross movement artifact, the EEG during periods of happy and disgust facial expressions was Fourier transformed and power in different frequency bands was calculated. Based upon the theory and evidence reviewed above, we hypothesized that the disgust periods would be associated with greater right-sided anterior activation than would the happy periods and that the happy periods would be associated with greater left-sided activation than would the disgust periods. Figure 1 presents the alpha power data for the frontal leads. As can be seen from this figure, disgust is associated with less alpha power (i.e., *more* activation) in the right frontal lead than is happiness, while happiness is associated with less alpha power in the left frontal lead than is disgust. The Hemisphere × Valence interaction was highly significant ($p < .0005$). This pattern of greater right-sided activation during disgust than during happiness was also found in the anterior temporal electrodes. Importantly, there were no significant Hemisphere × Valence interactions in the central or parietal regions, underscoring the specificity of the valence-related asymmetry to anterior brain regions.

We examined frontal asymmetry on an individual subject basis to determine how consistent the difference was between happy and disgust epochs. For each subject, we calculated an asymmetry index which expressed the asymmetry of frontal alpha power in a single metric. The index was log right minus log left alpha power. Higher numbers on this index denote greater relative left-sided activation. We computed this index separately for the happy and disgust periods. We found that 100% of the subjects showed a lower score on this index during the disgust than during the happy periods. The direction of this difference indicates greater right-sided frontal activation during the disgust than during the happy condition. We also found that there were large differences among individuals in their average asymmetry score (across emotion conditions). The difference between happy and disgust conditions appears to be superimposed upon subjects' basal levels of asymmetry. In the next part of this article, I show how such individual differences in asymmetry are related to characteristic differences in mood and affective reactivity.

In order to examine whether the procedures we used to verify the presence of an emotion (i.e., facial expression) actually made an important difference in uncovering patterns of asymmetry, we performed the type of analysis which is more typical in research on the psychophysiology of emotion. We simply compared all artifact-free EEG epochs extracted from the positive film clips with the comparable epochs extracted from the negative film clips. The epochs used for this analysis were selected irrespective of the subject's facial behavior. While the means were in the expected direction for the frontal leads, with the negative film clips producing more right-sided activation than the positive clips, we found no significant differences between these conditions on any of the measures of asymmetry. The lack of significant effects when the analyses were performed independent of facial behavior suggests that our method of using facial expressivity to flag epochs of peak emotional state was effective. In this study, significant between-condition differences in asymmetry were obtained only when facial expression was used to verify the presence of emotional states. We should note, however, that other studies in our laboratory (e.g., Davidson & Fox, 1982) and other laboratories (e.g., Ahern & Schwartz, 1985; Tucker, Stenslie, Roth, & Shearer, 1981) have found EEG differences between positive and negative emotional states without using facial expressive measures as an index of peak emotional intensity. Thus, the extraction of data during the presence of discrete facial expressions of emotion does not appear to be *necessary* for the emergence of hemispheric asymmetries relevant to emotion.

We recently completed a study in which robust differences in frontal brain asymmetry emerged during approach- and withdrawal-related emotion in the absence of extraction of epochs based upon facial behavior (Sobotka, Davidson, & Senulis, in press). In this experiment, we manipulated reward and punishment contingencies in the context of a video game-like task. The task consisted of a series of 400 trials, presented over the course of two experimental sessions, in blocks of 20 trials each. Half of the trials were potential reward trials and half potential punishment trials. Each trial began with the presentation of a fixation point, followed between 2 and 4 sec later by an arrow. The arrow was in either the up or the down position. An up arrow denoted that the trial was a potential reward trial and a down arrow indicated that the trial was a potential punishment trial. Four seconds following the presentation of the arrow stimulus, a square was presented in the center of the screen. This was the imperative stimulus to which the subject was required to respond as quickly as possible. The outcome of each trial was based upon the subjects' reaction time to the imperative stimulus. There were two possible outcomes on each trial. For reward trials, subjects could either win money or have no change in their earnings. For punishment trials, subjects could either lose money or have no change in their earnings. The amount of money which was won or lost on each trial was always $0.25. Subjects were told that they would receive $5 at the beginning of each session, which represented their starting sum of money in the game they were about to play. Subjects were instructed that they could win additional money as well as lose money from the $5 starting amount. They were also told that the amount of money they ended up with following the completion of the game would be theirs to keep.

For subjects to win money in the reward trials and stay even (i.e., not lose money) in the punishment trials, they were required to have a reaction time which was faster than the median reaction time from the previous block of trials. The computer which acquired the reaction time data thus updated the criterion reaction time on each trial block.

