# Symposium on Emotion

## EMOTION AND AFFECTIVE STYLE: Hemispheric Substrates

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**Abstract**—*Research on cerebral asymmetry and the experience and expression of emotion is reviewed. The studies described use electrophysiological procedures to make inferences about patterns of regional cortical activation. Such procedures have sufficient temporal resolution to be used in the study of brief emotional experiences denoted by spontaneous facial expressions. In adults and infants, the experimental arousal of positive, approach-related emotions is associated with selective activation of the left frontal region, while arousal of negative, withdrawal-related emotions is associated with selective activation of the right frontal region. Individual differences in baseline measures of frontal asymmetry are associated with dispositional mood, affective reactivity, temperament, and immune function. These studies suggest that neural systems mediating approach- and withdrawal-related emotion and action are, in part, represented in the left and right frontal regions, respectively, and that individual differences in the activation levels of these systems are associated with a coherent nomological network of associations which constitute a person's affective style.*

Emotions have often been conceptualized as reflecting primitive processes that are subserved by correspondingly primitive structures in the brain. This view was endorsed and strengthened by Papez's (1937) pioneering theoretical work in which he described a circuit comprising the hypothalamus, cingulate cortex, hippocampal formation, and their interconnections as forming the anatomical basis of the emotions. McLean (1949) later amplified this view and proposed his concept of the triune brain, with emotions controlled subcortically by the limbic system. This view of the anatomical basis of emotion has had an enormous impact in guiding research on the biology of emotion. Experiments performed within this tradition have usefully underscored the importance of certain subcortical sites in the regulation of emotional behavior. However, this view has also had the ill-fated effect of turning attention away from the potentially important role of various cortical regions in the regulation of emotional behavior. We now know that anterior cortical regions, possibly as a function of their connections with subcortical structures, play an important role in the control of emotions (see the review by Kolb & Taylor, 1990). From the very earliest observations on the role of the neocortex in emotion, important functional differences between the two hemispheres of the brain have been noted. This paper will present an overview of theory and research in this emerging area and summarize some of the implications of this work for understanding temperament, personality, and psychopathology.

### ON THE DIFFERENTIATED NATURE OF EMOTION

Many different behavioral and mental processes contribute to emotion. Sensory and perceptual processes are required to detect emotionally provocative stimuli, cognitive processes are often needed to appraise incoming stimuli, memory functions are sometimes invoked in the generation of emotional responses, and action often accompanies an emotion, functioning to either amplify or attenuate the response. Research on cerebral laterality and emotion has frequently been interpreted to be inconsistent, in part, because of the failure to differentiate among different subcomponents of emotion. It is clear from available research that the hemispheric substrates of the perception of emotional information are different from those associated with the generation of emotional responses (i.e., the experience and expression of emotion) (see Davidson, 1984, in press; Davidson & Tomarken, 1989, for reviews). This paper will focus on the hemispheric substrates of the experience and expression of emotion.

### EFFECTS OF UNILATERAL CORTICAL LESIONS ON EMOTIONAL BEHAVIOR: CLINICAL CLUES

The earliest suggestions that the left and right cerebral cortex contribute differently to the regulation of emotion came from observations on the effects of unilateral cortical lesions on emotional behavior (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 compared with comparable damage to the right hemisphere (e.g., Goldstein, 1939). More recent observations have confirmed and extended these early observations (Gainotti, 1972; Sackeim et al., 1982). Of particular importance to the research summarized in this article are studies by Robinson and his colleagues (e.g., Robinson, Kubos, Starr, Rao, & Price, 1984). These investigators have reported that it is damage specifically to the left frontal lobe that results in depressive symptomatology. Among patients with left-hemisphere lesions, they found that the closer the lesion to the frontal pole (assessed on the basis of computed tomographic scan evidence), the more severe the depressive symptomatology. Patients who developed mania subse-

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quent to brain injury were much more likely to have sustained damage to the right hemisphere, sparing the left.

The studies of affective changes in patients with unilateral brain injury suggest that the left frontal region is particularly important for certain forms of positive affect and when this region is damaged, depression is a likely consequence. I have conceptualized the frontal asymmetry as reflecting specialized systems for approach and withdrawal behavior, with the left frontal region specialized for the former and the right frontal region specialized for the latter. Following a brief description of the electrophysiological methods used, data will be presented which demonstrate that systematic changes in activation asymmetry in anterior cortical regions occur in response to experimentally elicited positive and negative emotion.

