

Chapter 6

Neuropsychological Perspectives on Affective Styles and Their Cognitive Consequences

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INTRODUCTION

Among the most striking features of human emotion is the variability that is apparent across individuals in the quality and intensity of dispositional mood and emotional reactions to similar incentives and challenges. Some people appear very resilient in the face of life's slings and arrows, while others decompensate quickly. Certain individuals show a dispositional tendency toward positive affect and success, while others are more prone to negative affect and failure. The broad range of differences in these varied affective phenomena has been referred to as "affective style" (Davidson, 1992; 1998). Differences among people in affective style appear to be associated with temperament (Kagan, Reznick & Snidman, 1988), personality (Gross, Sutton & Ketelaar, in press) and vulnerability to psychopathology (Meehl, 1975). Moreover, such differences are not a unique human attribute, but appear to be present in a number of different species (e.g. Davidson, Kalin & Shelton, 1993; Kalin 1993; Kalin, et al., 1998).

In the next section of this chapter, conceptual distinctions among the various components of affective style will be introduced and methodological challenges to their study will be highlighted. The third section will present a brief overview of the anatomy of two basic motivational/emotional systems—the approach and

withdrawal systems. The fourth section will consider individual differences in these basic systems, indicate how such differences might be studied and discuss the behavioral consequences of such individual differences. Finally, the last section will consider some of the implications of this perspective for the assessment and treatment of disorders of affect, and for plasticity.

THE CONSTITUENTS OF AFFECTIVE STYLE

Many phenomena are subsumed under the rubric of affective style. A concept featured in many discussions of affective development, affective disorders and personality is "emotion regulation" (Thompson, 1994). Emotion regulation refers to a broad constellation of processes that serve to either amplify, attenuate or maintain the strength of emotional reactions. Included among these processes are certain features of attention which regulate the extent to which an organism can be distracted from a potentially aversive stimulus (Derryberry & Reed, 1996) and the capacity for self-generated imagery to replace emotions that are unwanted with more desirable imagery scripts. Emotion regulation can be both automatic and controlled. Automatic emotion regulation may result from the progressive automatization of processes that initially were voluntary and controlled and have evolved to become more automatic with practice. We hold the view that regulatory processes are an intrinsic part of emotional behavior, and rarely does an emotion get generated in the absence of recruiting associated regulatory processes. For this reason, it is often conceptually difficult to distinguish sharply between where an emotion ends and regulation begins. Even more problematic is the methodological challenge of operationalizing these different components in the stream of affective behavior.

When considering the question of individual differences in affective behavior, one must specify the particular response systems in which the individual differences are being explored. It is not necessarily the case that the same pattern of individual differences would be found across response systems. Thus, for example, an individual may have a low threshold for the elicitation of the subjective experience (as reflected in self-reports) of a particular emotion but a relatively high threshold for the elicitation of a particular physiological change. It is important not to assume that individual differences in any parameter of affective responding will necessarily generalize across response systems, within the same emotion. Equally important is the question of whether individual differences associated with the generation of a particular specific emotion will necessarily generalize to other emotions. For example, are those individuals who are behaviorally expressive in response to a fear challenge also likely to show comparably high levels of expressivity in response to positive incentives? While systematic research on this question is still required, initial evidence suggests that at least certain aspects of affective style may be emotion-specific, or at least valence specific (e.g. Wheeler, Davidson & Tomarken, 1993).

In addition to emotion regulation, there are likely also intrinsic differences in

certain components of emotional responding. There are likely individual differences in the *threshold* for eliciting components of a particular emotion, given a stimulus of a certain intensity. Thus, some individuals are likely to produce facial signs of disgust upon presentation of a particular intensity of noxious stimulus, whereas other individuals may require a more intense stimulus for the elicitation of the same response at a comparable intensity. This suggestion implies that dose-response functions may reliably differ across individuals. Unfortunately, systematic studies of this kind have not been performed, in part because of the difficulty of creating stimuli that are graded in intensity and designed to elicit the same emotion. In the olfactory and gustatory modalities, there are possibilities of creating stimuli that differ systematically in the concentration of a disgust-producing component and then obtaining psychophysical threshold functions that would reveal such individual differences. However, the production of such intensity-graded stimuli in other modalities will likely be more complicated, although with the development of large, normatively rated complex stimulus sets, this may be possible. An example is the *International Affective Picture System* (Lang, Bradley & Cuthbert, 1995) developed by Peter Lang and his colleagues. This set includes a large number of visual stimuli that have been rated on valence and arousal dimensions and that comprise locations throughout this two-dimensional space. The density of stimulus exemplars at all levels within this space allow for the possibility of selecting stimuli that are graded in intensity for the sort of dose-response studies described above.

There are also likely to be individual differences in the *peak* or *amplitude* of the response. Upon presentation of a series of graded stimuli that differ in intensity, the maximum amplitude in a certain system (e.g. intensity of a facial contraction; change in heart rate, etc.) is likely to differ systematically across subjects. Some individuals will respond with a larger amplitude peak compared with others. Again, such individual differences may well be quite specific to particular systems and will not necessarily generalize across systems, even within the same emotion. Thus, the individual who is in the tail of the distribution in her heart rate response to a fearful stimulus will not necessarily be in the tail of the distribution in her facial response.