We recorded brain electrical activity from most of the standard 10/20 locations during the performance of the task. Of major interest to us was the frontal brain activity during the preparatory interval between the arrow and the imperative stimuli. The EEG during this period was Fourier transformed and power in the alpha band was extracted as described in the experiment above. As predicted, we found a significant Valence × Hemisphere interaction, with greater right frontal activation (i.e., less alpha power) during the punishment than during the reward trials. This

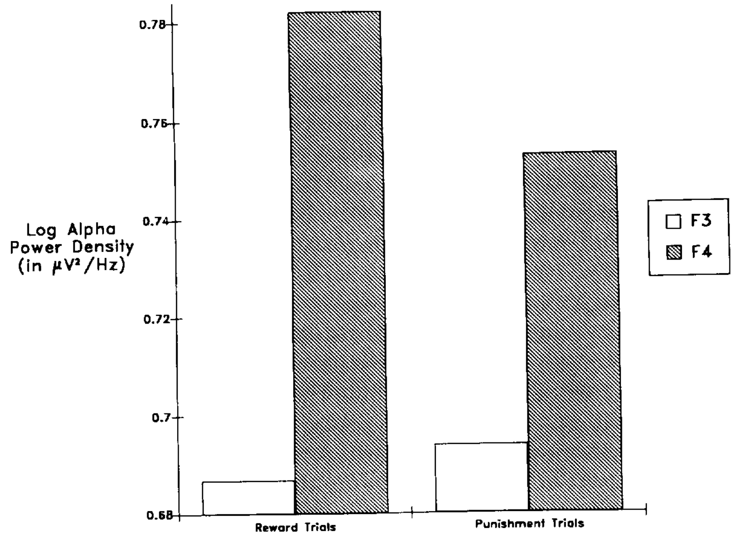

FIG. 2. Mean log-transformed alpha power for the left and right midfrontal regions (F3 and F4) during reward and punishment conditions. From Sobotka, Davidson, and Senulis (in press).

interaction was significant in both the midfrontal (F3/4) and the lateral frontal (F7/8) sites. These findings are displayed in Figs. 2 and 3. As can be seen from these figures, in both frontal regions the punishment condition is associated with less alpha power (i.e., more activation) in the right frontal lead than the reward condition. These data indicate that when reward and punishment contingencies are directly manipulated, frontal brain asymmetry changes in the direction of prediction, with greater right-sided activation present during the punishment condition than during the reward condition.

B. Studies in Infants

In a series of collaborative studies with Nathan Fox, we have found similar asymmetries in frontal brain activity during the experimental arousal of emotions in infants. These studies were designed to determine whether the cerebral asymmetries which we found to be associated with emotion in adults are present during the first year of life. In our first infant study (Davidson & Fox, 1982), we presented 10-month-old infants with a videotape of an actress displaying laughter and distress while EEG was recorded from the left and right frontal and parietal regions. We found that the positive condition elicited more left-sided frontal activation than the negative condition. This finding was obtained in two separate

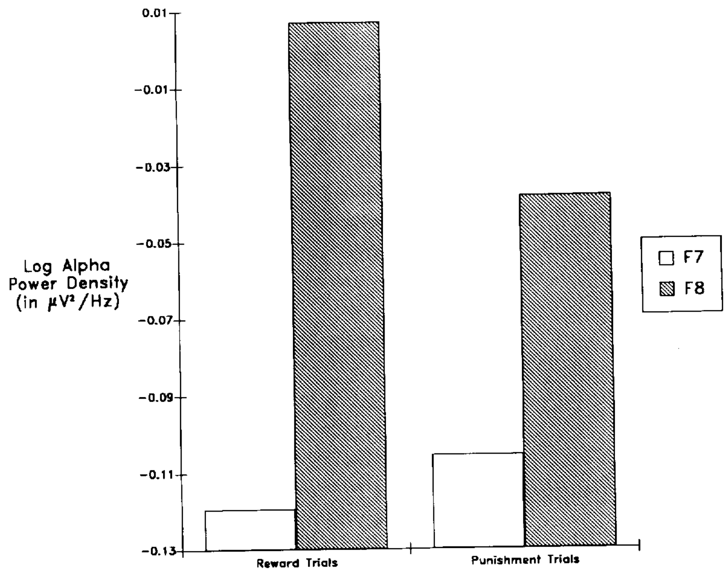

FIG. 3. Mean log-transformed alpha power for the left and right lateral frontal regions (F7 and F8) during reward and punishment conditions. From Sobotka, Davidson, and Senulis (in press).

samples of infants. In another study, we (Fox & Davidson, 1986) tested newborn infants to determine whether this asymmetry was present at birth. Neonates were presented with tastes which differed in hedonic valence while brain electrical activity was recorded. We found that tastes which produced facial signs of disgust were associated with more right-sided frontal activation than tastes which produced a more positive facial expression (sucrose).

