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INVITED REVIEW

Evolution and depression: issues and implications

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ABSTRACT

Depression is well recognized to be rooted in the down-regulation of positive affect systems. This paper reviews some of the social and non-social theories that seek to explain the potential adaptive advantages of being able to tone down positive affect, and how dysfunctions in such affect control can occur in some contexts. Common to most evolutionary theories of depression is the view that loss of control over aversive events and/or major resources/rewards exert downward pressure on positive affect. Social theories, however, suggest that it is loss of control over the *social* environment that is particularly depressogenic. Two evolutionary theories (the attachment-loss, and the defeat-loss theories) are briefly reviewed and their interaction considered. It is suggested that phenotypes for toning down positive affect, in the face of loss of control, may become more severe in the context of socially hostile, unsupportive and/or excessively competitive environments. The paper briefly considers how human competencies for self-evaluation in relation to others, rumination, self-criticism, and modern social contexts can accentuate dysfunctional expressions of affect regulation.

INTRODUCTION

Evolutionary approaches to psychopathologies can help illuminate how evolved functional systems (e.g. for specific emotions and moods) can come to be regulated by a variety of different processes, thus allowing for phenotype variation (McGuire & Troisi, 1998; Wilson, 1998). Just as 'panic disorder' might represent a maladaptive expression/phenotype of a *functional* anxiety system, due to conditioning or cognitive elaboration, so some depressions can represent maladaptive expressions of functional positive affect control systems (Nettle, 2004). Although certain genes may convey risk they may do so only in some environments and in others offer advantages because of phenotypic variation. As an example, the short allele of 5-HT transport gene has been linked to increased risk of depression in current and early stressful environments (Caspi *et al*. 2003). However, Suomi (1997, 1999) has reported that cross-fostering monkeys with this vulnerability to either highly responsive or low responsive mothers significantly affected their outcome, with those fostered to high responsive mothers doing well, but those with low responsive mothers faring poorly. Hence, this genotype may code for greater, possible phenotype variation which allows greater 'biological sensitivity to context' (Boyce & Ellis, 2005; Ellis *et al*. 2005).

The way genes can be turned on and off, and modified in their expression via life experiences, illustrates evolutionary theorists' concern with ontologies – that is learning can influence gene expression (Plomin & Crabbe, 2000). Evolutionary theory also debates the nature, forms and limits of experience on physiological maturation (Lickliter & Honeycutt, 2003). Phenotypes mature to fit (social) ecologies. Hence social environments (empathetic care *versus* neglect, abuse) and physical ecologies (e.g. food availability, threat from predators, parasites) impact on whole brain development and organization

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(Schore, 1994, 2001; Lickliter & Honeycutt, 2003; Boyce & Ellis, 2005). This analysis leads naturally to two questions: (1) What might be the possible advantages for phenotypes for *toning down* positive affect and motivation, and increase sensitivities to threat (anxiety and anger)? and (2) When can a phenotype be said to be maladaptive? (See Wakefield, 1999; Boyce & Ellis, 2005; for discussion of these issues.)

EVOLUTIONARY THEORIES

Many years ago Akiskal & McKinney (1975) suggested that although depression was a highly heterogeneous disorder it can be viewed as a common final pathway for a variety of previous and current stresses and personal vulnerabilities. The evolutionary question focuses on what kinds of stresses, that impinge on an animal such that activating the 'depression' pathway of lowered positive affect and increased negative affect, could have advantages. In fact there are a range of theories that consider the advantages of toning down positive affect and increasing negative affect. These can be divided in to two types: non-social and social theories.

