

Research article

Relationship of anhedonia and anxiety to social rank, defeat and entrapment

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Abstract

There is good evidence to suggest that depression is highly correlated with perceptions of low rank and subordinate status (i.e. feeling inferior, low-self esteem, feeling that others look down on the self, and submissive behaviour). However, it is possible for people to feel inferior and anxious, and behave submissively but not necessarily be depressed. More recently two other processes, defeat and entrapment, have attracted attention as possible processes linked specifically to depression and anhedonia. This research explored the relationship of these variables (social rank variables and defeat and entrapment) to two measures of hedonic tone (low positive affectivity and anhedonia) and anxiety in both a clinical and student population. All variables were strongly associated with lowered hedonic tone and anxiety. However, partial correlations, and a structural equation model fitted to the data from combined groups, suggests that perceptions of defeat play a specifically important role in anhedonia as measured by low positive affect. Framed within an evolutionary model the data suggest that the mechanisms which evolved to help animals accommodate and respond to defeats may have important regulatory effects over positive affect, reducing exploration of and engagement with the environment.

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1. Anhedonia

Anhedonia was first documented by Ribot (1896) as an inability to experience pleasure. Although regarded a core symptom of depression (Klein, 1974), Rush and Weissenburger (1994) note that only four out of the nine major classification systems require anhedonia as a criteria for melancholic/endogenous depression, raising concerns about these

diagnostic systems (Loas and Boyer, 1993; Loas et al., 1994). Moreover, anhedonia is not specific to melancholic depression. Akiskal and Weise (1992) argue that long standing anhedonia characterises dysthymia. Anhedonia has been linked to schizophrenia (Andreasen, 1982; Chapman et al., 1976; Katsanis et al., 1992) especially negative symptoms (Blanchard et al., 1994; Heinz et al., 1994), and may be a predisposing trait (Meehl, 1962; Berenbaum et al., 1990), or related to the chronicity and depressive features of the disorder (Harrow et al., 1977; Loas et al., 1996). Anhedonia is also a common feature in

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alcohol and drug dependent patients during withdrawal (Heinz et al., 1994), anxiety and adjustment disorders (Silverstone, 1991), and is associated with suicidal ideation (Robbins and Alessi, 1985; Oei et al., 1990) and successful suicide (Fawcett et al., 1990; Fawcett, 1993). For these and other reasons anhedonia has been recommended as worthy of study in its own right (Willner, 1993a,b; Snaith, 1993, 1995).

1.1. Anhedonia and positive affectivity

There are two different conceptualisations of anhedonia. The first, as typified by some diagnostic systems, employs anhedonia as a broad category encompassing general apathy with a marked lack of motivation to engage in almost all activities (Klinger, 1993), highly diminished interest or pleasure in those activities and a lack of 'gratification' (Beck, 1967). In this view anhedonia relates to a generalised lack of Positive Affectivity (PA) defined by Watson et al. (1988) as a dimension reflecting one's level of pleasurable engagement in the environment. This definition views anhedonic depression as the result of reductions in a range of positive affects such as joy, energy, enthusiasm, alertness, self-confidence and interest.

In contrast negative affect (NA), encompasses a broad range of negative mood states such as sadness, anger, guilt, disgust, and fear and is believed to be mediated by different neurophysiological systems to those of positive affect. Research has demonstrated that NA and PA are not opposite poles on a single dimension but are largely independent mood dimensions that have differential associations with anxiety and depression (Watson et al., 1988, 1995a,b; Watson and Clark, 1991; Clark and Watson, 1991). Watson and Clark developed the Mood and Anxiety Symptom Questionnaire (MASQ; Clark and Watson, 1991; Watson et al., 1995a,b) to specifically assess PA and NA. The MASQ has good discriminant validity between the anxiety and depressive disorders for clinical populations (Watson et al., 1995a,b; Jolly et al., 1994) and low positive affect has been shown to be the single most important discriminating feature of depression (see McGrath and Ratliff, 1993 for a review).