In more recent work with Fox (Fox & Davidson, 1988), we studied brain electrical activity during the expression of different facial signs of emotion in 10-month-old infants. Emotion was elicited via the approach of a mother and a stranger. Of prime interest to us was a comparison between two types of smiles. One of these involves activity in both the zygomatic muscle (cheek) *and* the orbicularis oculi (around the eye), while the other involves activity only in the zygomatic region. The difference between these two smile types was first described by the French anatomist Duchenne (1862). Duchenne's work figured heavily in Darwin's (1872) book *The Expression of the Emotions in Man and Animals.* According to Darwin's discussion, Duchenne suggested that the emotion of "frank joy" is accompanied by activity in both the zygomatic and the orbicularis oculi muscles, while smiles not associated with felt happiness are accompanied by activity only in the zygomatic region. Ekman and Friesen (1982) provided the first modern empirical support for this proposal by showing that smiles involving activity in both of these facial regions were much more highly correlated with self-reports of happiness than smiles produced by activity in the zygomatic region only. In light of this evidence, we were intrigued by the possibility that these two types of smiles could be discriminated electrophysiologically.

Artifact-free EEG data were obtained on 19 infants, all born to two right-handed parents. EEG was recorded from the left and right frontal and parietal regions and quantified in the same manner as described above for the studies with adults. Infants were exposed to episodes of both mother approach and stranger approach. Facial behavior and EEG were recorded in response to each episode. Facial behavior was coded with Ekman and Friesen's (1984) EM–FACS system, which is a streamlined version of FACS designed explicitly for the coding of facial behavior related only to emotion.

We first computed the incidence of each of the two smile types in response to both stranger and mother approach. Seventy-five percent of the infants displayed smiles without orbicularis oculi activity to the stranger, while in response to mother approach, 78% of the infants displayed smiles with orbicularis oculi activity. The difference in the frequency of occurrence of these two smile types is highly significant ($p <$ .005). In other words, smiles indicative of felt happiness were more likely to occur in the situation in which genuine positive affect would be expected (mother approach), while a potentially threatening situation (stranger approach) was more likely to elicit the other type of smile. We also coded the duration of the two smile types since Darwin (1872) suggested that the more "genuine" smiles (i.e., those with orbicularis activity) were longer in duration than the other type of smile. Our results confirmed Darwin's (1872) suggestion: the mean duration of smiles with orbicularis activity was 2.39 sec, while the mean duration of smiles without orbicularis activity was 1.49 sec ($p < .01$). The central question which we posed in this study was whether the two smile types could be discriminated on the basis of frontal brain electrical asymmetry. We specifically predicted that smiles with orbicularis activity would be accompanied by more relative left-sided frontal activation than the other smiles. As shown in Fig. 4, the data strongly supported this hypothesis. Consistent with the majority of our previous findings, regional specificity was once again indicated by the absence of significant differences in the parietal region (see Fig. 4).

We have recently examined EEG asymmetry during these two types of smiles in adults (Ekman, Davidson, & Friesen, 1990). In this study, we were also able to examine the relation between the duration of these smile types and the self-reports of emotion. We found that higher intensities of self-reported amusement were associated with increased du-

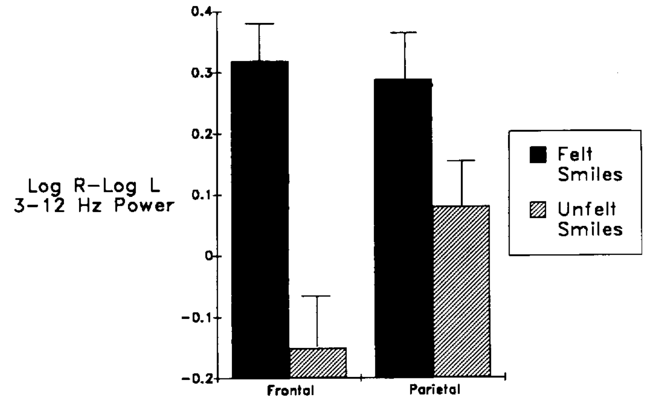

FIG. 4. Mean frontal (F3 and F4) and parietal (P3 and P4) asymmetry scores (log right minus log left power) for "felt" (i.e., with orbicularis oculi activity) and "unfelt" (i.e., without orbicularis oculi activity) smiles in response to mother and stranger approach in 10-month-old infants. Higher numbers on this laterality metric denote greater relative left-sided activation. Adapted from Fox and Davidson (1988).

ration of smiles with eye muscle involvement (r = .70), while the duration of smiles without eye muscle activity were not associated with self-reports of amusement (r = .14). Most importantly, smiles with orbicularis activity were associated with significantly more left anterior activation than smiles lacking orbicularis activity. This pattern of anterior asymmetry is precisely the same as that found to discriminate between these two smile types in infants.