NON-SOCIAL THEORIES

Control over aversive events

A number of theorists have postulated that depression ensues when individuals cannot control *aversive* events. This model, called 'learned helplessness' by Seligman and colleagues (Seligman, 1975; Peterson *et al*. 1993) has generated a great deal of animal and human research. The general idea is that when stressors are first encountered they ignite *invigorated* (anxiety and anger) behaviour to try to overcome them. If these coping options do not work there is then a change to a depressive-withdrawal coping strategy. To test this animals have been subjected to stresses they cannot control (e.g. electric shocks and cold water swims). Although there is good data that such experiences can disrupt a range of physiological systems (gonadal and stress hormones, immune functioning neuropeptides and transmitters) there remains doubt as to how far such disruptions (some of which can be of relatively short duration) can be taken as a model of depression (see Irwin, 2000). Some psychologists suggest an attributional model where it is explanations for lacking control that is crucial to human depression (e.g. Abramson *et al*. 1989).

Another example of an evolutionary model of this type has focused on problems arising from loss of control over stress; referred to as the arrested defences model (Gilbert, 1992, 2001; Dixon, 1998). This suggests that if a person or animal is threatened and highly motivated to escape or act aggressively there is elevated stress. However, many defences, such as fight and flight, were designed for short-term use and if they are aroused *but blocked or arrested* then chronic stress-activation can occur in these systems, exerting a 'toning down' effect on positive affect. Although control (and attributions for control) is a salient aspect of these theories, the arrested defences model focuses more specifically on blocked outputs of the defence system (e.g. entrapment/suppressed anger). There is now evidence that depression is associated with an elevated motivation to escape but feeling trapped (Brown *et al*. 1995; Gilbert & Allan, 1998; Farmer & McGuffin, 2003; Gilbert *et al*. 2004). There is also evidence that depressed people have elevated feelings of anger but can be fearful of their anger (Brody *et al*. 1999; Allan & Gilbert, 2002; Gilbert *et al*. 2004). Disturbances in fight and flight may link to the findings of changed activity in the amygdala in depression (Davidson *et al*. 2002) explaining why depressed people can experience increases in anxiety, irritability and even rage attacks (Fava *et al*. 1990). Indeed, van Praag (1998) has argued that dysregulation of anger and anxiety can underpin many depressions.

The value of awareness of possible, activated defences (e.g. like fight–flight–submission–clinging) that may be dysregulated, arrested or blocked, and distinguishing these processes from those of control attributions, may be especially important when formulating difficulties with patients. For example, a focus on the disruption to fight–flight might focus discussion on feelings of entrapment, wanting to run away (Gilbert, 2000; Swallow, 2000) and exploring when this may be useful to do (e.g. from an abusive spouse), when not (e.g. suicide as escape behaviour; O'Connor, 2003) and the perceived reasons for feeling unable to move on and trapped (e.g. lacking alternatives, resources help from others or shame and guilt; Gilbert

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et al. 2004). Leahy (2000) has suggested that people can remain stuck/trapped in unhelpful situations/relationships because they feel they have invested too much in them to let go or move on (called 'sunk costs') or have too much to lose (e.g. as for a recent case of a suicidal highly paid executive who hated his job, was being bullied and had early morning panic attacks, but feels he needs the income to sustain a way of life and his family). Explanations of arrested anger and depression might lead to more open discussion about brooding resentments that patients may fear to discuss or are ashamed of (Brody *et al*. 1999; Gilbert *et al*. 2004).

Control over positive events and goals

A different focus on control has been on *positive* events, rewards and goals. Two major theories in this domain are related to Klinger's (1975) model of incentive disengagement and Nesse's (2000) investment model. Klinger suggested that a reduction in positive affect helped to regulate motivation for incentives when the probability of achieving a reward becomes low. Thus disengagement results from a toning down of positive affect as incentives become unobtainable. Without this animals could continue to pursue their desires whether or not they were succeeding. Nesse (2000) suggested that downturns in positive affect could be adaptive in contexts where the pay-offs from effort and investment were low. Nesse's (2000) review highlights the fact that there is now agreement that there are complex interactions between pursuing goals and incentives, the value placed upon them, the perceived probability of success and consequence of failure – and mood. Being unable to control positive goals such as finding employment, or social engagement/isolation are well known to be depressogenic for some people, especially when people feel trapped and want to escape from low reward environments (Brown *et al*. 1995; Gilbert *et al*. 2004).