A second approach to anhedonia describes it as the result of dysfunction in the monoamine mediated reward systems (Klein, 1974; Willner, 1993b; Snaith, 1993). This conception of anhedonia does not focus on 'interest' or 'motivation', limiting its focus to anhedonia's more physical manifestations. Willner (1993a) suggests that anhedonic patients can remain 'interested' in hedonic experiences, but either anticipate that they will be unable to enjoy them, or are unable to enjoy them when they do engage in them. Loss of interest or lack of motivation may develop from repeated experiences of wanting but failing to feel pleasure or reward from various activities. Anhedonia as defined by lack of reward in specific sensory and appetitive experience has been measured by Snaith et al. (1995).

Despite differences in the degree of motivation in anhedonia both approaches clarify the need to distinguish effects on positive (reward system) affect and negative (punishment system) affect. Put simply, negative affects (e.g. anxiety) evolved to detect and cope threats while positive affects are related to engagement in resources seeking activities.

1.2. Social rank, defeat, entrapment and anhedonia

Theories of anhedonia range from the neurobiological (that there is a dysfunction in the mesolimbic dopamine system; e.g. Zacharko and Anisman, 1991; Papp et al., 1994) through to psychological explanations that focus on disengagement from incentives (Klinger, 1975). Evolutionary explorations of mood states consider their possible functional utility and typical situation elicitors (Nesse, 1998). A clue to anhedonia's function may be found in early data suggesting that positive affect is associated with social engagement and time spent socialising (Watson, 1988); the range of social activities engaged in (Watson et al., 1992) and the rated quality of social relationships (Berry and Hansen, 1996).

Price (1972) suggested that in group living animals one of the mediators of social engagement, social confidence and mood may be related to social rank (Gilbert, 1992; Gilbert, 2000a; Price et al., 1994). For example, it is not in the interests of lower ranking animals to be brimming with confidence, or

pursue vigorously biosocial goals such as mating or food resources, if this is likely to elicit attacks from more dominant others who are pursuing the same resources (Bernstein, 1980). A degree of inhibition in engagement in certain social activities, plus a readiness to submit when challenged, may have been adaptive for low rankers (Gilbert, 1992, 2000a; Price et al., 1994). However, while there is evidence that depressed people see themselves as inferior to others and tend to behave submissively (Allan and Gilbert, 1997), these variables are also associated with anxiety especially social anxiety (Gilbert, 2000b).

In fact, Price's (1972) original model of depression focused more on defeat than submissive behaviour and recent theory (Sloman and Gilbert, 2000) and research in depression have focused on two key social outcomes, or perceptions of current circumstances; social defeat and entrapment (Dixon, 1998). While defeat and entrapment are often highly associated with perceptions of low rank, these variables may also have specific effects on mood. Indeed, there is some evidence that defeat and entrapment may be more salient to depression than perceptions of low rank per se (Gilbert and Allan, 1998) and it has been found that life events that are experienced as humiliating defeats and/or entrapping are more depressogenic than loss events alone (Brown et al., 1995). There are also a number of studies that have shown that defeat has specific biological effects on animals social behaviour (Von Holst, 1986; Meerlo et al., 1996) and notably, on exploration and reward seeking behaviour (Henry, 1982). Laboratory studies on rodents show that repeated defeat experiences reliably result in physiological and behavioural consequences including: a decrease in offensive aggression (Lagerspetz and Sandnabba, 1982); an increase in defensive responses (Frischnecht et al., 1982); decreases in subsequent exploratory behaviour and increases in 'freezing' (Raab et al., 1986); weight loss (Adams and Boice, 1983; Raab et al., 1986); reduction of appetitive behaviours (Van de Poll et al., 1982) and disruption of escape learning (Williams and Lierle, 1988). Defeats seem to be associated with passivity, disengagement in the environment and from resource acquisition. It is possible therefore that perceptions of defeat and entrapment (being unable to move away from aversive environments) may be a key

variable that downgrades reward systems and is thus linked to anhedonia (see Gilbert, 2000a, for review).

1.3. *This study*

Given the data from animal studies, this study set out to explore the relationships between various measures of social rank (unfavourable social comparison and submissive behaviour), defeat and entrapment with those of affective tone. Although these variables have been shown to be associated with depression (e.g. Allan and Gilbert, 1997; Gilbert and Allan, 1998) we have no data on their specific relationship with positive affectivity. We also sought to explore the relative relationship of these variables to anhedonia and anxiety.

2. **Methods**

2.1. *Participants*

2.1.1. *Student group*

A total of 193 undergraduates (45 males and 148 females) participated in the study. The mean age was 22.9 years (S.D. = 7.7).