V. INDIVIDUAL DIFFERENCES IN ANTERIOR ASYMMETRY: A NEURAL SUBSTRATE FOR AFFECTIVE STYLE

A. Affective Reactivity and Vulnerability to Depression in Adults

In the first study described in the previous section, I noted that although 100% of the subjects showed a difference in the predicted direction between happy and disgust periods, these emotion-related differences were superimposed upon large individual differences in the overall magnitude and direction of asymmetry. In other research, we have found that a subject's overall (across task) EEG asymmetry during task performance is highly correlated with their asymmetry during a resting baseline (e.g., Davidson, Taylor, & Saron, 1979) and that anterior asymmetries during resting baselines are stable over time (Tomarken et al., 1990), with test–retest correlations ranging between 0.66 and 0.73 for different measures of anterior activation asymmetry. Over the past several years, we have performed a series of studies in both adults and infants which has examined the relation between individual differences in anterior activation asymmetry and dispositional mood, affective reactivity and psychopathology. Below I will present highlights of several components of this research effort, with an emphasis on studies of early differences in emotional reactivity and temperament.

We began our studies of individual differences in anterior asymmetry by comparing subjects who differed in dispositional depressive mood. We (Schaffer, Davidson, & Saron, 1983) selected subjects on the basis of their scores on the Beck Depression Inventory and compared a group of high and stable scorers to a group of low and stable scorers on resting frontal asymmetry. We found that the depressed subjects had less left frontal activation than the nondepressed subjects. We have recently replicated this finding on a group of clinically depressed subjects (Henriques & Davidson, 1991).

An important question concerning these findings with depressives is the degree to which they are state-dependent. Is the decrease in left frontal activation a marker of the state of depression or is it a more trait-like characteristic which marks an individual's vulnerability to depression. To obtain initial evidence relevant to this question, Henriques and I (Henriques & Davidson, 1990) compared remitted depressives to healthy controls who were screened for lifetime history of psychopathology. The remitted depressives all met Research Diagnostic Criteria (Spitzer, Endicott, & Robins, 1978) for major or minor depression within the past 2 years. All of the remitted depressives were currently normothymic, with no depressive symptomatology, and none were currently taking medication for their depression. We examined EEG during resting baseline conditions. We found that the remitted depressives, like the acutely depressed subjects, had significantly less left frontal activation than the healthy controls in the frontal region. This pattern was found for the anterior electrodes only, again underscoring the specificity of this asymmetry to the anterior cortical regions. Figure 5 presents the left and right hemisphere alpha power data from each of the regions from which we recorded for the remitted depressives and healthy controls.

These results indicate that the decreased left anterior activation which is characteristic of depression remains even when depression is remitted. In turn, these findings suggest that "depressogenic" asymmetry patterns may be a *state-independent* marker that indexes risk for depression. Clearly, to more comprehensively test this hypothesis, a prospective design is required in which subjects are classified on the basis of asymmetry patterns and followed-up over time. We would predict that, relative to comparison groups, a higher proportion of subjects who demonstrate decreased left anterior activation would develop subsequent psychopathology.

In two recent studies in adults (Tomarken, Davidson, & Henriques, 1990; Wheeler, Davidson, & Tomarken, in press), we examined the re-