SOCIAL THEORIES

The social theories of depression suggest that while control is a salient dimension of mood one cannot equate social and non-social stressors. First, social relationships are curial to survival, coping with adversities and reproduction and, thus, to lose control over these can seriously affect inclusive fitness. Second, unlike non-social stressors, social stressors are embedded in dynamic patterns of communication. Hence, an aggressive display by a dominant may be enough to make the subordinate stop what it is doing and become tense (Sapolsky, 1989). In fact depression itself can communicate important information about the self to another that regulates the interaction (Price *et al*. 2004). Third, social stressors come from the 'minds' of individuals who will be trying to co-create various social roles (e.g. eliciting care or support, dominating or responding to risks of aggression and rejection). Stresses and losses here relate to inabilities to *influence the mind of another*(*s*) in the co-creation of desired roles; for example, a person may feel unable to influence the mind of another to either stop attacks/criticism/rejection, or elicit valued roles such as sexual, supportive or affiliative. Such concerns focus on how minds co-regulate each other, and thus on social information-processing systems (Gilbert & McGuire, 1998; Cacioppo *et al*. 2000). Fourth, and more telling perhaps, has been research in the study of resilience. This has shown that life events alone are poor predictors of depression (and other psychopathologies) and early experiences of parenting, social support and personal meaning of events influence resilience to adversity (Masten, 2001).

Attachment and social affiliation model

The most well-known social evolutionary theory, that has had an enormous influence on thinking and research into possible origins of some psychopathologies, has been attachment theory (Bowlby, 1969, 1973 1980; Cassidy & Shaver, 1999). This model posits the existence of a menu of motivational, emotional and behavioural control systems that serve the function of keeping infant and mother in close contact with each other and for providing protection/security, resources (e.g. food) and comfort/soothing to the infant. When confronted by separation from mother, juveniles are at risk from a variety of dangers and show a protest–despair reaction. Protest is designed to engage in urgent searching and to *signal*/*communicate* distress to elicit help and/or reunion; i.e. the signal is designed to impact on others. Despair is a form of behavioural deactivation when protest does not work. For most mammals, a

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distressed/searching young individual on its own is in danger of attracting predators, getting lost and/or exhausted and starving. In such contexts sitting tight and waiting for the parent to return may be the best strategy for survival. Despair is thus designed to make an animal *stop signalling* and moving in the environment (hunker down/demobilize) when not to do so is dangerous.

These primitive strategies/mechanisms are still powerful human templates for coping with separations, with evidence for genetic differences in susceptibility to the intensity of protest–despair responses (Suomi, 1997, 1999). It is possible that more intense responses represent phenotypic variations that are sensitive to highly hostile environments (Boyce & Ellis, 2005). It is now known, from both animal and human studies, that depressed states are often triggered by social losses (Bowlby, 1980; Brown *et al.* 1995; Kendler *et al.* 2003) and the physiology of protest–despair has many overlapping features with depression (Reite & Field, 1985). Moreover, there is clear evidence that problematic early relationships, where parents do not act as soothing objects but are neglectful or abusive, impact on brain development and increase the risk of mood and other disorders (Schore, 2001; Teicher, 2002; Gerhardt, 2004).

Linked to the attachment approach is evidence that the availability and abilities to use social support impact on depression (Brown & Harris, 1978; Brown *et al.* 1986). Neurophysiological studies are beginning to illuminate these connections with findings that oxytocin is linked to affiliative behaviour (Carter, 1998), to the experience of social support, and has an inhibiting effect on cortisol and stress responses (Heinrichs *et al.* 2003). Poor abilities or opportunities to develop affiliative relationships may adversely impact on this stress buffering, positive affect system (Carter, 1998).

