Regional Brain Activity in Emotion: A Framework for Understanding Cognition in Depression

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A variety of cognitive characteristics have been shown to be associated with depressed moods. We propose that these tendencies are directly related to activity in specific regions of the brain. Using a comprehensive model of brain activity in emotion as a guide, we review the literature on cognitive function in depression and induced sad mood to provide evidence that depressed people are characterised by deficits and biases in performance on cognitive tasks that depend on regions of the brain that are more or less active in depression.

INTRODUCTION

The current Diagnostic and Statistical Manual of Mental Disorders (DSMIV; APA, 1994) identifies cognitive factors (e.g. indecisiveness, difficulties in thinking and concentrating) as fundamental components of depressive episodes and dysthymia. Numerous studies have also identified a variety of other cognitive characteristics associated with depressed moods. These findings have given rise to models of depression that have focused on cognitive factors as important in the aetiology and maintenance of the disorder (e.g. Beck, 1967, 1976; Bower, 1981, 1987; Teasdale, 1988). For the most part, these models have not considered physiological or neuropsychological concomitants of depression.

In a separate literature, converging evidence from a variety of paradigms in neuroscience has shown that depression is characterised by unique

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patterns of brain activity and function. Despite the fact that the same brain regions involved in depression are also fundamental for various aspects of cognition, the implications of these neuropsychological findings for cognitive processing in depression have rarely been explored (cf. George et al., 1994; Rubinow & Post, 1992).

Various brain regions are known to be specialised for particular kinds of cognitive processes. The extent to which a brain region is engaged in or recruited for the performance of a particular task, however, is reflected in the degree to which that region is active. Whereas we tend to think of specialised processes as relatively "hard-wired", the activity of a brain region is a dynamic process that can fluctuate and change. Thus, although a particular region might be specialised for a particular cognitive process, the extent to which it is active can vary (e.g. Levy, Heller, Banich, & Burton, 1983a; Levy & Trevarthen, 1976).

Activity of a brain region has been shown to correlate with performance on cognitive tasks for which that region is specialised. Performance advantages are typically accompanied by relative increases in activity of the specialised region during task performance, as measured by electroencephalographic (EEG) activity in the alpha band (Davidson, Chapman, Chapman, & Henriques, 1990; Doyle, Ornstein, & Galin, 1974; Galin & Ellis, 1975; Galin, Ornstein, Herron, & Johnstone, 1982; Green, Morris, Epstein, West, & Engler, 1992; McKee, Humphrey, & McAdams, 1973; Morgan, MacDonald, & Hilgard, 1974; Ornstein, Johnstone, Herron, & Swencionis, 1980), event-related brain potentials (ERPs; Deecke, Uhl, Spieth, Lang, & Lang, 1987; Galin & Ellis, 1975; Lang, Lang, Goldenberg, Podreka, & Deecke, 1987; Rasmussen, Allen, & Tate, 1977), and blood flow (George et al., 1993; Gur & Reivich, 1980; Lang et al., 1987). These results imply that at one extreme, an informationprocessing deficit could result if a brain region is inadequately activated during performance of a cognitive task for which that region is specialised. At the other extreme, an information-processing superiority could result for a particular task if the brain region specialised for that task is highly active. Moreover, relative activity or inactivity of a particular brain region could be associated with a tendency or bias to process or to avoid processing information in a particular way. It should be noted that measures of brain activity do not always reflect

It should be noted that measures of brain activity do not always reflect cognitive performance in this linear fashion. When examined in the context of task difficulty or repeated practice, better performance on same tasks has been associated with decreased brain activity (for a review, see Galin, Johnstone, & Herron, 1978; see also Haier et al., 1992). These effects have been attributed to various factors, including decreases in the use of nonessential brain areas, changes in cognitive strategies, and changes in task demands. In general, however, relatively greater activity for specialised

brain regions has been found to reflect better performance on the majority of tasks examined.

For the most part, researchers examining the neuropsychology of depression have focused on the relationship of regional brain activity to emotion, not to cognition. Although a few studies have been conducted examining brain activity and a very select subset of cognitive functions, such as attributional style (Davidson, in press), visuospatial abilities (Davidson, Chapman, & Chapman, 1987; George et al., 1994), and facial processing (Deldin, Keller, Gergen, & Miller, submitted), research examining cognition and brain activity in depression is clearly in its infancy. A somewhat larger literature on neuropsychological functioning in affective disorders has floundered in inconsistencies (for a review, see Silberman & Weingartner, 1986). Furthermore, a theoretical formulation explicating the relationship betwen various brain regions and cognition in depression has been lacking.