Another parameter that is likely to differ systematically across individuals is the *rise time to peak*. Some individuals will rise quickly in a certain response system, while others will rise more slowly. There may be an association between the peak of the response and the rise time to the peak within certain systems for particular emotions. Thus, it may be the case that, for anger-related emotion, those individuals with higher peak vocal responses also show a faster rise time, but to the best of my knowledge, there are no systematic data related to such differences.

Finally, another component of intrinsic differences across individuals is the *recovery time*. Following perturbation in a particular system, some individuals recover quickly and others recover slowly. For example, following a fear-provoking encounter, some individuals show a persisting heart rate elevation that might last for minutes, while other individuals show a comparable peak and rise

time but recover much more quickly. Of course, as with other parameters, there are likely to be differences in recovery time across different response systems. Some individuals may recover rapidly in their expressive behavior, while recovering slowly in certain autonomic channels. The potential significance of such dissociations has not been systematically examined.

The specific parameters of individual differences that are delineated above describe *affective chronometry*—the temporal dynamics of affective responding. Very little is known about the factors that govern these individual differences and the extent to which such differences are specific to particular emotion response systems or generalize across emotions (e.g. is the heart rate recovery following fear similar to that following sadness?). Moreover, the general issue of the extent to which these different parameters that have been identified are orthogonal or correlated features of emotional responding is an empirical question that has yet to be answered. For reasons that I hope to make clear below, affective chronometry is a particularly important feature of affective style and is likely to play a key role in determining vulnerability and resilience. It is also a feature of affective style that is methodologically tractable and can yield to experimental study of its neural substrates.

We also hold that affective style is critical in understanding the continuity between normal and abnormal functioning and in the prediction of psychopathology and the delineation of vulnerability. On the opposite side of the spectrum, such individual differences in affective style will also feature centrally in any comprehensive theory of resilience. The fact that some individuals reside “off the diagonal” and appear to maintain very high levels of psychological well-being despite their exposure to objective life adversity is likely related to their affective style (Ryff & Singer, 1998). Some of these implications will be discussed at the end of this article.

We first consider some of the neural substrates of two fundamental emotion systems. This provides the foundation for a consideration of individual differences in these systems and the neural circuitry responsible for such differences.

THE ANATOMY OF APPROACH AND WITHDRAWAL

Although the focus of my empirical research has been on measures of prefrontal brain activity, it must be emphasized at the outset that the circuit instantiating emotion in the human brain is complex and involves a number of interrelated structures. Preciously few empirical studies using modern neuroimaging procedures that afford a high degree of spatial resolution have yet been performed (see George et al., 1995; Paradiso et al., 1997, for examples). Therefore, hypotheses about the set of structures that participate in the production of emotion must necessarily be speculative and based to a large extent on the information available from the animal literature (e.g. LeDoux, 1987) and from theoretical accounts of the processes involved in human emotion.

Based upon the available strands of theory and evidence, numerous scientists

have proposed two basic circuits, each mediating different forms of motivation and emotion (see e.g. Gray, in press; Lang, Bradley & Cuthbert, 1990; Davidson, 1995). The approach system facilitates appetitive behavior and generates certain types of positive affect that are approach-related, e.g. enthusiasm, pride, etc. (for review, see Depue & Collins, in press). This form of positive affect is usually generated in the context of moving toward a desired goal (for theoretical accounts of emotion that place a premium on goal states, see Lazarus, 1991; Stein & Trabasso, 1992). The representation of a goal state in working memory is hypothesized to be implemented in dorsolateral prefrontal cortex. The medial prefrontal cortex seems to play an important role in maintaining representations of behavioral-reinforcement contingencies in working memory (Thorpe, Rolls & Maddison, 1983). In addition, output from the medial prefrontal cortex to nucleus accumbens (NA) neurons modulates the transfer of motivationally-relevant information through the NA (Kalivas, Churchill & Klitenick, 1993). The basal ganglia are hypothesized to be involved in the expression of the abstract goal in action plans and in the anticipation of reward (Schultz et al., 1995a,b). The NA, particularly the caudomedial shell region of the NA, is a major convergence zone for motivationally relevant information from a myriad of limbic structures. Cells in this region of the NA increase their firing rate during reward expectation (see Schultz et al., 1995a). There are likely other structures involved in this circuit which depend upon a number of factors, including the nature of the stimuli signaling appetitive information, the extent to which the behavioral-reinforcement contingency is novel or over-learned, and the nature of the anticipated behavioral response.