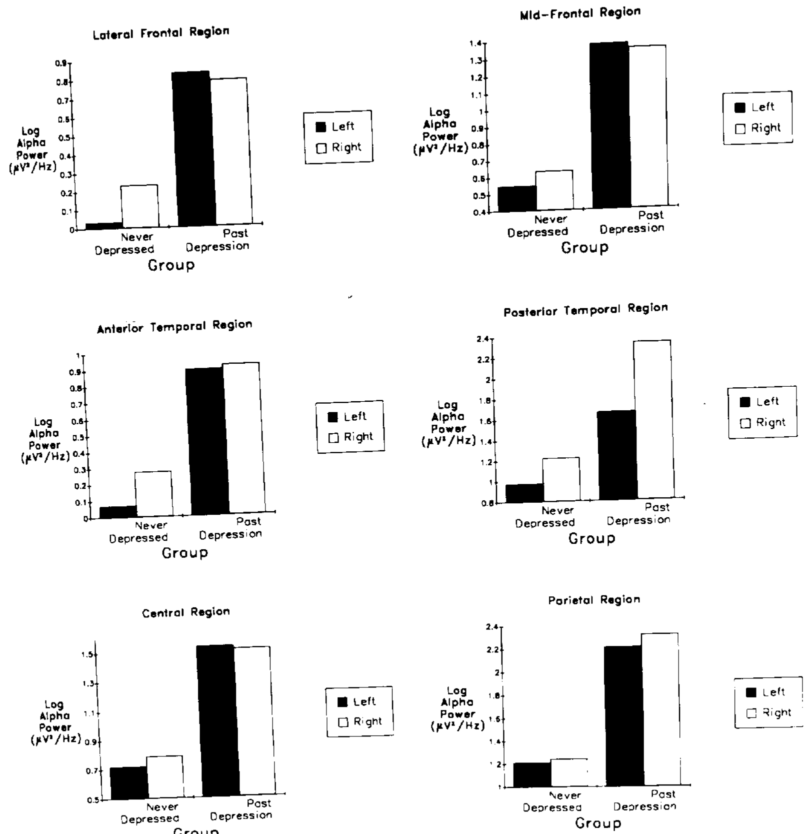

FIG. 5. Mean log-transformed alpha power in left and right hemisphere sites from the lateral frontal (F7 and F8), midfrontal (F3 and F4), anterior temporal (T3 and T4), posterior temporal (T5 and T6), central (C3 and C4), and parietal (P3 and P4) regions for subjects with a past depression and for those who were never depressed. From Henriques and Davidson (1990).

lation between individual differences in anterior asymmetry and reactivity to emotional film clips in normals. We hypothesized that subjects with greater right-sided frontal activation at rest would report more intense negative affect in response to film clips designed to elicit fear and disgust. In both studies, we found that measures of frontal activation asymmetry recorded prior to the presentation of the film clips accounted for significant variance in subjects' self-reports of negative affect in response to the clips. Subjects with greater relative right-sided frontal activation reported more intense negative affect to the clips. It should be noted that the studies included entirely independent groups of subjects and entirely different film clips. In the first study (Tomarken et al., 1990), the correlation between frontal asymmetry and global negative affect to the negative films was −.37. In the second study (Wheeler et al., in press), the correlations was −.48. The correlations are inverse since lower numbers on the asymmetry metric (log right minus log left alpha power) indicate greater relative right-sided activation. In both studies, the correlations between frontal asymmetry and positive affect were positive, and in the Wheeler et al. (in press) study it was significant (r = .48).[4] These data indicate that subjects with greater relative left-sided frontal activation at rest reported more positive affect in response to film clips designed to elicit happiness and amusement. It is important to note that all of these effects remained significant even when measures of mood at baseline were statistically partialled out. In other words, frontal asymmetry accounted for significant variance in emotional reactivity to film clip elicitors after the variance accounted for by measures of mood during baseline was statistically removed. This observation strengthens our suggestion that baseline anterior asymmetry is a state-independent measure of affective reactivity, but is itself unrelated to measures of phasic, unprovoked mood.

B. Implications for Early Childhood Temperament

In collaboration with Nathan Fox, we had the opportunity to examine the relationship between early manifestations of individual differences in emotional reactivity and frontal activation asymmetry. Among 10-month-old infants, there is substantial heterogeneity in the response to maternal separation. Some infants become distressed immediately and will cry as soon as their mother has departed. Other infants will show a very different pattern of response and evince relatively few signs of negative affect. We (Davidson & Fox, 1989) divided the 10-month-old infants into two groups on the basis of whether they cried or not in response to maternal separation lasting approximately 60 sec. We found that about half of our group cried within this time period and half did not. We recorded baseline measures of frontal and parietal activation from the two hemispheres approximately 30 min prior to subjecting the infants to the episode of maternal separation. We then examined EEG measures of frontal activation asymmetry during this preceding baseline period separately for the group of infants who subsequently cried and those who did not cry. We found a large difference in frontal asymmetry that predicted which infants would cry

[4] One possible reason for the generally more robust correlations between frontal asymmetry and measures of affective reactivity in the Wheeler et al. (in press) study compared with those of the Tomarken et al. (1990) study is the fact that in the former, two measures of resting asymmetry were obtained, 3 weeks apart. We then averaged the two measures together, for the subjects who were stable from time 1 to time 2 (i.e., those who showed little change in their asymmetry score from one occasion to the next). Thus, the analyses in this study are based upon more stable estimates of an individual's true frontal asymmetry.

and which would not cry. The criers had greater right-sided and less left-sided frontal activation during the preceding baseline period than with the noncriers. Parietal asymmetry from the same points in time failed to differentiate between the groups. To establish that the emotional states of the two groups of infants during the baseline period itself (when measures of brain activity were obtained) was comparable, we coded the facial behavior of the infants during this period. There were no differences in the frequency or duration of any facial signs of emotion during the baseline period between the infants who subsequently cried in response to maternal separation and those who did not. This suggests that our measures of regional brain activity were not reflecting phasic state differences between criers and noncriers. These data were the first to show that in infants, individual differences in frontal asymmetry predicts affective reactivity. The direction of the relation is identical to that observed in our studies with adults. Subjects who show greater relative right-sided frontal activation at rest are likely to express more intense negative affect in response to a stressful event than their more left-frontally activated counterparts.