Models of brain activity in depression have the capacity to provide an explicit framework for the investigation of cognitive function in this disorder. In previous research, we have proposed and researched such a model of brain function during different emotional states (for reviews, see Heller, 1990, 1993a, b; Heller & Nitschke, in press). The model is based on factor analytical studies depicting the psychological structure of emotions as represented along two dimensions—valence (pleasant/unpleasant) and arousal (high/low) (see Fig. 1). Briefly, valence is associated with activity of the anterior regions, such that pleasant valence is linked to greater left than right anterior activity and unpleasant valence to greater right than left anterior activity. The posterior regions are associated with the arousal dimension, with increased right parieto-temporal activity associated with low arousal.

As discussed at length elsewhere, subsequent research has both supported and refined this model (Heller & Nitschke, in press). Numerous studies using a variety of research paradigms have consistently found the anterior regions to be asymmetrically active during valenced states, in the direction predicted (for a review, see Heller, 1990). Other studies have shown that the right parietotemporal region is uniquely involved in various aspects of arousal, including global cortical activity, autonomic activity, anxious arousal, and behavioural arousal (Heller, 1990, 1993b; Heller, Nitschke, Etienne, & Miller, in press; Heller, Nitschke, & Lindsay, 1997).

The value of this model is that it provides a useful framework for predicting how specific patterns of brain activity should be associated with both emotional and cognitive functions. Because brain activity in particular regions should be reflected in performance for the cognitive

VALENCE DIMENSION (Frontal)

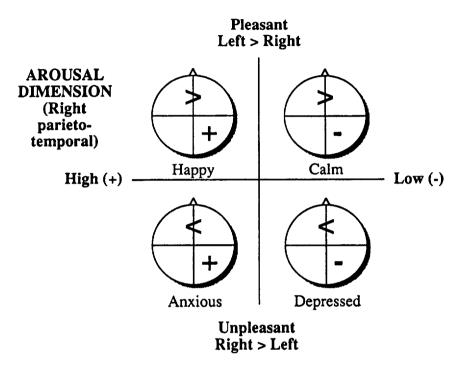


FIG. 1. A neuropsychological model of emotion hypothesising patterns of brain activity during different emotions dependent on relative activity of right posterior and anterior regions. The right posterior region is differentially involved in the arousal dimension (depicted here as the x-axis), whereas the anterior regions are involved in the valence dimension (depicted here as the y-axis). Higher activity of the right posterior region is associated with higher levels of arousal (+), whereas lower activity of this region is associated with lower levels of arousal (-). Higher left compared to right anterior activity is associated with unpleasant valence, whereas higher right compared to left anterior activity is associated with unpleasant valence. The circles symbolise the brain, with the top two quadrants representing the left and right anterior regions and the bottom two quadrants representing the left and right posterior regions. Each circle portrays the pattern of brain activity that would be expected to accompany the emotion stipulated beneath. (Adapted from Heller, 1993b.)

functions specialised to those regions, the model allows us to make explicit predictions about the nature of a wide variety of cognitive functions in depression. The model also allows us to modulate our predictions about cognition when depression is coincident with other emotional states, such as anxiety.

A primary goal of this article is, therefore, to argue that the patterns of brain activity associated with depression are intrinsically related to many of the cognitive characteristics that have been described in depression. Using our model as a guide, we will review the findings for brain activity in depression. Then, we will draw from the literature on cognitive function in depression to provide evidence that depressed people are characterised by deficits in performance on tasks that depend on regions of the brain that are less active in depression. Ultimately, we hope to construct a more comprehensive account of the neuropsychological foundations of cognition in depression than has previously been accomplished. By necessity, many of these associations will be inferential, as there is a limited amount of empirical research linking neurophysiological and cognitive processes. Nonetheless, the time is ripe for the interface of these two areas in depression, especially with the advancing technologies in the field of cognitive neuroscience that make it more feasible to examine brain activity during the performance of relevant cognitive tasks.

BRAIN ACTIVITY IN DEPRESSION

Various methodologies have been used to examine brain activity and function in depression, including neurodynamic techniques, electrocortical measures (EEG, ERPs), and behavioural measures, such as dichotic listening, tachistoscopic presentation, and the Chimeric Faces Test (CFT; Levy, Heller, Banich, & Burton, 1983b) that are believed to index lateralised cognitive processes and biases. Populations have included people with regional brain damage (see Depression and Regional Specialisation of Cognitive Functions section below), people classified as depressed in various ways, and people who have been induced into sad moods. Although studies of clinical depression, psychometrically defined depression, and sad mood will all be reviewed here, it remains to be seen whether they are addressing the same phenomenon. The number of consistent findings across these populations suggests some commonality; on the other hand, some inconsistencies in this literature could be in part due to the heterogeneity of the samples studied.