2.1.2. *Patient group*

This was a mixed clinical group consisting of 81 psychiatric in-patients (32 males and 49 females; mean age 36.8 years, S.D. = 13). selected from three acute wards at Derby City hospital. 58% had a diagnosis of primary depression (including major, postnatal and bipolar depression) while the other 42% diagnoses were of secondary depression comorbid with eating disorders, schizophrenia, personality disorders and stress reactions. Diagnoses was by the treating psychiatrist using ICD-10 criteria. The mean Beck Depression Inventory score was 26.7 (S.D. = 14) and range 5–49 with 74.7% having a BDI score greater than 15. As the study was on anhedonia rather than depression specifically, those with comorbid disorders were included. Each patient was sufficiently orientated to understand the protocol, sign an ethics consent form and complete the self-report questionnaires. No patient was floridly psychotic. The range of scores reflect the differing points in recovery.

2.2. Measures

2.2.1. Mood and Anxiety Symptoms Questionnaire (MASQ) — short form

The MASQ was developed by Watson and Clark (1991) to test the Clark and Watson (1991) tripartite model of anxiety and depression (Watson et al., 1995a,b). The generation of the items and their allocation to the subscales was guided by the symptom criteria of the revised third edition of the Diagnostic and Statistical Manual of Mental Disorders (DSM-111-R; American Psychiatric Association, 1987). The short form used here does not include the 'General Distress: Mixed Symptoms Scale', which contains items that appear in the symptom criteria of both anxiety and mood disorders. Hence, the short form MASQ comprises four subscales. The 12-item General Distress: Depressive Symptoms (GDD) reflect depressed mood and relatively non-specific symptoms of mood disorder (e.g. self-blame, pessimism, feelings of disappointment and failure). The 11-item General Distress: Anxious Symptoms (GDA) reflect undifferentiated anxious mood and symptoms of anxiety disorder (e.g. inability to relax, upset stomach). The eight item Anhedonic Depression (AD) subscale reflects 'loss of interest' and 14 reverse-keyed items reflecting 'High Positive Affect'. The Anxious Arousal (AA) subscale consists of 17 items reflecting somatic tension and hyperarousal.

2.2.2. Snaith–Hamilton Pleasure Scale (SHAPS)

This 14-item scale was constructed to measure hedonic tone in a general psychiatric population (Snaith et al., 1995). The scale items were based on pleasurable experiences most frequently cited by a general population and cover four areas of potential hedonic experience (eating, pastimes, social interaction, and sensory experience). For each item, participants indicate whether they agree or disagree that they would enjoy the experience (scored 0 and 1, respectively). For example "I would enjoy reading a book, magazine or newspaper" (Item 9). Hence scores can range between 0 and 14, with higher scores indicating higher levels of anhedonia. Snaith et al. (1995) found the scale to have satisfactory reliability and validity and that "few respondents in the general public scored over 2" (p. 100) but most

patients scored more than 2. In this study the Cronbach α value for the clinical population was 0.86 for the clinical population and 0.74 for the student population.

2.2.3. Social comparison scale

Measures of social comparison assess perceptions of personal inferiority and low rank. A social comparison scale using a semantic differential methodology developed previously (Allan and Gilbert, 1995) was used in this study. This measure asks subjects to make a global social comparison of themselves in relation to others with a series of bipolar constructs. For example, the scale asks "in relation to others I generally feel"

Inferior 1 2 3 4 5 6 7 8 9 10 Superior

In this 11-item scale, constructs were chosen in discussion with other clinicians about the salient dimensions used by patients and taps judgements concerned with rank (inferior–superior), attractiveness, and how a person judges themselves 'to fit in' with or be like others (same–different, insider–outsider). Low scores on this scale indicate general inferiority (low rank) self-perceptions. This scale has been used in other studies and has satisfactory reliability and validity (Allan and Gilbert, 1997). In this study the Cronbach α for the clinical population was 0.96 and 0.90 for the student population.