In a very recent study using PET with ^{18}F -labeled deoxyglucose (FDG), we (Sutton et al., 1997) presented aversive or appetitive pictures during the FDG uptake procedure in separate sessions. We found significant left-sided metabolic increases during the appetitive condition in inferior prefrontal cortex, nucleus accumbens and superior prefrontal, premotor and motor regions. The significant left-sided focus of these metabolic increases was confirmed by formally testing the condition \times hemisphere interactions for these regions. Similar findings have recently been reported by Thut et al. (1997) in response to monetary reward. These data imply that, at least in humans, the circuitry for appetitive (and aversive) emotion is lateralized. Such a functional neuroanatomical arrangement may be advantageous in helping the brain to compute affective value (for additional discussion of this issue, see Davidson, 1998).

It should be noted that the activation of this approach system is hypothesized to be associated with one particular form of positive affect and not all forms of such emotion. It is specifically predicted to be associated with *pre-goal attainment positive affect*, that form of positive affect that is elicited as an organism moves closer toward an appetitive goal. *Post-goal attainment positive affect* represents another form of positive emotion that is not expected to be associated with activation of this circuit (for a more extended discussion of this distinction, see Davidson, 1994). This latter type of positive affect may be phenomenologically experienced as contentment or joy (although conventional emotional terms ap-

pear inadequate in capturing these hypothesized differences) and is expected to occur when the prefrontal cortex goes off-line after a desired goal has been achieved. Cells in the NA have also been shown to decrease their firing rate during post-goal consummatory behavior (e.g. Henriksen & Giacchino, 1993).

Lawful individual differences can enter into many different stages of the approach system. Such individual differences and their role in modulating vulnerability to psychopathology will be considered in detail below. For the moment, it is important to underscore two issues. One is that there are individual differences in the tonic level of activation of the approach system which alters an individual's propensity to experience approach-related positive affect. Second, there are likely to be individual differences in the capacity to shift between pre- and post-goal attainment positive affect and in the ratio between these two forms of positive affect. Upon reaching a desired goal, some individuals will immediately replace the just-achieved goal with a new desired goal, and so will have little opportunity to experience post-goal attainment positive affect, or contentment. There may be an optimal balance between these two forms of positive affect, although this issue has never been studied.

There appears to be a second system concerned with the neural implementation of withdrawal. This system facilitates the withdrawal of an individual from sources of aversive stimulation and generates certain forms of negative affect that are withdrawal-related. Both fear and disgust are associated with increasing the distance between the organism and a source of aversive stimulation. From invasive animal studies and human neuroimaging studies, it appears that the amygdala is critically involved in this system (e.g. LeDoux, 1987). Using functional magnetic resonance imaging (fMRI), we have recently demonstrated for the first time activation in the human amygdala in response to aversive pictures, compared with neutral control pictures (Irwin et al., 1996). In addition, the temporal polar region also appears to be activated during withdrawal-related emotion (e.g. Reiman et al., 1989; but see Drevets et al., 1992). These effects, at least in humans, appear to be more pronounced on the right side of the brain (for reviews, see Davidson, 1992, 1993). In the human PET and electrophysiological studies, the right frontal region is also activated during withdrawal-related negative affective states (e.g. Davidson et al., 1990b). In the recent FDG-PET study from our laboratory mentioned above (Sutton et al., 1997), we observed increased glucose metabolism in response to aversive pictures (compared with appetitive pictures) in the right prefrontal cortex (Brodmann's area 9) and amygdala. In addition to the prefrontal and temporal polar cortical regions and the amygdala, it is also likely that the basal ganglia and hypothalamus are involved in the motor and autonomic components, respectively, of withdrawal-related negative affect (see Smith, De Vita & Astley, 1990).

The nature of the relation between these two hypothesized affect systems also remains to be delineated. The emotion literature is replete with different proposals regarding the interrelations among different forms of positive and negative

affect. Some theorists have proposed a single bivalent dimension that ranges from unpleasant to pleasant affect, with a second dimension that reflects arousal (e.g. Russell, 1980). Other theorists have suggested that affect space is best described by two orthogonal positive and negative dimensions (e.g. Watson & Tellegen, 1985; Cacioppo & Bernston, 1994). Still other workers have suggested that the degree of orthogonality between positive and negative affect depends upon the temporal frame of analysis (Diener & Emmons, 1984). This formulation holds that when assessed in the moment, positive and negative affect are reciprocally related, but when examined over a longer time frame (e.g. dispositional affect), they are orthogonal. It must be emphasized that these analyses of the relation between positive and negative affect are all based exclusively upon measures of self-report, and therefore their generalizability to other measures of affect are uncertain. However, based upon new data from our laboratory showing reciprocal relations between metabolic activity in the left prefrontal cortex and the amygdala (Davidson et al., in preparation), we believe that one function of positive affect is to inhibit concurrent negative affect. It seems likely that the presence of negative affect would interfere with the generation of pre-goal attainment positive affect and with the production of approach behavior. It would therefore be adaptive for negative affect to be inhibited during the generation of certain forms of positive affect. Of course, the time course of this hypothesized inhibition and the boundary conditions for its presence remain to be elucidated in future research.

INDIVIDUAL DIFFERENCES IN ASYMMETRIC PREFRONTAL ACTIVATION: WHAT DO THEY REFLECT?