For the anterior regions, a prominent finding has been asymmetric activity during depressed mood states. In studies of EEG alpha, depression has been associated with less left than right anterior activity (Allen, Iacono, Depue, & Arbisi, 1993; Henriques & Davidson, 1990, 1991; Schaffer, Davidson, & Saron, 1983). Consistent with the EEG findings, numerous positron emission tomography (PET) studies have reported deficiencies in left anterior activity (Baxter et al., 1985, 1989; Bench, Friston, Brown, Frackowiak, & Dolan, 1993; Bench et al., 1992; George et al., 1994; Martinot et al., 1990). However, blood flow studies have also reported

significant (e.g. Baxter et al., 1989) or marginally significant (e.g. Bench et al., 1992) reductions in right anterior brain activity for depressed patients. Taken together, these results suggest that regional asymmetries in anterior activity may be superimposed upon or co-occur with bilateral anterior or global decreases in activity (see Sackeim et al., 1990).

For the posterior regions, we have argued that depression is characterised by deficient activity in the parietotemporal area of the right hemisphere, except when anxiety is comorbid (Heller, Etienne, & Miller, 1995; Heller et al., in press; Heller & Nitschke, in press). In EEG, ERP, and blood flow studies that report positive findings, depression is typically associated with less right posterior activity (Deldin et al., submitted; Flor-Henry, 1979; Henriques & Davidson, 1990; Post et al., 1987; Uytdenhoef et al., 1983). Studies that have directed information to one or the other hemisphere using lateralised paradigms, such as dichotic listening or tachistoscopic presentation, have also found specific deficits for the right hemisphere in depressed people and in induced sad mood (for a review, see Bruder, 1995; see also Banich, Stolar, Heller, & Goldman, 1992; Ladavas, Nicoletti, Umilta, & Rizzolatti, 1984). On the CFT, a free-vision task of face-processing that typically elicits a left hemispatial bias suggesting greater right hemisphere activation, studies have reported smaller left-hemispatial biases for depressed than nondepressed participants for clinical depression (Jaeger, Borod, & Peselow, 1987) and for psychometrically defined depression (Heller et al., 1995; Keller et al., submitted).

In this brief review, we have ignored some of the inconsistencies that have been reported in this literature; for example, the findings reviewed earlier have not always been replicated for depression (e.g. Baxter et al., 1985; Drevets et al., 1992; Nitschke, Heller, Etienne, & Miller, 1995; Tomarken & Davidson, 1994) or sad mood (e.g. George et al., 1995), and other regions of the brain have also been reported as either hyper- or hypoactive in depression (e.g. Sackeim et al., 1990). Elsewhere, we have argued for the importance of comorbidity with anxiety and of subtypes of depression in explaining the reported discrepancies (Heller et al., 1995; Heller & Nitschke, in press). It is also not clear whether the patterns of anterior brain activity associated with depression disappear on remission. Henriques and Davidson (1990) found evidence of similar patterns of brain activity in remitted depressives; however, Baxter et al. (1989) reported an increase of left (but not right) anterior activity following successful treatment. Despite these complicating factors, there is nonetheless compelling evidence that in many cases depression is associated with reductions or deficiencies in left anterior and right posterior activity. It now remains to examine the cognitive specialisations of the areas implicated in depression.

DEPRESSION AND REGIONAL SPECIALISATION OF COGNITIVE FUNCTIONS

Anterior Regions

Emotional Valence. There is a preponderance of evidence from a variety of research paradigms that anterior asymmetries are associated with valence (for a review, see Heller, 1990). More left than right anterior activity has been consistently associated with pleasant affect and happy mood states, whereas the converse has been found for unpleasant affect and sad mood states. This pattern has emerged in studies of brain-damaged populations (Gainotti, 1972; Robinson, Kubos, Starr, Rao, & Price, 1984; Sackeim et al., 1982), patients undergoing the WADA test (Ahern et al., 1994; Lee, Loring, Meador, Flanigin, & Brooks, 1988; Lee, Loring, Meador, & Brooks, 1990), right versus left hemisphere ECT (Cohen, Penick, & Tarter, 1974; Decina, Sackeim, Prohovnik, Portnoy, & Malitz, 1985), EEG studies following mood induction (Davidson, Schwartz, Saron, Bennett, & Goleman, 1979; Davidson, Schaffer, & Saron, 1985), and EEG research on facial expressions of emotion (Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Ekman, Davidson, & Friesen, 1990). Moreover, the same pattern of anterior EEG asymmetries has been associated with pleasant and unpleasant affect (Tomarken, Davidson, Wheeler, & Doss, 1992) as well as with pleasant and unpleasant affect in response to emotion elicitors such as film clips (Tomarken, Davidson, & Henriques, 1990; Wheeler, Davidson, & Tomarken, 1993).