The findings in both adults and infants provided the foundation for a current study in our laboratory on relations between temperament and frontal asymmetry. Kagan and his colleagues (e.g., Kagan, Reznick, & Snidman, 1988) have been studying the temperamental construct of behavioral inhibition for the past 10 years. Behavioral inhibition refers to the young child's tendency to withdraw and/or freeze in situations of novelty or unfamiliarity. Behaviorally inhibited children at 2½ years of age would likely withdraw in response to a novel object, such as a robot. Such a child would also be unlikely to approach a stranger, to climb through a toy tunnel, or to interact with a same-sex peer. In a novel peer play situation, behaviorally inhibited children spend the majority of their time in close proximity to their mothers, without playing or interacting in any way. While Kagan and his colleagues have studied autonomic differences between inhibited and uninhibited children, there have been no studies on central nervous system differences between these groups. We therefore embarked upon a longitudinal study whose principal aims were to determine if inhibited children showed greater relative right-sided frontal activation than uninhibited children and to examine relations between frontal asymmetry and measures of behavioral inhibition over time.

To select groups of inhibited and uninhibited children, we adopted the procedures that Kagan and his colleagues had developed (Kagan et al., 1988). At 31 months of age, we tested 386 children in a peer play session. The children were randomly selected from birth announcements in the newspaper. Two unfamiliar same-sex peers came to the laboratory with their mothers and were escorted to a large play room. The mothers were instructed to sit on chairs and fill out an extensive series of questionnaires. They were instructed not to interact with their children. There were age-appropriate toys on the floor in the play room, including a toy tunnel through which the children could crawl. At Minute 10 of the play session, the experimenter brought a remote-controlled robot into the room. The robot began to speak and walk toward each of the children. It was controlled by an experimenter behind a one-way mirror. After remaining in the room for 3 min, the robot said that it was tired and had to go home to take a nap. The experimenter then entered the room and removed the robot. At Minute 20, a stranger entered the room who was not seen before by either child. The stranger was holding a tray on which were placed several very interesting looking toys. The stranger invited the children to play with the toys. After 3 min, the stranger left the tray of toys on the floor for the children to play with and then departed. The play session ended at Minute 25.

During the entire play session, two observers were positioned behind a one-way mirror to code the behavior of each child. The major measures which were coded included the total time the child was proximal to mother (within arm's length) and not interacting, the latency to touch the first toy, the latency to speak the first utterance, the latency to approach the robot, the latency to approach the stranger, and the latency to enter the tunnel. On the basis of these measures, we selected three groups of children for our longitudinal study. The criteria we used were based on the work of Kagan et al. (1988), but were more stringent. The inhibited children were those who spent more than 9.5 min (of a total of 25 min) proximal to mother and also met four of the following five additional criteria: (1) latency of $\geq$3 min to touch their first toy, (2) latency of $\geq$3 min to speak their first utterance, (3) no approach to the robot, (4) no approach to the stranger, and (5) latency of $\geq$10 min to enter the tunnel. The criteria for the uninhibited children were all of the following: (1) total duration of time proximal to mother $\leq$30 sec, (2) latency of $\leq$30 sec to touch their first toy, (3) latency of $\leq$60 sec to speak their first utterance, (4) latency of $\leq$60 sec to approach the robot, (5) latency of $\leq$60 sec to approach the stranger, (6) latency of $\leq$60 sec to take a toy from the stranger, and (7) enter the tunnel at some point during the session. In addition to selecting groups of inhibited and uninhibited children, we also selected a group of middle children who showed values in the midrange for all of the measures described above. We selected approximately 28 subjects in each of the three groups, balanced evenly by sex. The average duration of time spent proximal to mother among children in the inhibited and uninhibited groups underscores the magnitude of the difference between the two extreme groups. The inhibited children remained proximal to their mothers for an average of 1171 sec (of a total of 1500 sec—25 min—representing 78% of the total time) while the uninhibited children were proximal to their mothers for an average of 9 sec (representing less than 1% of the total time).