This section will present a brief overview of recent work from my laboratory that was designed to examine individual differences in measures of prefrontal activation and their relation to different aspects of emotion, affective style and related biological constructs. These findings will be used to address the question of what underlying constituents of affective style such individual differences in prefrontal activation actually reflect.

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

imposed upon more tonic individual differences in the direction and absolute magnitude of asymmetry (Davidson & Tomarken, 1989).

During our initial explorations of this phenomenon, we needed to determine whether baseline electrophysiological measures of prefrontal asymmetry were reliable and stable over time and thus could be used as a trait-like measure. Tomarken et al. (1992) recorded baseline brain electrical activity from 90 normal subjects on two occasions, separated by approximately 3 weeks. At each testing session, brain activity was recorded during eight 1-minute trials, four eyes open and four eyes closed, presented in counterbalanced order. The data were visually scored to remove artifacts and then Fourier-transformed. Our focus was on power in the alpha band (8–13 Hz), although we extracted power in all frequency bands (for a discussion of power in different frequency bands and their relation to activation, see Davidson et al., 1990a). Using the asymmetry measures derived from each of the eight 1-minute trials as the data, we computed coefficient alpha as a measure of internal consistency reliability, separately for each session. The coefficient alphas were quite high, with all values exceeding 0.85, indicating that the electrophysiological measures of asymmetric activation indeed showed excellent internal consistency reliability. The test-retest reliability was adequate, with intraclass correlations ranging from 0.65 to 0.75, depending upon the specific sites and methods of analysis. The major finding of import from this study was the demonstration that measures of activation asymmetry based upon power in the alpha band from prefrontal scalp electrodes showed both high internal consistency reliability and acceptable test-retest reliability to be considered a trait-like index.

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

On the basis of our prior data and theory, we reasoned that extreme left and extreme right frontally activated subjects would show systematic differences in dispositional positive and negative affect. We administered the trait version of the Positive and Negative Affect Scales (PANAS; Watson, Clark & Tellegen, 1988) to examine this question and found that the left-frontally activated subjects reported more positive and less negative dispositional affect than their right-frontally activated counterparts (Tomarken et al., 1992; see Figure 6.1). More recently, with Sutton (Sutton & Davidson, 1997), we showed that scores on a self-report measure designed to operationalize Gray's concepts of Behavioral Inhibition and Behavioral Activation (the BIS-BAS scales; Carver & White, 1994) were even more strongly predicted by electrophysiological measures of prefrontal asymmetry than were scores on the PANAS scales (see Figure 6.2). Subjects with greater left-sided prefrontal activation reported more relative BAS

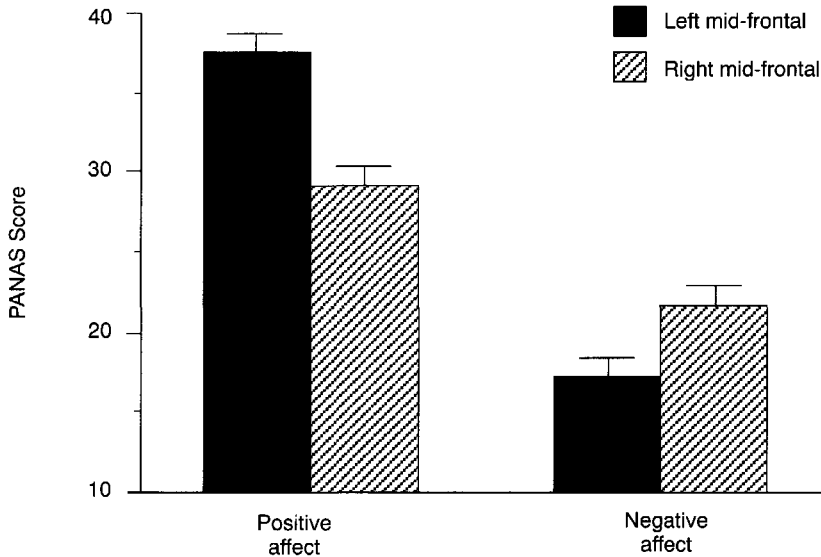


Figure 6.1 Dispositional positive affect (from scores on the PANAS-General Positive Affect Scale) in subjects who were classified as extreme and stable left-frontally active ($n = 14$) and extreme and stable right-frontally active ($n = 13$) on the basis of electrophysiological measures of baseline activation asymmetries on two occasions separated by three weeks. Reproduced from Tomarken et al. (1992), with permission

to BIS activity, compared with subjects exhibiting more right-sided prefrontal activation. Importantly, in each of these studies, measures of asymmetry from posterior scalp regions derived from the identical points in time showed no relation with the affect variables. In the Sutton & Davidson (1997) study, where we had a sufficiently large sample size, we tested the significance of the difference in the magnitude of correlation between measures of activation asymmetry in anterior and posterior regions and the BAS-BIS scores. We found that the prefrontal asymmetry measures were significantly more highly correlated with the affect measures than the measures of posterior asymmetry from the identical periods, underscoring the specificity of this relation to the anterior scalp region.