The extensive literature on cognitive biases in depression is very pertinent to this relationship between anterior asymmetries and emotional valence. Attention, memory, and judgement biases in depression have been reported by numerous researchers (for reviews, see Gotlib & MacLeod, in press; Gotlib, Gilboa, & Kaplan, in press). Gotlib and colleagues concluded that depressed people attend more strongly to unpleasant than to pleasant stimuli, fail to avoid unpleasant stimuli (whereas nondepressed people avoid such stimuli), show better recall of unpleasant than pleasant information, and make more negative judgements about hypothetical and actual life events. Several studies have also shown that cognitive biases are not present in remitted depressives (e.g. Gotlib & Cane, 1987; McCabe & Gotlib, 1993), consistent with the PET findings of increased left anterior activity following successful treatment of depression (Baxter et al., 1989).

The findings are perhaps most salient for memory biases, especially on explicit memory tasks (for reviews, see Gotlib et al., in press; Mineka & Sutton, 1992). Although studies on implicit memory tasks that depend primarily on perceptual features have found no evidence for a memory

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bias (Denny & Hunt, 1992; Watkins, Mathews, Williamson, & Fuller, 1992), a recent study using a conceptually driven implicit memory task did find a memory bias for depression despite finding no implicit memory deficit (Watkins, Vache, Verney, Mathews, & Muller, 1996). This set of cognitive biases ties in neatly with the association of less left than right anterior activity for unpleasant emotional valence as indicated by our model.

Executive Functions. The anterior regions of the brain have also been shown to be specialised for a class of behaviours that have, rather loosely. been referred to as "executive functions". These behaviours include judgement, planning, abstract thinking, metacognition (i.e. "thinking about thinking"), cognitive flexibility (i.e. flexibility in strategy use), ability to generate alternate strategies, verbal fluency, initiative, and motivation. Damage to this area of the brain does not affect the knowledge base of the person; rather, it affects the degree to which that stored information can be accessed, strategically deployed, and adaptively applied to routine or novel situations (e.g. Stuss & Benson, 1986). Deficits are observed in sequencing tasks (Petridies & Milner, 1982), in the ability to shift response set and modify strategies in task performance (e.g. Cicerone, Lazar, & Shapiro, 1983), in the evaluation of a situation and the use of cues and extra information in the environment to guide behaviour (Alivisatos & Milner, 1989), and in the ability to monitor behaviour or performance accurately (e.g. Luria, 1966). Furthermore, the frontal lobes have been described as selectively involved in effortful (i.e. controlled) but not automatic processing (Banich, 1997).

In addition, there are differences between the left and right anterior regions. For example, the left is more involved in verbal fluency and sequencing, whereas the right is more involved in design fluency and recency judgements (for a review, see Banich, 1997). However, Banich also reviews evidence that many of the deficits observed for executive functions occur after damage to either side of the brain.

A selected review of the literature suggests that depressed people display deficits in many of the cognitive activities we have described as dependent on anterior functions. Various studies have indicated that depressed people are poor problem-solvers (for reviews, see Hartlage, Alloy, Vazquez, & Dykman, 1993; see also Klein, Fencil-Morse, & Seligman, 1976; Klein & Seligman, 1976; Price, Tryon, & Raps, 1978). There is also substantial evidence of deficits for other types of effortful processing, such as explicit memory, general learning, and reading (for a review, see Hartlage et al., 1993). In contrast, Hartlage and colleagues reviewed the evidence indicating that depression is not associated with tasks reliant on automatic processing. The distinction between effortful and automatic processing

has received the most focus in studies of memory, for which depressed people have predominantly been found to have explicit but not implicit memory deficits (for reviews, see Johnson & Magaro, 1987; Roediger & McDermott, 1992; see also Watkins et al., 1996). Similarly, depressed children performed more poorly than nondepressed children on an effortful memory task (the Children's Auditory Verbal Learning Test), but not on an automatic memory task (Lauer et al., 1994).

Other types of anterior brain function have also been found to be compromised in depression. On the Halstead-Reitan Categories Test, typically considered to measure anterior brain functioning, depressed patients performed more poorly than controls, a deficit which improved on remission (Savard, Rey, & Post, 1980). Roth and Rehm (1980) found that depressed patients were less accurate than nondepressed patients in their estimation of the amount of positive and negative feedback received, a deficit that was not due to memory differences for personally relevant adjectives. As pointed out by Slife and Weaver (1992), these findings indicate that although their knowledge and memories were unaffected, their metacognitive skills were deficient. Using a mathematical estimation task, Slife and Weaver showed that both induced depression and psychometrically defined depression were associated with inaccurate predictions about problem-solving abilities in relation to the task, as well as with inaccurate ratings of performance. Furthermore, this rating inaccuracy increased with severity of depression. Importantly, there was no evidence that the rating inaccuracy was due to a negative response bias or lower expectations for success on the part of the depressives. Similarly, depressed children were less accurate than nondepressed children on a metamemory task, particularly for judgements of memory capacity (Lauer et al., 1994).