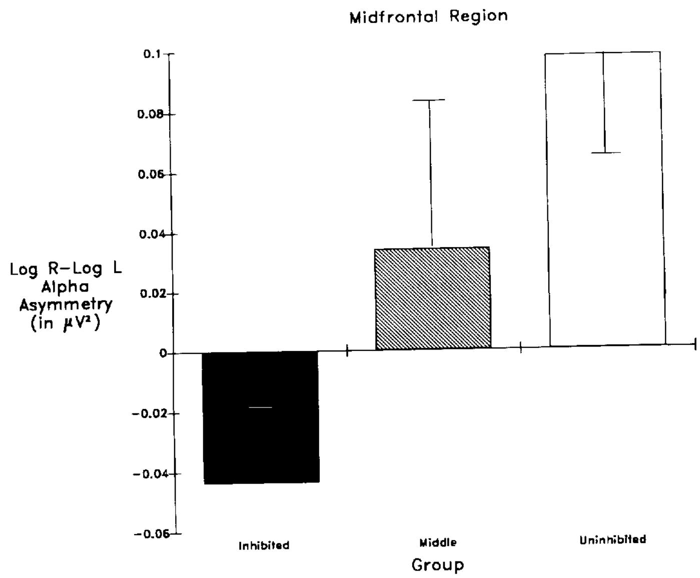

FIG. 6. Mean asymmetry scores (log right minus log left power in the 7- to 10-Hz band—the toddler alpha frequency range) for the midfrontal electrodes for inhibited, middle, and uninhibited children. Higher numbers on this metric denote greater relative left-sided activation. Adapted from Davidson, Finman, Straus, and Kagan (1992).

We tested the longitudinal cohort at 38 months of age in a session during which we recorded brain electrical activity at rest and in response to several tasks. To date, we have analyzed the data for the resting baselines. Our major prediction was that inhibited children would show greater relative right-sided frontal activation than their uninhibited counterparts. Middle children were hypothesized to fall in between. Figure 6 presents the frontal asymmetry data for the three groups. As in previous figures, negative asymmetry scores indicate greater right frontal activation and positive scores indicate left frontal activation. As can be seen from this figure, inhibited children show right frontal activation, while the uninhibited children show the opposite pattern. The middle children fall predictably in between the two extreme groups.

For theoretical reasons, it is important to ascertain how the two hemispheres are contributing to this group difference in asymmetry. If the primary difference among the groups is in the withdrawal-related component, we would expect the inhibited children to show *more* right frontal activation than the uninhibited children. However, if the fundamental difference between the groups is in the approach-related component, we would expect the inhibited children to show *less* left frontal activation

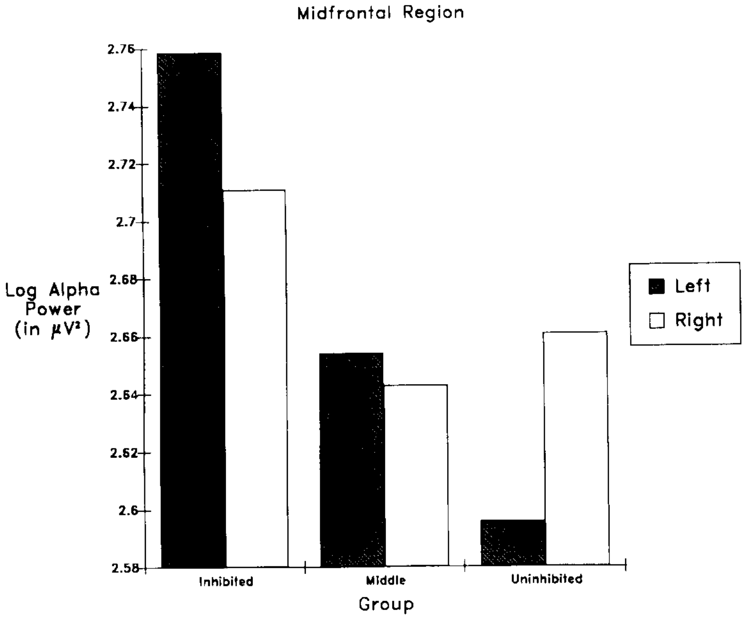

FIG. 7. Mean log-transformed power in the 7- to 10-Hz band in the left and right midfrontal region for inhibited, middle, and uninhibited children. Adapted from Davidson, Finman, Straus, and Kagan (1992).

than their uninhibited counterparts. This latter pattern would suggest that inhibited children show deficits in approach-related behavior and emotion, rather than accentuated withdrawal-related behavior. Most accounts of behavioral inhibition have implied a strong linkage to fear and anxiety. On this view, the difference among groups should be most pronounced in the right frontal region. Figure 7 presents the frontal EEG data for each of the three groups separately by hemisphere. The Group × Hemisphere interaction was highly significant ($p = .0003$). As can be clearly seen from this figure, the difference among the groups is exclusively in the left hemisphere, with the inhibited children showing more power (i.e., less activation) in this region than the other two groups. These data clearly indicate that the group difference is in the approach-related system and suggest that it would be most appropriate to characterize the inhibited children as showing deficits in a frontal approach system, rather than hyperactivation in a frontal withdrawal system.