2.2.4. Submissive Behaviour Scale

This scale was developed from the work of Buss and Craik (1986) who asked subjects to identify typical submissive behaviours. The most highly agreed upon items (16 items) were chosen to construct the submissive behaviour scale (Gilbert and Allan, 1994; Allan and Gilbert, 1997). It includes items such as; "I agreed I was wrong even though I knew I wasn't". The measure is a response scale based on behavioural frequency. The scale focuses on social behaviour and is not intended to provide a measure of anxiety or depression. Subjects respond by giving their estimated frequency of these behaviours on a five point scale. This scale has satisfactory internal consistency and test–retest reliability (see Allan and Gilbert, 1997). In this study the Cronbach α for the clinical population was 0.92 and 0.85 for the student population.

2.2.5. Other as Shamer Scale (OAS)

To look at the extent to which people think others look down on them and place them in subordinate positions we used a measure of external shame (Goss et al., 1994). This can be contrasted with internal shame which is how the self judges the self (e.g. I see myself as inadequate). The external shame scale (OAS) used here taps global judgements of how people think others see them (e.g. “I think other people see me as inadequate”). The scale consists of 18 descriptions of feelings or experiences. Subjects respond on a five point scale indicating how often they feel this way (ranging from 0=never, to 4=almost always). Previous research using OAS has found satisfactory internal consistency (Allan et al., 1994). The scale offers a measure of beliefs of “being looked down on” (seen as low-rank) by others, which is a salient dimension of external shame or stigmatising shame (Gilbert, 1998). In this study the Cronbach α for the clinical population was 0.96 and 0.92 for the student population.

2.2.6. External Entrapment Scale

This 10-item external entrapment scale was designed to measure perceptions of entrapment by external situations and escape motivation (e.g. “I am in a relationship I can’t get out of; I have a strong desire to escape from things in my life”). Respondents indicate on a five-point scale of ‘not at all like me’ to ‘extremely like me’. The scale has satisfactory psychometric properties (Gilbert and Allan, 1998). In this study the Cronbach α for the clinical population was 0.89 and 0.86 for the student population.

2.2.7. Defeat Scale

This 16-item scale was designed by Gilbert and Allan (1998) to measure a sense of failed struggle and losing social rank (e.g. I feel defeated by life; I feel I have lost important battles in my life; I feel I have lost my standing in the world). Items focus on feelings and perceptions of defeat and loss of social standing. Participants respond on a five-point scale indicating the extent to which each item describes their feelings (0=not at all to 4=extremely). The scale has previously been found to have satisfactory psychometric properties (Gilbert and Allan, 1998). In this study the Cronbach α for the clinical popula-

tion was 0.88 for the clinical population and 0.83 for the student population.

3. Results

3.1. Descriptive statistics

The means, standard deviations and intercorrelations, for both students and patients, are shown in Table 1. *t*-Tests showed significant differences between the two groups on all scales used ($P < 0.01$). The social rank derived scores are similar to those obtained in previous studies with students and patients (Allan and Gilbert, 1995, 1997; Gilbert and Allan, 1994, 1998). The student scores for the four subscales of the MASQ are similar to those obtained by Watson et al. (1995a).

3.2. Association of the SHAPS and the MASQ subscales with the rank-derived scales

Table 1 provides the full correlation matrix for all variables (patients upper table, students lower table). In both groups the social-rank variables were significantly associated with both the general distress depression (GDD), anhedonia (AD) the Snaith–Hamilton Pleasure Scale (SHAPS) and anxiety measures (GDA and AA). The variables of defeat and entrapment performed well, showing very robust correlations with all the MASQ subscales. The SHAPS was significantly associated with all the MASQ subscales, but given that this was $r = 0.57$ for students and $r = 0.51$ for patients, it appears that these scales are probably measuring different dimensions of anhedonia.

It can also be seen that defeat and entrapment, which represent perceptions of one’s current circumstances, are highly correlated with social rank evaluations such as feeling inferior to others, thinking that others look down on the self, and behaving submissively.