Involuntary subordination

Other social theories have focused on the regulators of mood in the context of social conflict, and the way dominant and subordinate animals regulate conflict (Price, 1972; Price & Sloman, 1987). This has been referred to as the social rank theory of depression where involuntary subordination is highly linked to depression (Gilbert, 1992, 2000). This model was developed by Price (1972) who noted early ethological observations that depressed-like states occur in animals and humans who have been defeated and lose rank, and subordinates who are regularly harassed or threatened by more dominant animals and cannot escape (MacLean, 1990). It is known that even in 'primitive' animals social rank can affect physiological systems and responses. For example, Yeh *et al.* (1996) have shown that in subordinate crayfish, serotonin suppresses firing in the neurones controlling tail flick (a threat response) but it increases probability of firing in dominants. Harber *et al.* (1981) found that in rhesus monkeys given amphetamine (which releases dopamine), dominant animals increased their threat, chase and attack behaviours, while subordinates increased their submissive behaviour (e.g. fear grimace and turning away). These were independent effects from separate groups and not the result of the dominant animals threatening more and subordinates submitting more as a result of the drug. There is evidence that subordinates are more stressed (as measure by cortisol) than dominant animals, and take longer to physiologically recover from stressors than dominants (Sapolsky, 1989; Levitan *et al.* 2000). The threat displays of a dominant are capable of suppressing the serotonin of subordinates (Raleigh *et al.* 1984; Gilbert & McGuire, 1998). Grant *et al.* (1998) found lower D2 receptors among subordinate monkeys, hypothesizing that the stress of subordination produced a down-regulation of D2 receptors in monkeys. Shively (1999) also found that the stress of social subordination is associated with down-regulation of D2 receptors and poorer regulation of the hypothalamic–pituitary–adrenal (HPA) system. The social exchanges of harassment/threats of dominants on subordinates can mark child–parent, peer, marital and other forms of relating and may link to work on the pathological influence of high expressed emotion in families (Gilbert, 2004) and abuse (Andrews, 1998).

Such data, from the study of subordinate profiles, may also mirror work showing depression and suicide are linked to (lower) socio-economic status, especially for men (Taylor *et al.* 2005). Ostler *et al.* (2001) found depression differs between GP practices and that 48·3% of this variation could be accounted for by poverty and socio-economic status. In both animal and human groups low-ranking individuals seem to

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be at increased risk from psychological and physical disorders linked to the stress of occupying that position (Wilkinson, 1996). These evolved *social* regulators of physiological systems have not impacted on drug research that only studies syndromes, not individual and social differences.

Social defeats

Price's original model, however, focused on social defeat. There is growing evidence that in monkeys (Shively *et al*. 1997) and rodents (Rygula *et al*. 2005) social defeats and social harassment set in motion a set of *long*-lasting physiological and behavioural responses that appear depression-like (Gilbert, 2000; Levitan *et al*. 2000). Indeed, the social defeat model is now regularly used to model depression in animals (Rygula *et al*. 2005). The function of these depressed states in a social rank context are two-fold: (1) to down-regulate an animal/person's goal pursuits and behaviour and avoid directly challenging dominants (or seeking resources, e.g. sexual contacts) that could stir their attack, and keep a low and vigilant profile; and (2) to impact on the mind of the dominant such that the dominant either accepts a submission and/or sees them as inhibited/timid/compliant and 'out of action' and, therefore, as no threat to him/her (Price, 1972). Allen & Badcock (2003) have further developed these ideas to suggest that depression is linked to social threat and non-consciously engaging a risk-averse strategy. These risk-averse strategies (be they linked to social loses or defeats and entrapments) may be triggered outside conscious control or desire, and run as psychobiological organizing programmes.

The social rank model, that considers involuntary subordination and defeats, helps to make sense of the fact that human depression is significantly associated with subjective experiences of low self-esteem (Price, 2000), 'self-as-inferior-to-others', elevated submissive behaviour, beliefs that others are 'looking down' and being critical/rejecting of the self (Allan & Gilbert, 1997; Buunk & Brenninkmeyer, 2000; Gilbert *et al*. 2002), and why depression is commonly linked to abuse, bullying and social conflicts (Gilbert, 2004). Gilbert & Allan (1998) found that the subjective experience of defeat was a more powerful predictor of depression than hopelessness. The subjective experience of defeat has also been shown to have a special and powerful relationship to feeling inferior and anhedonia (Gilbert *et al*. 2002). Rooke & Birchwood (1998) found that loss of status, sense of defeat and entrapment are powerfully related to depression in people suffering from schizophrenia. Willner & Goldstein (2001) studied 76 stressed mothers and found that entrapment and defeat mediated the link between depression and stress. It is when stress is associated with a sense of personal defeat and entrapment that stress is particularly associated with depression.