Other studies have indicated that depressed patients show deficits in the use of organising strategies that would help them in task performance. For category learning, Smith, Tracy, and Murray (1993) found that depressed participants were impaired in performance when the task required a flexible analytical strategy. Similarly, Weingartner, Cohen, Murphy, Martello, and Gerdt (1981) found that depressed people failed to use spontaneously encoding operations that would facilitate later recall. However, when the task provided them with organising information, they were able to make use of it to improve their performance.

Based on a series of studies yielding similar results to those reported by Weingartner et al. (1981), Hertel (1994) argued that impaired memory in depressed people is not due to a lack of effort or to a limited capacity to attend to or process information. Rather, she posited that cognitive resources are sufficient, whereas the initiative to deploy them is lacking. For example, nondepressed participants, whose performance was superior to that of the depressed patients, appeared to make use of an implicit

strategy for recognising words they had previously seen (Hertel & Hardin, 1990). When depressed patients were explicitly directed to use such a strategy, their performance improved to the level of the nondepressed group. In another study, Hertel and Rude (1991) found that depressed people in an unfocused condition performed more poorly than nondepressed people on an unintentional learning task. However, when part of the task imposed a focus on the critical information, the deficit disappeared.

Other research has found that providing depressed individuals with problem-solving strategies leads to improved performance (Abramson, Alloy, & Rosoff, 1981; Silberman, Weingartner, & Post, 1983). However, when such strategies are not provided, research on decision making has found that depressed individuals use a smaller amount of available relevant information (Conway & Giannopoulos, 1993). In sum, evidence that depressed people perform at normal levels when given explicit strategies suggests that the fundamental deficit is in initiative and in strategic use of information, cognitive functions that are strongly dependent on the frontal lobes.

One area of anterior function not highlighted in the cognitive literature on depression is working memory, which is integrally tied to executive functions, including those compromised in depression. Working memory is the portion of memory that temporarily holds information used in the performance of a task. Several studies have localised working memory in the prefrontal cortex (Funahashi, Bruce, & Goldman-Rakic, 1989; Goldman-Rakic, 1987; Jonides et al., 1993); however, other regions have also been identified (for a review, see Raichle, 1993; see also Jonides et al., 1993). Although speculative, if difficulties in working memory interfere with a depressed individual's abilities to keep information about and objectives of a task in mind, deficits in initiative, strategy generation, and cognitive flexibility should ensue. Future research on the neuropsychology of cognitive processing in depression is needed to address whether working memory is impaired in depressed individuals.

Studies that have examined the cognitive characteristics associated with induced pleasant and unpleasant affect also suggest that unpleasant affect is associated with a decrease in the cognitive processes associated with frontal lobe function (for a review, see Isen, 1990). In both adults and children, pleasant affect facilitates creative problem-solving, more flexible thinking, and a more integrated organisation of cognitive material. These findings for pleasant affect are consistent with the reports of compromised cognitive flexibility, problem-solving skills, and organising strategies in depression reviewed earlier. Clore, Schwarz, and Conway (1994) reviewed other evidence on cognitive processing and mood that are highly consistent with the findings for depression and again implicate anterior regions of the brain. They argued that pleasant affect is associated with a focus on

heuristic processing (generalisations, information integration, global or top-down processing), more cognitive flexibility, and more novel responses. In contrast, they asserted that sad affect is associated with a reduction in abstract thinking, less cognitive flexibility, and fewer novel responses.

In summary, evidence from a variety of sources suggests that depressed people show biases or deficits on cognitive tasks that involve functions of the anterior brain regions. Given the present state of research, the relative contribution of the left versus the right hemisphere to the executive functions altered in depression is not known. Thus, definitive statements pertaining to the anterior asymmetries hypothesised by our model are not warranted at this time. Compromised executive functions in depression may be related to decreases in bilateral anterior activity, decreased left anterior activity alone, or less left than right asymmetric activity.