It is instructive to consider the possibility that our sample of inhibited children is more extreme than samples that have been studied previously by Kagan's group. Certainly, the magnitude of the difference between our extreme groups on the play session variables (e.g., time proximal to mother) is greater than that which Kagan observed in his sample. It is also possible that there are different subtypes of inhibition, with one subtype characterized by approach-related deficits and the other characterized by accentuated withdrawal tendencies. Our grouping procedures may have inadvertently selected for subjects in the former category. A testable prediction which follows from our initial finding is that our sample of inhibited children should not differ from uninhibited children in their propensity to display withdrawal-related negative affect in response to appropriate elicitors. Rather, they should be more prone to sadness and depression-like reactions following situational elicitors of these emotions. We intend to examine these predictions in the course of our future longitudinal work.

The pattern of decreased left frontal activation we found among our inhibited children is similar to the pattern we have reported in depressives. It is important to emphasize that this pattern is viewed as a marker of *vulnerability* to emotion and behavior which is associated with deficits in the approach system. Such vulnerability will become expressed as psychopathology only in response to relatively extreme life stresses. Thus, only a small percentage of affected individuals (i.e., those with the marker) would be expected to actually develop an affective disorder. However, a larger percentage might be expected to have subclinical characteristics such as dysthymic mood, shyness, and decreased dispositional positive affect. It will be of interest to examine these children as they confront increasingly more complex life challenges (e.g., entry into school) to help define what the environmental circumstances are that predispose individuals with decreased left frontal activation to exhibit depression-related symptomatology.

It will be equally of interest to study the children at the opposite extreme. It is not clear whether the uninhibited children are likely to display impulsive behavior and show an oversensitivity to reward contingencies. We are currently testing some of these hypotheses in our assessment of the children at 4½ years of age.

VI. SUMMARY AND CONCLUSIONS

This article presented an overview of recent research on anterior asymmetries associated with emotion and individual differences in emotional reactivity, psychopathology, and temperament. I proposed that the anterior regions of the two cerebral hemispheres are specialized for approach and withdrawal processes, with the left hemisphere specialized for the former and the right for the latter. Using electrophysiological measures of regional cortical activation, data were presented which demonstrated that the experimental arousal of approach-related positive affect was associated with left anterior activation while arousal of withdrawal-related negative affect was associated with right anterior activation. In the second half of the article, evidence was presented which indicated that individual differences in patterns of anterior asymmetry are stable over time and predict important features of affective style—an individual's dispositional emotional profile, including characteristic patterns of emotional reactivity as well as mood. The possible antecedents of such adult individual differences were examined in the context of our longitudinal study of temperament, where we found that behaviorally inhibited 3-year-old children show less left frontal activation than their behaviorally uninhibited counterparts.

We believe that the phasic state effects we can produce through the experimental arousal of positive and negative emotion are superimposed upon the more tonic individual differences in baseline measures of anterior asymmetry. These individual differences are clearly present early in life and show important associations with reactivity to situational challenges in the laboratory, including maternal separation and exposure to novelty and unfamiliarity. Among the most important unanswered questions is the degree to which these individual differences are modified through experience. For example, will frontal asymmetry parallel behavioral changes in a child who at age 4½ years is considerably less inhibited than he was at 3 years of age (when he showed pronounced left frontal hypoactivation)? A related question concerns the variability in frontal asymmetry observed among the groups. Clearly not all children who show decreased left frontal activation are inhibited. Are the children who show decreased left frontal activation but are not currently inhibited more likely to *become* inhibited with development? Or can we identify anything in the home environments of children with decreased left frontal activation who are not inhibited which buffered them from the expression of behavioral inhibition? These are some of many important questions which longitudinal study of these children can begin to answer.

From the data already available, it is clear that asymmetry in the anterior cortical regions is significantly associated with emotion and emotional reactivity. It will be important for future research to characterize both the proximal and the distal causes of this asymmetry. The study of proximal causes will necessarily require the examination of subcortical and neurochemical contributions. Distal causes will inevitably be some combination of heritable and early environmental factors. Virtually no information on either of these classes of causal factors is currently available. We have every reason to think that future research on this topic will be as exciting and revealing as the recent work has been.

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