In humans, the *subjective* experiences of *personal* inferiority in defeat are also crucially important. For example, Ehlers *et al*. (2000) point out that many victims of torture may feel defeated and sign false confessions, but may not feel *inwardly or personally inferior or defeated* in the sense that one has lost autonomy/identity. Mental defeat, however, is defined as, 'the perceived loss of all autonomy, a state of giving up in one's mind all efforts to retain one's identity as a human being with a will of one's own' (p. 45). They found that mental defeat, in this context, was also associated with total subordination, such as feeling merely an object to the other, loss of self-identity, prepared to do whatever the other asked, and not caring if one lives or dies. Those who experienced mental defeat had more chronic post-traumatic stress disorder (PTSD) symptoms and higher depression. Ehlers *et al*. (2000) indicate that refusing to feel *personally* inferior to one's torturers (e.g. one is morally superior to them) might help to limit mental defeat. Gilbert (1992, see pp. 209–217) noted these themes (of feeling controlled by others and not caring if one lives or dies, feeling one had lost one's identity) to be common in some depressions.

Perceptions of defeat and inferiority need not be related to direct interpersonal social conflicts, however, but to perceived failures in being able *to compete* for (social) resources, such as securing caring, supportive or sexual relationships, obtaining meaningful employment, or sufficient material resources to reduce the stress of chronic life difficulties of, for example poverty (Gilbert, 1992, 2004; Morriss & Morriss, 2000; Allen & Badcock, 2003). Brenninkmeyer *et al*. (2001) explored symptoms of burnout (which

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has overlapping features with depression, e.g. fatigue) and found inferiority interacted with burnout feelings to significantly predict levels of depression.

The interaction between affiliation and social rank/defeat

The attachment and social rank theories of depression are complementary evolutionary theories (Sloman *et al*. 2003). Both draw attention to the social dynamics of depression and suggest why non-social theories may be limited, especially for humans (Gilbert, 2004). Even an uncontrollable event, such as facing death, does not inevitably lead to depression especially in the context of feeling one is loved and cared for, which can link to spiritual beliefs as sources of comfort, and buffer against depression (Aldridge, 2000). As noted above, resilience to adversity (losses, defeats and setbacks) can arise from early, positive experiences of parenting, social support and personal meaning of events (Masten, 2001). In a major meta-analysis of subordinate stress in monkeys Abbott *et al*. (2003) found that cortisol levels in subordinates were predicted by two key variables. First, the rates of conflicts and stressors experienced, and second subordinate opportunities for affiliative kin and supportive interactions. This is intriguing because affiliative interactions may stimulate oxytocin and oxytocin can inhibit cortisol and lower stress (Carter, 1998). Oxytocin is also linked to an opiate system that can produce a calming form of positive affect (Depue & Morrone-Strupinsky, in press).

Another research paradigm that reveals an important link between personal failure and social affiliation comes from the work of Baldwin and colleagues (see Baldwin, 2005, for reviews). They found that the depressive impact of various personal failures depends on the accessibility of both conscious and non-conscious representations of others. For example, Baldwin & Holmes (1987) found that people who were primed with a highly evaluative relationship, and who then failed at a laboratory task, showed depressive-like responses of blaming themselves for their failure and drawing broad negative conclusions about their personality. Conversely, individuals who were instead primed with a warm, supportive relationship were much less upset by the failure and attributed the negative outcome to situational factors rather than personal shortcomings. In another study students were asked to generate research ideas and were then subliminally primed (outside of conscious awareness) with either the approving or disapproving face of the department professor. Those primed with the disapproving face rated their ideas more unfavourably than those primed with the approval face. Negative s*elf*-evaluation was *non-consciously* linked to approval/disapproval of another (see Baldwin & Dandeneau, 2005, for reviews of this work). Perhaps this suggests that subordinate self-perceptions are more accessible in the context of failure when the social environment is potentially hostile/rejecting. Hence, the degree to which people are able to access warm and supportive, or condemning and critical, other-to-self and self-to-self-scripts and memories has a central bearing on emotional and social responses to events and self-evaluation (see Baldwin, 2005; Mikulincer & Shaver, 2005, for reviews). In a study with adolescents Irons & Gilbert (2005) found that the link between insecure attachment and depression was mediated via rank concerns (feeling inferior and submissive behaviour) but this was not so for securely attached adolescents.