Posterior Regions

Depressed people have also been shown to display deficits on tasks associated with cognitive functions of the right posterior regions of the brain. This has been suggested by a rather extensive literature in which neuropsychological research has been carried out with depressed patients. These studies typically administered full or partial neuropsychological batteries and were therefore able to examine relative right- versus leftside differences (e.g. performance of the nondominant compared to the dominant hand on the Tactual Performance Test), which serves as a way to evaluate relative function of the contralateral hemisphere. Such neuropsychological batteries also assess performance on right hemisphere tasks (e.g. judgement of line orientation, three-dimensional constructional praxis, spatial association learning, subtests of the WAIS-R Performance scale) compared to left hemisphere tasks (e.g. vocabulary, verbal learning, subtests of the WAIS-R Verbal scale). Often, indices of abnormality were computed based on multiple tests comparing right versus left hemisphere performance. In general, despite criticisms of limitations in some studies (e.g. Miller, Fujioka, Chapman, & Chapman, 1995), depression has been rather consistently associated with impairments on right but not left hemisphere tasks (Berndt & Berndt, 1980; Flor-Henry, 1976; Flor-Henry, Fromm-Auch, & Schopflocher, 1983; Fromm & Schopflocher, 1984; Goldstein, Filskov, Weaver, & Ives, 1977; Gruzelier, Seymour, Wilson, Jolley, & Hirsch, 1988; Kronfol, Hamsher, Digre, & Waziri, 1978; Miller et al., 1995; Rubinow & Post, 1992; Sapin, Berrettini, Nurnberger, & Rothblat, 1987; Silberman & Weingartner, 1986; Silberman et al., 1983).

Confusions and conflicts arose in this literature in part because authors were attempting to argue that depression was uniquely associated with

pathology of one hemisphere or the other. As pointed out by Silberman and Weingartner (1986), evidence was inconclusive regarding relatively greater right hemisphere dysfunction in affective illness, because some neuropsychological studies also found impairments on traditional left hemisphere tasks as well. These concerns can be resolved by considering a caudal distinction as well as a lateral one. Our model predicts that deficits would be present for both hemispheres, but that for the left they would primarily reflect anterior functions, and for the right, primarily posterior functions. Although it is difficult to evaluate comprehensively the caudality of all tasks that have been used in this literature, our model provides a framework for integrating these apparently conflicting findings.

A separate line of research examining depressed children using various neuropsychological tasks has also supplied evidence for posterior right hemisphere dysfunction (for a review, see Brumback, 1988). Brumback and colleagues described a hemisyndrome of right cerebral dysfunction that they argue is commonly associated with depression in children. The description of this syndrome is essentially the same as that described in the literature on nonverbal learning disabilities (Rourke, 1988). Characteristics include left-sided pathognomonic signs indicating right hemisphere dysfunction, large discrepancies between Verbal and Performance IO in favour of the former, and deficits in visuospatial skills. In addition, children with nonverbal learning disabilities have been shown to have significant difficulties in social functioning and social/emotional adjustment (Rourke, 1988). Many of these problems have been attributed to deficits in the ability to interpret nonverbal information, such as facial expression, voice prosody, and gesture, which is strongly associated with right posterior functioning (e.g. Ahern et al., 1991; Etcoff, 1984a, b; Heilman, Bowers, Speedie, & Coslett, 1984).

Deficits in social functioning have also been extensively described in right brain-damaged patients (see Lezak, 1995). In addition, there is a large literature describing deficits in the ability to express and interpret emotional information after damage to the right hemisphere (for reviews, see Borod, 1993; Bowers, Bauer, & Heilman, 1993), suggesting that the processing of emotional material is an aspect of cognition modulated by posterior right hemisphere regions. Although we are not aware of studies directly linking deficits in emotional information processing with subsequent impairments in social functioning, case studies and clinical observation strongly suggest such a connection (Lezak, 1995).

Few studies have examined emotional information processing in depressed patients from a neuropsychological perspective. However, a number of studies have found depressed patients to display impaired recognition of affect in facial expression (Feinberg, Rifkin, Schaffer, & Walker, 1986; Persad & Polivy, 1993; Rubinow & Post, 1992). These

results are consistent with other evidence of right hemisphere deficits in specialised cognitive domains. Clearly, much more research is needed, but it may be that such deficits contribute to the social difficulties exhibited by depressed people.

Although social functioning in depression has not been examined from a neuropsychological perspective, there is a substantial literature demonstrating that depressed people have significant difficulties in relationships, including marital, family, and community interactions (for a review, see Barnett & Gotlib, 1988). Problematic interpersonal behaviours, such as slow and monotonous speaking, poor eye contact, poor timing in verbal interchanges, and use of awkward gestures, are all phenomena of depression (Barnett & Gotlib, 1988) that have been described in patients with right hemisphere damage (Lezak, 1995) and in people diagnosed with nonverbal learning disabilities (Rourke, 1988).