## THE USE OF SCALP-RECORDED MEASURES OF BRAIN ELECTRICAL ACTIVITY TO INFER PATTERNS OF REGIONAL CORTICAL ACTIVATION

Several important considerations apply in the choice of methods to study regional brain activity underlying emotion. First, the time resolution of the method must match the time scale of the emotional phenomena under study. Spontaneous manifestations of emotion are often brief and frequently unpredictable. For example, many facial expressions of emotion are present for as little as 1 to 2 s, and they can occur at different times for different subjects in response to the same emotionally provocative stimulus. An ideal method of assessing regional brain activity would be one capable of capturing such brief periods marked by specific expressive signs. For other purposes, it is also important to record physiological activity over much longer intervals of time. One of the most exciting new areas in psychophysiological research on emotion is the study 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.

A second important consideration in the choice of methods to assess regional brain activity is that they be relatively noninvasive. More than most manipulations, the experimental arousal of emotion interacts heavily with contextual factors, and its success depends on the maintenance of an appropriate social context. Invasive procedures, such as certain types of positron emission tomography (PET) imaging, are not very conducive to the arousal and maintenance of positive affect. Also, if common procedures are to be used in research with adults and young children, noninvasive methods are a must.

For these various reasons, most of my work has used scalp-recorded measures of brain electrical activity to make inferences about regional cortical activation. The electroencephalogram (EEG) is noninvasive, has a fast time resolution, and can easily be used with persons of all ages. Moreover, it is suitable for studies of episodic emotional events, as well as stable individual differences. Examples of each of these types of research will be presented later.

The principal measure extracted from the EEG in the research I will highlight in this paper is power in the alpha band, which in adults is defined as activity between 8 and 13 Hz. A wealth of evidence indicates that power in this frequency band is inversely related to activation in adults (Shagass, 1972). In the studies I will describe on infants, power in a lower frequency band was the dependent measure since this represents the functional equivalent of adult alpha activity (Davidson & Fox, 1989; Davidson & Tomarken, 1989). The measures of band power are computed from the output of a Fast Fourier Transform, which decomposes the brain activity into its underlying constituent frequencies.

## THE EFFECTS OF SPECIFIC EMOTIONAL AROUSAL ON BRAIN ACTIVITY

In collaborative research with Ekman (Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Ekman, Davidson, & Friesen, 1990), normal subjects were exposed to short film clips designed to elicit happiness/amusement and disgust. We chose these emotions for study because of their association with approach and withdrawal behavior, respectively. During film viewing, we recorded brain electrical activity and unobtrusively videotaped the subjects' facial behavior. The facial behavior was coded with Ekman and Friesen's (1978) Facial Action Coding System. Using this system, we identified the onset and offset times of different facial expressions of emotion. These times were then entered into our computer system so that brain activity coincident with the expressions could be extracted. Special procedures were used to remove muscle and other artifacts from the EEG (see Davidson, 1988). The EEG data revealed greater right-sided anterior activation (both frontal and anterior temporal) during the disgust than happy facial expression conditions. Notably, 100% of the subjects showed the effect in the predicted direction. However, the asymmetry difference between disgust and happy periods was superimposed upon wide-ranging individual differences in the direction and magnitude of asymmetry. As will be described later, these individual differences in asymmetry are relatively stable over time and are associated with different features of dispositional mood and affective reactivity.

With Ekman, I also had the opportunity to compare the brain activity during two types of smiles. One form of smiling includes the contraction of both the zygomatic muscle, which pulls the mouth corners up, and the *orbicularis oculi*, which causes wrinkling in the external canthi (crow's-feet). We have labeled this smile type the Duchenne smile, since it was Duchenne (1862/1990) who first described it in detail and suggested that only this form of smiling was associated with the felt experience of happiness. Other smiles specifically do not include the presence of crow's-feet. Such smiles may be produced in a variety of different situations, and include the masking of negative affect and social signaling in the absence of any felt experience of happiness. Based on our model, we predicted that the Duchenne smiles would be associated with greater left-sided anterior activation compared with other smiles. Measures of frontal and anterior temporal brain activity confirmed this prediction (Ekman et al., 1990). Moreover, only the duration of Duchenne smiles was correlated with self-reports of happiness and amusement; the duration of other smiles was not. A study of 10-month-old infants exposed to episodes of mother and stranger approach also found similar differences in frontal brain asymmetry between Duchenne and other smiles (Fox & Davidson, 1988). In very recent work, Ekman and I (Ekman & Davidson, 1991) had subjects voluntarily produce Duchenne and other smiles and found that they differed significantly in anterior temporal asymmetry in the same direction as was found in the studies examining spontaneous smiling.