We also hypothesized that our measures of prefrontal asymmetry would predict reactivity to experimental elicitors of emotion. The model that we have developed over the past several years (see Davidson, 1992; 1994; 1995 for background) features individual differences in prefrontal activation asymmetry as a reflection of a diathesis which modulates reactivity to emotionally significant events. According to this model, individuals who differ in prefrontal asymmetry should respond differently to an elicitor of positive or negative emotion, even when baseline mood is partialled out. We (Wheeler, Davidson & Tomarken, 1993) performed an experiment to examine this question. We presented short film clips designed to elicit positive or negative emotion. Brain electrical activity

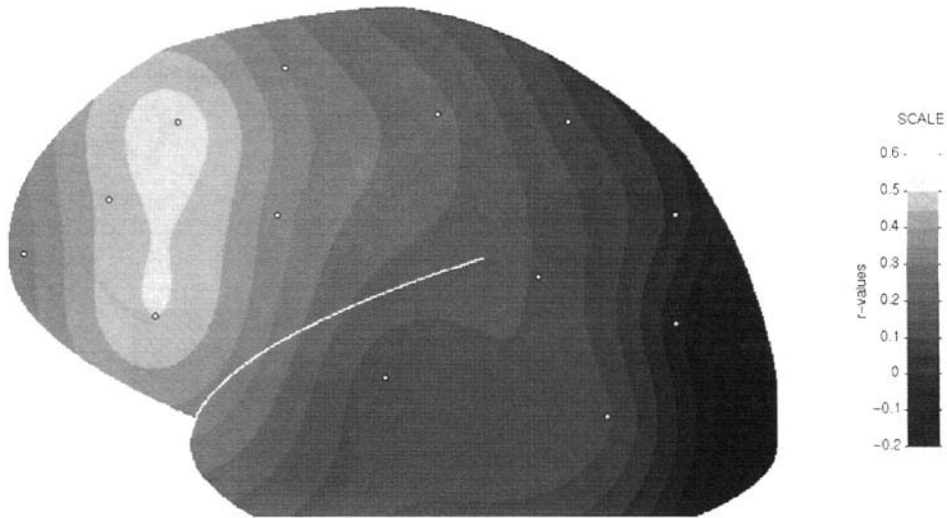


Figure 6.2 Relations between electrophysiological measures of asymmetry and the difference between the standardized score on the Behavioral Activation and Behavioral Inhibition Scales (BAS/BAS scales; Carver & White, 1994), $n = 46$. Electrophysiological data was recorded from each subject on two separate occasions separated by 6 weeks. The BIS/BAS scales were also administered on these two occasions. Data were averaged across the two time periods prior to performing correlations. The topographic map displays the correlations between alpha power asymmetry (log right minus log left alpha power; higher values denote greater relative left-sided activation) and the difference score between the standardized BAS minus BIS scales. After correlations were performed for each homologous region, a spline-interpolated map was created. The top end of the scale denotes positive correlations. The figure indicates that the correlation between the BAS–BIS difference score and the electrophysiology asymmetry score is highly positive in prefrontal scalp regions, denoting that subjects with greater relative left-sided activation report more relative behavioral activation compared with behavioral inhibition tendencies. The relation between asymmetric activation and the BAS–BIS difference is highly specific to the anterior scalp regions, as the correlation drops off rapidly more posteriorly. The correlation in the prefrontal region is significantly larger than the correlation in the parieto-occipital region. Reproduced from Sutton & Davidson (1997), with permission

was recorded prior to the presentation of the film clips. Just after the clips were presented, subjects were asked to rate their emotional experience during the preceding film clip. In addition, subjects completed scales that were designed to reflect their mood at baseline. We found that individual differences in prefrontal asymmetry predicted the emotional response to the films even after measures of baseline mood were statistically removed. Those individuals with more left-sided prefrontal activation at baseline reported more positive affect to the positive film clips and those with more right-sided prefrontal activation reported more negative affect to the negative film clips. These findings support the idea that individual differences in electrophysiological measures of prefrontal activation asymmetry mark some aspect of vulnerability to positive and negative emotion

elicitors. The fact that such relations were obtained following the statistical removal of baseline mood indicates that any difference between left and right frontally activated subjects in baseline mood cannot account for the prediction of film-elicited emotion effects that were observed.

In a very recent study, we (Davidson et al., in preparation) examined relations between individual differences in prefrontal activation asymmetry and the emotion-modulated startle. In this study, we presented pictures from the *International Affective Picture System* (Lang, Bradley & Cuthbert, 1995) while acoustic startle probes were presented and the EMG-measured blink response from the orbicularis oculi muscle region was recorded (see Sutton et al., 1997 for basic methods). Startle probes were presented both during the 6-second slide exposure as well as 500ms following the offset of the pictures, on separate trials.¹ We interpreted startle magnitude during picture exposure as providing an index related to the peak of emotional response, while startle magnitude following the *offset* of the pictures was taken to reflect the recovery from emotional challenge. Used in this way, startle probe methods can potentially provide new information on the time course of emotional responding. We expected that individual differences during actual picture presentation would be less pronounced than individual differences following picture presentation, since an acute emotional stimulus is likely to pull for a normative response across subjects, yet individuals are likely to differ dramatically in the time to recover. Similarly, we predicted that individual differences in prefrontal asymmetry would account for more variance in predicting magnitude of recovery (i.e. startle magnitude post-stimulus) than in predicting startle magnitude during the stimulus. Our findings were consistent with our predictions and indicated that subjects with greater left-sided prefrontal activation show a smaller blink magnitude following the offset of the negative stimuli, after the variance in blink magnitude *during* the negative stimulus was partialled out. Measures of prefrontal asymmetry did not reliably predict startle magnitude during picture presentation. The findings from this study are consistent with our hypothesis and indicate that individual differences in prefrontal asymmetry are associated with the time course of affective responding, particularly the recovery following emotional challenge.