A number of additional aspects of information processing in depressed people and people induced into sad moods may be related to right hemisphere functions, although a great deal of further research is needed. Several authors have argued that the right hemisphere (particularly posterior regions) plays an important role in locating information in a larger social, environmental, and ecological context (for a review, see Heller, 1994; see also Gardner, Brownell, Wapner, & Michelow, 1983; Grossman, 1988). This concept is illustrated in the tendency for patients with right hemisphere damage to attribute specific features of categories in an indiscriminate or inappropriate manner (e.g. drawing a picture of a "potato bush"; Grossman, 1988). Based on findings that right brain-damaged patients tend to violate the overall reality of a verbal narrative in favour of irrelevant or nonsensical details, Gardner et al. argued that the right hemisphere has a unique ability to assess "plausibility", or the likelihood that a particular event is appropriate with reference to a particular context. Remarkably similar to Gardner and colleagues' description of the behaviour of right brain-damaged patients, depressed patients failed to recall the central aspects of a story they were asked to memorise, but recalled more specific items than did controls (Leight & Ellis, 1981). Similarly, Basso, Schefft, Ris, and Dember (1996) found questionnaire-defined depression to be directly associated with a local (i.e. detail) bias and inversely related with a global (i.e configural) bias on a perceptual judgement task of visual processing.

Along these lines, Clore et al. (1994) reviewed evidence that individuals in pleasant mood states are more likely to rely on heuristic processing strategies that simplify information configurations and intuitive decision strategies (more typical of right hemisphere information processing). In contrast, they argued that depressed mood is associated with greater attention to details and more systematic information processing (more

typical of left hemisphere information processing), which is consistent with the focus on specific items or details observed in depressed patients (e.g. Basso et al., 1996; Leight & Ellis, 1981).

In other research, Isen, Means, Patrick, and Nowicky (1982) showed that happy people were more likely to rely on simplistic response strategies in that they produced judgements biased by the ease to which exemplars came to mind (e.g. the "availability heuristic"; Tversky & Kahneman, 1973). Happy people were also less attentive to the substance of arguments in persuasion situations, responding more to relatively superficial heuristic cues (Bless, Bohner, Schwarz, & Strack, 1990; Mackie & Worth, 1989; Worth & Mackie, 1987). Consistent with a heuristic as opposed to a systematic strategy, people in a pleasant mood following a success experience responded more quickly and efficiently on a decision-making task (Isen & Means, 1983). Similarly, other researchers have reported that sad individuals were more systematic in information-processing strategies on a visual attention task (Gotlib, McLachlan, & Katz, 1988) and in processing a persuasive message (Bless et al., 1990). Because the posterior right hemisphere is uniquely suited for processing contextual, relational, and global information, whereas the posterior left hemisphere for systematic processing of details, this set of findings is consistent with other evidence that sad or depressed mood is associated with reduced right hemisphere activity.

A number of studies have also examined the tendency to resort to stereotypes in decision making (for a review, see Bodenhausen, in press). These findings suggest that happy people are more likely to engage in this type of information processing than sad or depressed people, which is consistent with the tendency of happy people to resort more to superficial heuristic cues and to attend less to the specific details of a situation than depressed people do. Although few studies have examined this particular information-processing style from a neuropsychological perspective, the available evidence suggests that it is likely to reflect right as opposed to left hemisphere processing (e.g. Zaidel & Kasher, 1989).

The cognitive-processing strategies outlined here correspond rather well with distinctions that have been made between right hemisphere (heuristic) and left hemisphere (detail-oriented) information-processing styles (for a review, see Heller, 1994). Indeed, Clore et al. (1994) presented evidence that depression and sad affect are associated with better performance on some detail-oriented tasks than is pleasant affect, consistent with earlier suggestions that relative activity of a certain brain region could be reflected in superior or inferior performance for tasks specialised to that region or in a bias to process information in a particular way. More specifically, the reduced right posterior activity in depression might result in the tendency to utilise left hemisphere information-processing strategies.

Also addressed in the literature is the possibility that the posterior right hemisphere plays a special role in aspects of arousal (for reviews, see Heller, 1993b; Heller et al., 1997; Wittling, 1995). Furthermore, the right hemisphere may be involved in modulating the responses of the hypothalamic-pituitary-adrenal axis (HPA; Heller, 1993b). Given that abnormalities of the HPA axis are well established in depression, it will be important in future studies of depression to consider further the role of the right hemisphere in various arousal systems (e.g. behavioural arousal, cortisol secretion, autonomic functions; see Heller et al., in press) and potential indirect effects on aspects of cognition such as speed and efficiency of information processing.

In summary, a large number of cognitive findings reported in the literature on depression and pleasant/unpleasant mood states implicate posterior regions of the brain. Furthermore, these findings are highly consistent with the reduced levels of right posterior activity reported for depression in neurodynamic, EEG, dichotic listening, tachistoscopic, and CFT studies.