It was hypothesised that defeat has a particularly important relationship with reduced positive affect (anhedonia). However, the correlations show that both anxious arousal and anhedonia are significantly associated with defeat. Partial correlations in the depressed group were calculated to examine associa-

Table 1
Mean, standard deviations and correlations (two-tailed Pearson r values) of all scales and both samples

	Social comparison	Submissive behaviour	Other as shamer	External entrapment	Defeat	SHAPS	GDD	AD	GDA	AA
Social comparison		−0.64**	−0.59**	−0.61**	−0.76**	−0.54**	−0.70**	−0.72**	−0.47**	−0.35**
Submissive behaviour	−0.45**		0.63**	0.56**	0.66**	0.47**	0.70**	0.55**	0.65**	0.53**
Other as shamer	−0.47**	0.59**		0.72**	0.73**	0.40**	0.69**	0.53**	0.57**	0.47**
External entrapment	−0.30**	0.42**	0.55**		0.72**	0.52**	0.70**	0.63**	0.51**	0.39**
Defeat	−0.43**	0.54**	0.70**	0.62**		0.49**	0.80**	0.79**	0.56**	0.42**
SHAPS	−0.22**	0.17**	0.25**	0.33**	0.40**		0.55**	0.57**	0.51**	0.39**
GDD	−0.46**	0.50**	0.65**	0.65**	0.78**	0.47**		0.79**	0.77**	0.63**
AD	−0.44**	0.44**	0.56**	0.59**	0.71**	0.51**	0.75**		0.54**	0.36**
GDA	−0.30**	0.41**	0.51**	0.59**	0.56**	0.39**	0.71**	0.62**		0.83**
AA	−0.22**	0.29**	0.47**	0.46**	0.47**	0.27**	0.64**	0.44**	0.67**	
Student Mean	61.3	23.8	21.53	10.0	17.3	1.5	24.1	58.2	20	25.9
S.D.	12.4	8.8	11.07	7.6	10.5	2.1	9.0	15.6	6.9	8.8
Patient Mean	43.0	35.3	38.7	20.5	38.1	4.7	39.4	80.1	28.8	37.3
S.D.	20.6	13.2	18.26	11.2	18	3.9	13.5	20.4	9.3	14

Patients upper table, students lower table; GDD, General distress–depressive symptoms; AD, Anhedonic depression; GDA, General distress–anxious symptoms; AA, Anxious arousal; SHAPS, Snaith–Hamilton Pleasure Scale.

*, $P < 0.05$; **, $P < 0.01$.

tions between the defeat and the MASQ anhedonic depression subscale and the SHAPS but controlling GDA and AA anxiety. Defeat remained significantly correlated with AD ($r = 0.67$) and SHAPS ($r = 0.30$) after controlling for anxiety. However, when controlling for depression (GDD) and anhedonia (AD), the correlation of defeat with anxiety arousal was ($r = 0.05$) i.e. it became nonsignificant. This suggests that defeat may have a more powerful impact on positive affect systems than it does on negative affect systems.

Based on the finding that the relationship between anxious arousal with defeat disappears when anhedonia and general distress depression are controlled, we wanted to explore these relationships in more detail. Recall that we have suggested that defeat is particularly related to lowered positive affect. Moreover, it would seem possible for one to have high negative affect (feel anxious) but not necessarily feel defeated, trapped or depressed.

To test the differential impact of the social rank variables on anhedonic depression and anxious arousal from the MASQ, the groups were combined (for $n = 274$) and a structural equation model was specified (using AMOS 4.0), in which standardised versions of the affect variables (anhedonic depression and anxious arousal) were regressed onto four of the social rank variables (defeat, entrapment,

social comparison and shame). This model is equivalent to a multivariate regression model. However, by specifying the model within a structural equation model framework it enables us to test the differential impact of the rank variables, defeat and entrapment on anxious arousal and anhedonic depression. The model was first estimated with all parameters free to vary (this model is a saturated model, with 0 df, and so automatically fits the data). The model was then re-estimated four times, each time the paths from one of the independent variables (defeat, entrapment, shame, and social comparison) to the two dependent variables (MASQ anhedonic depression and anxious arousal) were constrained to be equal. By constraining the parameters, the model is no longer saturated, and hence can be tested. The χ^2 value, and its associated probability value, provide a test of significance of difference of the two parameters. The model is given in Fig. 1 with the appropriate statistics given in Tables 2 and 3.