In addition to the studies described above using self-report and psychophysiological measures of emotion, we have also examined relations between individual differences in electrophysiological measures of prefrontal asymmetry

¹ In this initial study on the recovery function assessed with startle probe measures, we had only a single post-stimulus probe at 500ms following the offset of the picture. Readers may be surprised that the interval between the offset of the picture and the presentation of the probe was so short. However, it should be noted that these emotional pictures are not particularly intense and so the lingering effects of emotion following the presentation of such pictures is likely not to last very long in most individuals. Future studies will probe further out following the offset of the picture. Since at most only a single probe can be presented for each picture, so that habituation effects are minimized, each new probe position requires a substantial increase in the overall number of pictures presented. There is a finite limit to the number of pictures contained in the IAPS. Even more importantly, we have found that it is critical to keep the picture viewing period to well under 1 hour to minimize fatigue and boredom.

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

Recently, in collaboration with Kalin, our laboratory has been studying similar individual differences in scalp-recorded measures of prefrontal activation asymmetry in rhesus monkeys (Davidson, Kalin & Shelton, 1992, 1993). Recently, we (Kalin et al., 1998) acquired measures of brain electrical activity from a large sample of rhesus monkeys ($n = 50$). EEG measures were obtained during periods of manual restraint. A sub-sample of 15 of these monkeys were tested on two occasions four months apart. We found that the test-retest correlation for measures of prefrontal asymmetry was 0.62, suggesting similar stability of this metric in monkey and man. In the group of 50 animals, we also obtained measures of plasma cortisol during the early morning. We hypothesized that if individual differences in prefrontal asymmetry were associated with dispositional affective style, such differences should be correlated with cortisol, since individual differences in baseline cortisol have been related to various aspects of trait-related stressful behavior and psychopathology (see e.g. Gold, Goodwin, & Chrousos, 1988; Tomarken et al., 1996). We found that animals with right-sided prefrontal activation had higher levels of baseline cortisol than their left-frontally activated counterparts (see Figure 6.3). Moreover, when blood samples were collected 2 years following our initial testing, animals classified as showing extreme right-sided prefrontal activation at age 1 year had significantly higher baseline cortisol levels when they were 3 years of age compared with animals who were classified at age 1 year as displaying extreme left-sided prefrontal activation. These findings indicate that individual differences in prefrontal asymmetry are present in non-human primates and that such differences predict biological measures that are related to affective style.

AFFECT-COGNITION INTERACTION: TOP-DOWN INFLUENCES OF PREFRONTAL CORTEX

The prefrontal cortex is uniquely situated, with extensive cortico-cortical connections to posterior perceptual processing regions (e.g. Goldman-Rakic, 1987) and

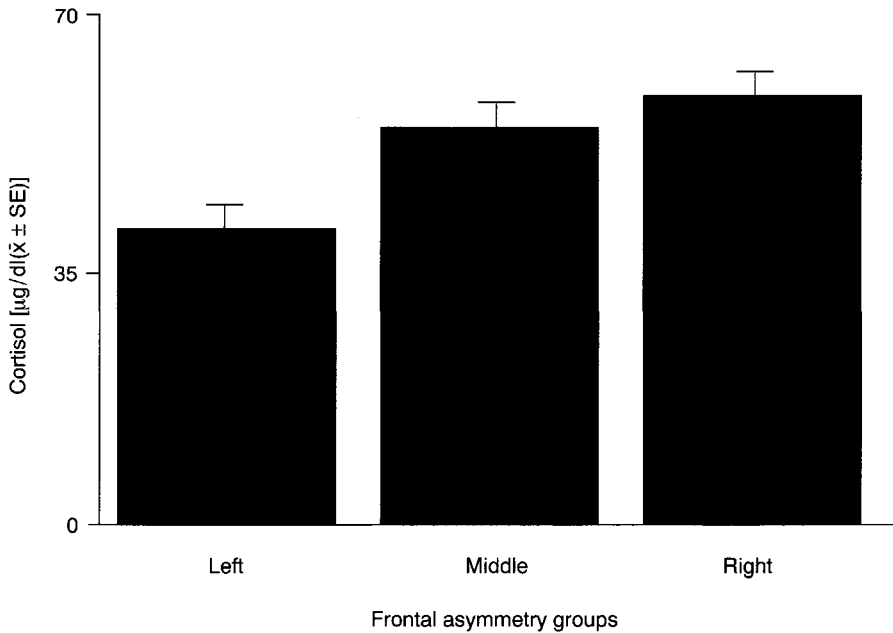


Figure 6.3 Basal morning plasma cortisol from 1 year-old rhesus monkeys classified as left ($n = 12$), middle ($n = 16$) or right ($n = 11$) frontally activated, based upon electrophysiological measurements. Reproduced from Kalin et al. (1998), with permission