The emerging picture points to depression, and the toning down of positive affect, as outcomes in the face of social adversity, where one feels inferior to others, defeated in being able to reach valued goals, and the social environment is perceived as potentially rejecting and condemning. Intriguingly Keller & Nesse (2005) have recently found some evidence in mild low mood that the nature of the stressor predicts symptom profiles. They found that social loss events tended to predict crying and sadness while thwarted goals are associated with pessimism and fatigue symptoms. This may indicate that loss events trigger protest-type responses, whereas failures to reach goals trigger a more defeat-like profile. Since they did not control for the perceived helpfulness of, or rejection in, the social environment it is impossible to know if such 'defeats' exert their impact on mood primarily because the social context was perceived as unsupportive, rejecting and/or to result in changes in social status and standing.

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ADAPTIVE AND MALADAPTIVE DEPRESSIONS

Evolutionary theories do not suggest that all depressions or anxieties are necessarily adaptive in all environments. In fact phenotypes can operate outside their adaptive range when they are: too easily triggered, too intense, frequent or long lasting. Understanding which depressions are adaptive in which contexts is complex, for much depends on the associated reproductive costs and benefits, and frequency dependent selection (Wilson, 1998; Wakefield, 1999). The reasons phenotypes can come to function maladaptively have been articulated by Nesse & Williams (1995) and Gilbert (2001). Space does not allow exploration of these here, but we can mention two key aspects.

Integration of new with old functions relate to how new and old functional abilities operate and are choreographed together (MacLean, 1990), as for example, the way our earlier evolved threat detection-response systems (e.g. for anxiety) can overwhelm logical thinking (LeDoux, 1998). Price *et al*. (2004) argue that different brain areas can control different elements of depression and that at times these can conflict, as in someone who loses energy, but remains cognitively committed to try to pursue goals, or someone who becomes angry but consciously fears anger and inhibits expression.

Some depressions may arise as a result of new adaptations within the brain; e.g. the moderating effects of cortical mechanisms on limbic affect/motivation systems (Henry, 1993) and new competencies for thinking. For example, human depressions have been linked to our evolved human capacities for self-reflective thinking (Beck *et al*. 1979), rumination (Lyubomirsky *et al*. 1999), anticipating a (poor) future, and meta-cognition (Sheppard & Teasdale, 2000). While such competencies can offer huge advantages in flexibly adapting to an environment, the trade-off depends on their focus and how they are used. Just as we can stimulate sexual arousal via internal thoughts and images, or stimulate excitement via anticipation of positives, so humans can stimulate depression pathways by their own self-focused (negative) thoughts and images. Related to this is the way that humans can be self-critical to such an extent that they literally beat themselves down into a depression and are 'harassed' repeatedly by their on negative self-evaluations (see Gilbert, 2004; Gilbert & Irons, 2005, for reviews). This 'self-harassment' concept has also been used to explore some of the depression associated with voice hearing in psychosis (Gilbert *et al*. 2001) and as a target for psychological interventions (Gilbert & Irons, 2005).