Table 2 shows that there is a significantly higher association of defeat with anhedonic depression than anxiety (anxious arousal) when the relationships with the other rank variables are held constant. Entrapment however failed to show a significantly differential impact on anhedonic depression, indicating that it is defeat which has the more specific impact on anhedonia. Social comparison narrowly failed to

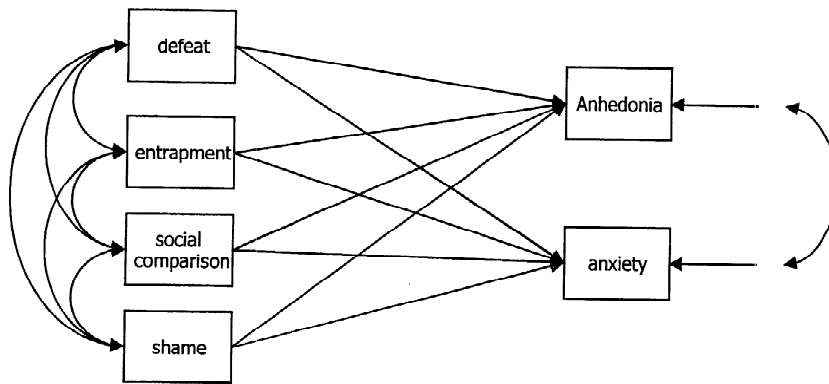


Fig. 1. Path diagram showing relationships between social rank variables, anhedonia (anhedonic depression) and anxiety (anxious arousal).

Table 2
Estimates (*P* values) for standardised regression weights and χ^2 values (*P* values)

	Anxiety	Anhedonia	χ^2 change
Defeat	0.253 (0.008)	0.591 (<0.001)	9.659 (0.002)
Social comparison	-0.026 (0.722)	-0.175 (0.001)	3.339 (0.068)
Entrapment	0.188 (0.014)	0.208 (<0.001)	0.057 (0.812)
Shame	0.213 (0.012)	-0.075 (0.208)	8.814 (0.003)

The columns labelled Anxiety (anxious arousal) and Anhedonia (anhedonic depression) show the standardised regression weights, and their associated probability values. The column labelled χ^2 change shows the change in χ^2 when the values are fixed to be equal, and the *P* value associated with that χ^2 (1df), this provides a test of significance of difference of the two parameters.

show a statistically significant differential impact on anhedonic depression at the conventional 0.05 level (*P* = 0.068). Nonetheless, given that this finding was

close to significance, it is worth considering the possibility that internal feelings of low rank (i.e. personal inferiority, as measured by social comparison) may be an important perception affecting positive affect. It is therefore of interest that external shame (thinking that others look down on the self), unlike social comparison, appears to have a more specific impact on anxious arousal. As noted elsewhere (Gilbert, 1998) one need not feel personally inferior (internal shame) even if one believes others see the self negatively. Hence it may be when a sense of low rank (inferiority) is internalised (as personal inferiority, or internal shame) that the inhibiting effects on positive affect switch in. In other words, one can worry about what others think about the self and feel anxious but not necessarily see oneself as inferior, and thus be less likely to experience reduced positive affect. Although we did not set out to explore the distinction of internal shame (how one feels about oneself) and external shame (how one thinks others feel about the self), and their relative and differential impacts on positive

Table 3
Correlations for the combined group (*n* = 274) on variables used in the structural equation model

Shame	1.000					
Defeat	0.795	1.000				
Entrapment	0.712	0.754	1.000			
Social comparison	-0.675	-0.724	-0.598	1.000		
Anhedonia	0.662	0.815	0.705	-0.677	1.000	
Anxiety	0.565	0.582	0.545	-0.465	0.562	1.000
	Shame	Defeat	Entrapment	Social Comparison	Depression	Anxiety

All correlations *P* < 0.001. Anhedonia, MASQ, anhedonic depression; Anxiety, MASQ anxious arousal.

and negative affect, this data indicates this as a possible fruitful avenue for further research (Gilbert, 1998).

4. Discussion

There is now good evidence that subordinate and dominant animals are physiologically different (Henry, 1982; Ray and Sapolsky, 1992; Sapolsky, 1989) and engage their social environments in different ways (Bernstein, 1980). Subordinates are generally less confident, less explorative and more timid. However, though anxious and stressed they are not necessarily depressed but may be vulnerable to depression (and anhedonia) because they are likely to suffer higher rates of defeats and entrapments than the more dominant who have more control over their social environments. However, even the relatively dominant can suffer serious defeats. For such reasons, in a recent publication (Sloman and Gilbert, 2000), we choose to focus on what we called involuntary defeat strategies rather than subordinate strategies (as in Price et al., 1994) because subordinate strategies can involve a wide variety of behaviours and affects (e.g. social anxiety) that need not be depressogenic as such, although maybe a vulnerability factor. Indeed, the structural equation model indicated that shame (thinking others look down on the self) is more highly related to anxious arousal than to anhedonia. Hence, it is important to separate the evolved mechanisms regulating positive and negative affect systems, and here we have suggested that defeats are intimately linked to positive affect systems and their behavioural outputs (e.g. explorative behaviours and social engagement).