We conducted a parallel set of studies with infants to determine at what age differential lateralization for approach- and withdrawal-related emotions emerges (see Davidson & Fox, 1988, for review). In a study with newborn infants (tested within the first 72 hr of life) who were presented with tastes differing in hedonic tone, those tastes associated with facial signs of disgust produced significantly greater right-sided frontal activation compared with a sucrose solution condition, which produced predominantly facial signs of interest (Fox & Davidson, 1986). From these data, it appears that differential anterior lateralization for emotion is present at birth.

## INDIVIDUAL DIFFERENCES IN ASYMMETRIC ANTERIOR ACTIVATION: A BIOLOGICAL SUBSTRATE OF AFFECTIVE STYLE

A number of investigators working in the field of lateralization have underscored the distinction between hemispheric specialization and hemispheric activation (e.g., Levy, 1983). Individual differences in hemispheric activation are superimposed upon relatively invariant patterns of hemispheric specialization. Hemispheric specialization refers to the functional efficiency or capability of a hemispheric region. For example, among right-handed individuals, areas in the left temporal lobe are specialized for certain linguistic processes. However, there are differences among people in the degree to which this region might be tonically activated, and these variations in activation patterns have functional consequences. Most germane to this paper are individual differences in activation asymmetry in anterior cortical regions. We have recently found that baseline electrophysiological measures of frontal and anterior temporal activation asymmetry are relatively stable over time, with test–retest correlations varying between .65 and .75 over a 3-week time interval. Moreover, such measures have excellent internal consistency reliabilities, with alpha coefficients in the .90s (Tomarken, Davidson, Wheeler, & Kinney, in press). In a series of studies in children and adults, we have repeatedly found that baseline frontal asymmetry predicts important qualities of dispositional mood, psychopathology, temperament, reactivity to emotionally provocative events, and other emotion-relevant biological indices. I will briefly summarize key components of this evidence.

In light of the neurological data on the emotional consequences of left anterior lesions, we first studied differences between depressed and nondepressed individuals on EEG measures of frontal asymmetry. We (Schaffer, Davidson, & Saron, 1983) found that subclinically depressed subjects had significantly less left frontal activation compared with their nondepressed counterparts. We have recently observed the same phenomenon in a sample of clinically depressed patients (Henriques & Davidson, 1991). Most important, it appears that the difference between depressed and nondepressed subjects does not depend on the acute symptoms of depression, but rather is a trait difference between the groups, since remitted depressives who are currently normothymic also exhibit hypoactivation in the left frontal region (Henriques & Davidson, 1990).

We have also studied individual differences in anterior asymmetry in normal subjects. As part of a large study, we tested approximately 100 individuals on two occasions, separated by an interval of 3 weeks. With such a large initial sample, we could identify subgroups of subjects with extreme left frontal activation and extreme right frontal activation on both occasions and then compare them on a number of psychological and biological characteristics. We found that the left frontal subjects reported more positive and less negative dispositional affect compared with their right frontally activated counterparts (Tomarken, Davidson, Wheeler, & Doss, in press).

In three independent studies (Tomarken, Davidson, & Henriques, 1990; Wheeler, Davidson, & Tomarken, 1991), we have also found that subjects with greater baseline right frontal activation report more intense negative affect in response to film clips designed to elicit such emotion compared with subjects showing greater baseline left frontal activation. Subjects with greater baseline left frontal activation tend to report more positive affect in response to positive film clips compared with right frontally activated subjects.