extensive connections to limbic structures such as the amygdala (e.g. Amaral et al., 1992). By virtue of its unique pattern of anatomical connectivity, the prefrontal cortex is likely to play an important role in top-down influences on brain regions that are critical components of circuitry required for many complex emotional and cognitive functions. The role of the prefrontal cortex in three aspects of cognition–emotion interaction will be featured in this section. First, the influence of the prefrontal cortex on posterior cortical regions, and the cognitive consequences of such influence, will be described. Second, the role of the prefrontal cortex in biasing preattentive processes will be illustrated with data from a new study. Third, the role of the prefrontal cortex in emotion regulation will be briefly discussed. These three functions of the prefrontal cortex underscore the importance of this structure for both emotion and cognition and highlight its role in understanding the interaction between certain key aspects of thought and feeling.

One function of the cortico–cortical connections from the dorsolateral prefrontal cortex to posterior cortical regions is inhibitory. For example, Knight (1991) reviewed data from his laboratory and others showing sensory gating deficits following damage to the dorsolateral prefrontal cortex. Evoked potentials elicited in response to sensory stimuli are enhanced in patients with prefrontal damage, implying that the prefrontal cortex is exerting top-down

inhibitory control over posterior processing regions. One important implication of this prefrontal inhibitory influence over posterior processing regions is that prefrontal activation asymmetries may be reciprocally related to posterior activation asymmetries (for review, see e.g. Davidson, 1995). A number of studies that have used either electrophysiological or hemodynamic imaging methods have reported findings consistent with this notion (e.g. Davidson, Schaffer & Saron, 1985; Wood, Flowers & Naylor, 1991). For example, in a study examining patterns of EEG activation in response to the presentation of lateralized faces, we observed a reciprocal relation between frontal and parietal activation asymmetry, particularly among depressed subjects. Wood, Flowers & Naylor (1991) have reported a similar pattern of inverse relations between blood flow asymmetry measures derived from anterior and posterior cortical regions.

What are the cognitive consequences of such reciprocal relations between anterior and posterior cortical asymmetry? In several previous studies, we have found that depressed subjects show a pattern of relative right-sided prefrontal activation (caused primarily by decreased left-sided prefrontal activation; Henriques & Davidson, 1990, 1991). We reasoned that such a prefrontal pattern should be associated with less relative right-sided posterior activation. This hypothesis leads to the prediction of performance decrements on cognitive tasks known to require right posterior activation, such as certain measures of visuospatial cognition. Some studies have reported such performance decrements in depressed subjects (e.g. Bruder, 1995; Heller, Etienne & Miller, 1995; Jaeger, Borod & Peselow, 1987). In a recent study, Henriques & Davidson (1997) administered psychometrically-matched verbal (word finding) and spatial (dot localization) tasks known to differentially elicit relative left vs. right-sided posterior EEG activation (Davidson, Chapman, Chapman & Henriques, 1990a) to depressed and non-depressed subjects. As predicted, based upon the model described, depressed subjects showed a specific differential performance deficit, with impairment in the dot localization task compared with controls. Importantly, the groups did not differ in response to the verbal task. Non-depressed subjects showed the expected pattern of EEG changes with task—greater right-sided central and parietal activation during the spatial compared with the verbal task. In contrast, the depressed subjects failed to show any difference in posterior EEG asymmetry between the two tasks. These findings are consistent with the idea that relative left-sided prefrontal hypoactivation among the depressed subjects is associated with relative right-sided posterior hypoactivation, thus resulting in a failure among the depressed subjects to activate the right posterior region in response to the dot localization task.

A variety of evidence implicates the prefrontal cortex in attentional control and vigilance (e.g. Pardo et al., 1990; Posner & Petersen, 1990). Based on the view that the prefrontal cortex plays an important role in directing attention, we recently examined whether individual differences in electrophysiological measures of prefrontal asymmetry predict attentional biases to positive or negative stimuli (Sutton, Davidson & Rogers, 1996). In this study, subjects were first assessed for baseline electrophysiological measures of activation asymmetry on

two occasions separated by 6 weeks. In a third session, held between 4 and 28 months following the EEG sessions, subjects were tested on a simple choice task where two word-pairs were presented simultaneously, with one word pair on the left and the other on the right of a computer monitor. The subject was instructed to choose the word-pair that "went together best". Word-pairs were previously categorized as either negative (e.g. "hurt-cry"), neutral (e.g. "mail-box") or positive (e.g. "happy-glad") on the basis of prior ratings. Word-pairs were matched on the degree of similarity in meaning, as rated in a prior study. One-third of the trials consisted of negative-neutral pairs, one-third of positive-neutral pairs and one-third of negative-positive pairs. We predicted that subjects with greater relative left-sided activation would be biased toward processing the positive word pairs and would therefore select more of the positive word pairs as going together best. Particularly among subjects whose prefrontal EEG asymmetry was stable across testing occasions, those with greater relative left-sided activation selected more of the positive word pairs ($r = 0.40$). These findings suggest that individual differences in prefrontal activation asymmetry bias attention selectively toward positive or negative stimuli in our environment. Such selective attentional biases might act to maintain and preserve the dispositional affective characteristics of individuals who differ in their trait-levels of prefrontal activation asymmetry.