QUESTIONS FOR FUTURE RESEARCH

In general, it will be important to consider that most tasks depend on more than one brain region for efficient performance. Furthermore, there are often multiple strategies that the brain can call on to carry out a task. Therefore, we will need to disentangle carefully the various cognitive demands imposed by any one task and then examine the relationship between the task components and the patterns of brain activity exhibited by depressed and nondepressed people. For example, the literature on information processing in affective states tends to lump together the concepts of top-down processing, flexible thinking, and capacity for novel responses (see Clore et al., 1994). Our neuropsychological perspective suggests that these concepts are distinguishable. For example, some aspects of top-down processing may rely on specialisation of right posterior regions for processing relational information (i.e. "seeing the forest instead of the trees"), whereas flexible thinking may be more dependent on functions of the anterior regions.

It is also likely that a consideration of the neuropsychological findings will lead us to investigate novel ways in which cognition may be affected in depression. For example, the right parietotemporal region has been found to be specialised for the pragmatic aspects of language (e.g. Hough, 1990; Kaplan, Brownell, Jacobs, & Gardner, 1990). Included among these are the perception of intonation, language contours, conversational conventions, and complex narrative comprehension. One might argue that these aspects of language are critical for successful treatment

in conventional forms of therapy, and hence, important to investigate as possibly impaired in depression.

It will also be crucial to deal with the issue of comorbidity. The evidence that patterns of brain activity in left anterior and right posterior regions are discrepant for depression and certain types of anxiety, such as anxious apprehension (e.g. worry) and anxious arousal (e.g. panic) (Heller et al., in press; Heller & Nitschke, in press; Keller et al., submitted), suggests that cognitive concomitants of depression and anxiety may be similarly confounded. Anxiety has been shown to promote less systematic thinking in the processing of persuasive appeals (Baron, Burgess, Kao, & Logan, 1990; Jepson & Chaiken, 1991). This is in direct contrast to the evidence that sad moods are associated with more systematic information-processing and consistent with predictions based on our model that anxious arousal would be associated with increased, as opposed to decreased, right posterior activity (Heller & Nitschke, in press). Similarly, Bodenhausen (in press) reviews evidence that stereotyping is seen more often in anxiety, happiness, and states of heightened arousal, and less often in sadness. If stereotyping, as suggested earlier, is more characteristic of a right hemisphere cognitive style, these data are consistent with the notion that right posterior regions are relatively more active in anxious arousal and happiness, and less active in sadness and depression. Given the high rates of comorbidity reported for depression and anxiety (Akiskal, 1990; Alloy, Kelly, Mineka, & Clements, 1990; Heller et al., 1995; Hiller, Zaudig, & Rose, 1989), it appears imperative that future studies examining the neuropsychology and cognition of depression attend to the possible effects of anxiety.

Finally, it remains unclear as to whether the patterns of brain activity and cognitive function described here as characteristic of depression are present regardless of mood state. As noted earlier, Henriques and Davidson (1990) reported findings consistent with a trait view, whereas other studies find that patterns of brain activity (e.g. Baxter et al., 1989) and performance on cognitive tasks (e.g. Barnett & Gotlib, 1988; Gotlib & Cane, 1987; Kronfol et al., 1978; McCabe & Gotlib, 1993) normalise with remission of depression. The work by Miranda and Persons on dysfunctional attitudes in depression (e.g. Miranda & Persons, 1988; Miranda, Persons, & Byers, 1990) may inform future research in this area. They argued that dysfunctional attitudes are traits (i.e. vulnerability factors) that are mood-state dependent. Specifically, previously depressed people showed more dysfunctional beliefs than never-depressed people when in an induced or naturally occurring unpleasant mood, but not when in a pleasant mood. Similarly, Teasdale and Dent (1987) found that after a negative mood induction, remitted depressives exhibited a memory bias for unpleasant words, whereas subjects with no history of depression did

not; without the negative mood induction, no group differences emerged. Following this pattern, previously depressed people might show less left anterior and right posterior activity than never-depressed people only when in an unpleasant mood. It will thus be crucial to measure current mood, as well as depression, in future research examining remitted depression.

In summary, we have made an attempt to formulate a more comprehensive account of cognition in depression from a neuropsychological perspective than has previously been attempted. Although it was not possible to review the entire literature on aspects of cognition in depression, we were able to draw on a variety of sources to suggest that there are clear parallels between the predictions that would be made on the basis of brain activity data and the cognitive characteristics that have been identified in depression. The conceptual integration of the neuropsychological and cognitive concomitants of depression attempted here suggests the need for greater interdisciplinary collaboration between researchers in cognitive neuroscience, clinical psychology, cognitive psychology, and emotion.

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