There is much in cognitive-behavioural and other psychotherapies that seek to help depressed people by breaking up these 'feedback loops' between thinking, feeling and behaving that continue to stimulate depressive defences/systems. Research is beginning to explore the physiological impact of psychotherapy (Cozolino, 2002; Schwartz & Begley, 2002; Davidson *et al*. 2003). Developing psychological therapies specifically because they can stimulate neural pathways is yet to impact on psychotherapy but is being used for other disorders such a post-stroke rehabilitation (Taub, 2004). From an evolutionary point of view, in altering some physiological systems, psychotherapy might help re-set low-mood, defensive strategies, making psychotherapy a means of changing phenotype expressions.

Contextual overload, constraint and niche change, can arise when modern life-styles overload physiological systems; for example the cardiovascular system was not designed to cope with high fat foods, low exercise and smoking. *Contextual constraint*, occurs where new environments constrain adaptive behaviours; i.e. human marriage systems may constrain escape behaviour from an abusive other. *Rapid niche change*, occurs when change results in new demands or inputs. The rising rates of diabetes and heart disease, for example are linked to dietary changes in sugar and salt intake (Smith, 2002). Dietary alteration (e.g. low omega-3 or folate intake) may be linked to some depressions with genetic individual differences increasing risk. There is increasing concern over the toxic industrial chemicals in our environment and their impact on physical and mental health. All these point to evolved limits in our abilities to adapt to environment variation.

Although civilization has brought many advantages and comforts it also has many down sides. Relative poverty (Ostler *et al*. 2001), low social support (Brown *et al*. 1986), intense

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individualized competitiveness (Wilkinson, 1996; Kasser, 2002), alcohol use, high social conflicts in families or communities where individuals can not escape from each other, and war, have all long been implicated in depression. These social dynamics may vary greatly from some primate and early human, small-stable group-living, based on mutual support and relative freedom to distance oneself from hostile others (Boehm, 1999). As such they represent new stresses of modern life. Social conditions and relationships can be breeding grounds for depression and other disorders, in part via their impact on various neurophysiological mediators of phenotypes (Pani, 2000). Any preventive endeavours will need to address environmental factors, as it is the environment that sculptures phenotypes for depression, and can push some beyond their adaptive ranges. Neurophysiological patterns in (some) depression(s) may be the signatures of these effects not their cause.

CONCLUSION

This short review has not explored all the various evolutionary theories that have been suggested for depression, nor has it sought to explain variations in the reproductive strategies that might underpin depression (Wilson, 1998). Rather it is suggested that depression (as the toning down of positive affect) commonly emerges from the activation of defensive strategies that evolved in pre-human times. Our brains appear to be wired to tone down positive affect in contexts of poor attachment and affiliation. In addition, people compete for social resources and when this competition is going badly (people think they are failing, and or/are inferior, shamed and defeated), especially in the context of perceived unhelpful social environments and negative schema of others (Baldwin, 2005), depression can be triggered. Moreover, for humans, harassment and attacks do not just arise from the external world but can become part of self-to-self relating, with good evidence that self-criticism and self-attacking are sources for depression (see Gilbert & Irons, 2005 for a review). The power of affiliation to buffer against stress, offers one reason for trying to help people develop supportive affiliative relationships, and learn to be self-compassionate. These may stimulate internal (opiate-oxytocin based) soothing systems (Carter, 1998; Gilbert & Irons, 2005).

An evolutionary analysis can help us think about evolved strategies that can regulate psychobiological patterns of activity, often outside consciousness, and their function. Individual differences stalk this territory, and biological, psychological and social theorists are calling for better integrative research (Eisenberg, 1986) and, individually tailored therapies. Humans did not evolve *de novo*, and legacies of past adaptations, and new social environments, can be sources of much personal misery. Social stresses, in the form of social harassment, social insecurities and elevated competitive behaviour, defeats and lack of affiliative relations are key sources of depressed states for rodents, monkeys and humans. Defensive toning down of positive affects in these contexts seems to be part of evolved design. Under what conditions we should call such phenotypic expressions pathological, is not easy to say. Clearly, however, treating and preventing depression requires a biopsychosocial focus that recognizes our evolved needs and vulnerabilities.

DECLARATION OF INTEREST

None.

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