As part of one of the studies referred to above, we collected blood samples from the subjects in the left and right extreme frontal asymmetry groups and assayed the samples for a number of immune measures (Kang et al., in press). There were three converging lines of evidence which led us to hypothesize possible differences between the groups in immune function. First, a number of reports have indicated that certain subgroups of depressives have compromised immune function (e.g., Schleifer, Keller, Bond, Cohen, & Stein, 1989). Given the findings indicating differences between depressed and nondepressed individuals in frontal activation asymmetry, the finding of decreased immunocompetence among depressives suggested a relation between relative right-sided frontal activation and lowered immune function. Second, several recent studies in which the investigators examined the effects of unilateral cortical lesions on immune function in animals have shown that left-sided lesions result in a much more pronounced impairment in immune function compared with lesions of the right neocortex (e.g., Renoux, Biziere, Renoux, Guillaumin, & Degenne, 1983). Finally, Geschwind's theory (Geschwind & Galaburda, 1985) argued for a strong relation between laterality and immunity based on common influences during embryogenesis. Geschwind proposed that testosterone is the common factor influencing both cerebral asymmetry and immunity. Testosterone delays the development of the left hemisphere and also retards the growth of the thymus.

When we compared extreme right and left frontally activated subjects (Kang et al., in press), we found that the right-activated group had significantly lower natural killer (NK) cell activity compared with the left-activated subjects. NK activity is one of the measures which best differentiate between depressives and controls and between mice with left versus right neocortical lesions.

In recent work, we have determined that individual differences in frontal activation asymmetry are present within the first year of life (Davidson & Fox, 1989). Earlier, I described a study on the effects of hedonically positive and negative tastes on newborn asymmetry. That study was not designed to examine individual differences. In this more recent work, we assessed whether individual differences in baseline measures of frontal asymmetry predicted an infant's response to a subsequent affective challenge. Among 10-month-old infants, those who cried in response to 1 min of maternal separation had greater right-sided frontal activation during a prior baseline measure (obtained about 30 min before exposure to maternal separation) compared with infants who showed no evidence of crying within the 1-min period. We found no differences in facial signs of positive or negative emotions assessed during the baseline period between babies who subsequently went on to cry and those who did not. Thus, baseline frontal asymmetry predicted reactivity to a subsequent stressful event independent of concurrent mood.

These findings suggested to us that individual differences in frontal asymmetry may be related to early childhood temperament. We are currently in the midst of conducting a longitudinal study of three groups of children. The inhibited group is characterized as shy, wary, and reticent to approach novel objects and people. The uninhibited group is very outgoing and sociable. We have also included a middle group who display intermediate values on the measures used to classify the two extreme groups. The children were first selected on the basis of behavioral measures during a peer play session at 30 months of age (based on the procedures of Kagan, Reznick, & Snidman, 1988). There are approximately 25 children per group. We assessed baseline measures of regional cortical activation at 38 months of age using our quantitative electrophysiological procedures and found that the inhibited children showed significantly less left-sided frontal activation compared with the uninhibited children (Davidson, Finman, Straus, & Kagan, 1991). The middle group fell, predictably, in between. These findings are the first to show that frontal asymmetry is directly related to an important form of childhood temperament. The disposition to approach or not approach novel and unfamiliar objects and people varies greatly among young children. This is among the most stable temperament constructs yet investigated (Reznick et al., 1986) and shows a substantial heritable influence (Matheny, 1989). The pattern of left frontal hypoactivation displayed by the inhibited children is similar to that observed in adult depressives. In this light, it is interesting to note that in a study comparing the offspring of depressed patients and healthy controls, it was found that the incidence of childhood inhibition was significantly higher among offspring of depressives (Kochanska, 1991).

## SUMMARY AND CONCLUSIONS

This paper presented a brief overview of recent research on anterior asymmetries associated with emotion, affective style, 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. Data were presented which indicated that the experimental arousal of certain positive and negative emotions is accompanied by phasic shifts in activation in the left and right frontal regions. These state effects are present in the newborn period. I argued that such phasic changes in activation asymmetry are superimposed upon more tonic trait differences among subjects. These individual differences in baseline anterior asymmetry are related to dispositional mood, reactivity to emotionally provocative events, psychopathology, immune function, and temperament. It will be important for future research to characterize both the proximal and the distal causes of this anterior asymmetry. The proximal causes will necessarily require the examination of subcortical and neurochemical contributions. Such studies must be conducted either with animals or in humans using more invasive methods to make inferences about regional brain function (e.g., PET imaging can provide detailed information on metabolic and neurochemical activity throughout the brain). Distal causes will inevitably involve some combination of heritable and early environmental factors. The next decade of research on the hemispheric substrates of emotion should be even more exciting than the previous one has been.

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