Although there are individual differences in response to defeats (Von Holst, 1986) a defeated and trapped animal may need to significantly curtail its exploration and resource acquiring behaviours. As Dixon (1998) noted, defeated and trapped rodents are particularly vulnerable to becoming passive and withdraw to the periphery of the territory (disengagement). Human research has also suggested this linkage, in that when people are depressed they feel defeated, trapped and inferior (e.g. Brown et al., 1995; Gilbert and Allan, 1998). Thus we argued that defeats may have evolved to have direct effects on

lowering positive affect and render an individual less active and engaging in a potentially hostile and/or low pay off environment. Whatever mechanisms control these behaviours, these potential states of mind (socially withdrawn, passivity, low explorative behaviour and low positive affect) have been noted in many species. Hence, for genetic or other reasons, it may be the mechanisms that evolved to cope with entrapped defeats (rather than just low rank) which are active in anhedonic depression. Indeed, our structural equation model indicated that perceptions of defeat have more powerful effects on anhedonic depression than on anxious arousal.

This finding does not imply that anhedonic depression is always caused by defeats. Rather it suggests that there may be mechanisms that evolved to regulate positive affect and engagement with the environment by tracking defeats. Such a mechanism(s) may be under genetic and/or environmental control. Genes may control the threshold for triggering of defeat states and the 'depth' of the state once triggered, giving rise to individual differences. This implies that experiences of defeat and entrapment can be both causes and/or consequences of anhedonia but these experiences (feeling anhedonic, and feeling defeated and trapped) are linked together because of the way these mechanisms evolved.

Our measure of defeat focuses on 'losing important battles' and 'loss of social standing' in an effort to capture the typical evolved context of defeats, (i.e. they are associated with some fall in a perceived hierarchy and reduced access to resources). We have not measured defeat that captures a sense of failure but which does not imply falling in some hierarchy. However, we strongly suspect that defeats that do not carry these meanings (falling in some hierarchy and losing access to valued resources) are less likely to be depressogenic, although firm evidence for this is yet to be obtained.

There are other possible interpretations for these findings. It could be that it is the loss of control that is central to anhedonia rather than specific internal mechanisms linking affect with social rank and defeat (Gilbert, 2000a). For example, a number of studies indicate that exposure to inescapable stressors and social defeat both reliably induce anhedonia (Zacharko and Anisman, 1991; Plaznik et al., 1989; Koolhaas et al., 1990). Willner et al. (1987) and

Willner et al. (1992) found that even relatively mild stressors, such as cage tilting, change of cage mates, overnight illumination and short periods of food and water deprivation generated anhedonia for up to 4 months in rats. It is important to note that escapable footshocks, defeats and other 'stressors' do not induce anhedonia (Willner, 1993b) which suggests it is not the nature of the stressor event itself but the entrapment (unable to get away) that may be pathogenic.

Willner (1993b) further notes that there is a striking similarity between forms of response following inescapable electric shocks (a physical stressor) and social defeat (a psychological stressor). Both inescapable shock and defeat increase immobility and prolonged freezing responses (Koolhaas et al., 1990; Van Dijken et al., 1992) and results in decreases in social dominance (Williams, 1982). Other studies highlight the importance of subordinate social status as environmental determinants of vulnerability to anhedonic responses (Korte et al., 1991; Kudryatseva et al., 1991). Hence, the intimate nature between social status and social control requires further research. It is possible that it is via their influence on social control (access to resources and disengagement from hostile or low pay off environments) that these social rank variables evolved to exert their effects.

Understanding what mechanisms may have evolved for the control of affect, and their evolved functions may offer insights into which mechanisms become activated in different psychopathologies (Nesse, 1998; Gilbert, 2001). This does not imply that these mechanisms, such as those which evolved to be triggered by defeats in the natural environment, are operating adaptively in serious depression. Rather it suggests the value of trying to understand the natural regulators of positive and negative affect and then to explore how these may become dysfunctional.

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