The prefrontal cortex also appears to play an important role in emotion regulation. The component of emotion regulation subserved by the prefrontal cortex that is probably the most well characterized is the inhibition of negative affect. As noted earlier, there are extensive descending connections from the prefrontal cortex to the amygdala (Amaral et al., 1992). The glutamatergic efferents from the prefrontal cortex likely synapse on GABA neurons (Amaral et al., 1992), and thus provide an important inhibitory input to the amygdala. LeDoux and his colleagues (Morgan, Romanski & LeDoux, 1993; but see Gewirtz, Falls & Davis, 1997) demonstrated in rats that lesions of the medial prefrontal cortex dramatically prolong the maintenance of a conditioned aversive response. In other words, animals with medial prefrontal lesions retain aversive associations for a much longer duration of time than normal animals. These findings imply that the prefrontal cortex normally inhibits the amygdala as an active component of extinction. In the absence of this normal inhibition, the amygdala remains unchecked and continues to maintain the learned aversive response.

As noted in Section IV above, we (Davidson et al., in preparation) have recently observed that subjects with greater left-sided prefrontal activation show increased inhibition of startle magnitude following the offset of a negative emotional stimulus. These findings imply that subjects with this pattern of prefrontal activation are able to more rapidly terminate a negative emotional response once it is elicited. New findings using PET from my laboratory indicate that in normal subjects, glucose metabolism in the left medial and the lateral prefrontal cortex is strongly reciprocally associated with glucose metabolic rate in the amygdala (Abercrombie et al., 1996). Thus, subjects with greater left-sided prefrontal

metabolism have lower metabolic activity in their amygdala. These findings are consistent with the lesion study of LeDoux and colleagues and imply that the prefrontal cortex plays an important role in modulating activity in the amygdala. At the same time, the left prefrontal cortex is also likely to play a role in the maintenance of reinforcement-related behavioral approach. Perhaps the damping of negative affect and shortening of its time course facilitates the maintenance of approach-related positive affect.

IMPLICATIONS AND CONCLUSIONS

Earlier in this chapter, the constituents of affective style were described. We considered individual differences in threshold, peak amplitude, rise time to peak, and recovery time. Together, these constitute parameters of affective chronometry and dictate important features of the time course of affective responding. Following a description of the functional neuroanatomy of the approach and withdrawal systems, individual differences in prefrontal activation asymmetry were discussed and their relation to affective style described. The final section considered the role of the prefrontal cortex in the top-down control of affect-cognition interactions. Three aspects of prefrontal involvement in affect-cognition interaction were described: (a) prefrontal inhibition of posterior cortical zones; (b) prefrontal control of affect-relevant attentional processes; and (c) prefrontal inhibition of the amygdala and its role in regulation of negative affect.

The questions that are featured in this chapter are more tractable now than ever before. With the advent of echoplanar methods for rapid functional MR imaging, sufficient data can be collected within individuals to examine functional connections among regions hypothesized to constitute important elements of the approach and withdrawal circuits discussed above. Individual differences in different aspects of these systems can then be studied with greater precision. fMRI methods also lend themselves to address questions related to affective chronometry. In particular, we can calculate the slope of MR signal intensity declines following the offset of an aversive stimulus to provide an index of the rapidity of recovery from activation in select brain regions. PET methods using new radioligands that permit quantification of receptor density for specific neurotransmitters in different brain regions is yielding new insights directly relevant to questions about affective style (see e.g. Farde, Gustavsson & Jönsson, 1997). Trait-like differences in affective style are likely reflected in relatively stable differences in characteristics of the underlying neurochemical systems. Using PET to examine such individual differences promises to provide important syntheses between neurochemical and neuroanatomical approaches to understanding the biological bases of affective style.

Affective neuroscience seeks to understand the underlying proximal neural substrates of elementary constituents of emotional processing (Davidson & Sutton, 1995). In this chapter, I have provided a model of the functional

neuroanatomy of approach and withdrawal motivational/emotional systems and illustrated the many varieties of individual differences that might occur in these systems. Research on prefrontal asymmetries associated with affective style and their cognitive consequences was used to illustrate the potential promise of some initial approaches to the study of these questions. Modern neuroimaging methods used in conjunction with theoretically sophisticated models of emotion and cognition offer great promise in advancing our understanding of the basic mechanisms giving rise to affective style and its cognitive consequences.

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