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Essay

Territory, Rank and Mental Health: The History of an Idea

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Abstract: We trace the development of ideas about the relation of mood to social rank and territory. We suggest that elevated mood enabled a person to rise in rank and cope with the increased activities and responsibilities of a leadership role, while depressed mood enabled a person to accept low rank and to forego the rewards associated with high rank. This led to the concept of a trio of agonist/investor strategy sets, each consisting of escalating and de-escalating strategies, one set at each of the three levels of the triune forebrain. Depressed mood can be seen as a de-escalating (appeasement) strategy at the lowest (reptilian) level; this should facilitate de-escalation at the highest (rational) level, but sometimes this rational level de-escalation is blocked (e.g., by stubbornness, courage, pride or ambition) and then clinical depression may ensue. These evolved psychobiological mechanisms survived the partial transition from agonistic to prestige competition. We discuss difficulties which have arisen with our ideas, and their implications for clinical work and research.

Keywords: agonistic competition, escalation/de-escalation, depressive illness, evolutionary epidemiology, social rank (hierarchy), territory

Introduction

About thirty years ago four psychiatrists, independently, started to think about mood and anxiety disorders from an ethological, functional, adaptational and evolutionary perspective.

Albert Demaret, who is an ornithologist as well as a psychiatrist, observed that his patients with elevated mood behaved rather like birds strutting and swaggering about on their own territories, whereas his depressed patients behaved like birds on another bird's territory, hopping furtively about and not inclined to break into song (Demaret, 1971, 1979). He thought that if evolution had designed the contrasting social roles of territory owner and non-territory owner, then it should also have designed behaviors to fit those roles, and what could be better fitted to perform that function than elevated and depressed mood? Unfortunately Demaret (who practices in Belgium) did not publish in English, and so his ideas have not received the attention they deserve in the UK and US.

Russell Gardner, Jr., who was Professor and Chair of Psychiatry in North Dakota (and later became Harry K. Davis Professor of Psychiatry in Galveston, Texas), was impressed by the similarity between patients with elevated mood and normal leaders, and suggested that mania communicated leadership intent but out of context (Gardner, 1982, 1988). His patients were communicating high rank signals in the absence of high rank; and likewise his depressed patients communicated inappropriately low rank. He thought that these rank signals had ancient evolutionary origins. He stressed the need for a normal physiology of mood changes in both man and animals – reconceptualizing them as “communicational states”. To clarify those extreme mood changes which are seen by clinicians he suggested a new discipline of sociophysiology should investigate how these might normally operate (Gardner, 1997).

John Price had come under the influence of Niko Tinbergen while reading Psychology at Oxford, and later, while working in the Emergency Clinic at the Maudsley Hospital in London, he was impressed by the similarity between his depressed patients and the low ranking long-tailed macaque monkeys seen in a film shown by ethopharmacologist Michael Chance (Price, 1967, 1969, 1972, 1998). Looking back at those hen-pecked animals, he thought that if they could talk and were allowed access, they would be queuing up at the Emergency Clinic to complain of anxiety, depression and widespread aches and pains. It seemed obvious that if you had to have social hierarchies, you had to have behaviors appropriate to the different positions in the hierarchy that individuals came to adopt, and especially you had to have behaviors to mediate going up and down the hierarchy – and it seemed that elevated and depressed mood were “tailor-made” to contribute to the performance of that task. Literature describing hierarchies in non-human primates was scarce at this time, the most informative were those by Zuckerman (1932) and DeVore and Hall (1965).

Leon Sloman (1976, 1979, 2000) pointed out that neurotic depression and anxiety impair function, so that, to the extent that depression is the result of failure to achieve, the depressed person will achieve even less than he did before, resulting in a vicious circle or positive-feedback situation between depression and impairment of function. Such a state of maladaptation would impair breeding success, compounded also by assortative mating for maladaptation. Moreover, the original causes of failure to achieve, which are likely to be related to small genetic differences in skill and intelligence, will be magnified by this

positive-feedback process, thus accelerating the evolution of abilities including intelligence. Because this formulation was criticised for being a “group selectionist” argument (Pitman, 1981), Sloman (2000) changed the premise by focussing on the “cycle of adaptation” associated with success. This is based on the notion that success leads to feelings of mastery, and improves self-confidence and assists the individual to rise to new challenges. The “maladaptive cycle” is now relabelled as an unravelling of the cycle of adaptation. Healthy adaptation involves either prevailing in the competitive struggle or a ready acceptance of defeat. Failure to achieve this can lead to the negative cycle of clinical depression.

These ideas converged on the conclusion that the phenomena we were observing in the clinic were part of an evolved mechanism for creating and managing social asymmetry – the asymmetry between the owners of territories and non-owners, and the asymmetry between high-ranking individuals and low-ranking individuals. States of high and low mood appeared adapted not only to create asymmetry, but also to maintain asymmetry once established, and to reverse asymmetry in the cases of loss of rank or territory. It seemed likely that more intense mood states were required for the creation and reversal of asymmetry than for the maintenance of asymmetry.

After formulating these ideas, it came as a pleasant surprise to learn that they had already been anticipated by a Norwegian zoologist who was the first to describe social hierarchy (or peck order) in animals. Thorlief Schjelderup-Ebbe (1935) described a low-grade depression in his low-ranking hens and a severe, life-threatening depression in alpha birds who were deposed from their high status. It seemed unlikely that “neurotic” (mild) and “endogenous” (severe) depression had a separate phylogeny stretching back to the common ancestor of domestic hens and human beings, but rather that the very nature of hierarchies was likely to give rise to different mood states to subserve change in rank on the one hand and the maintenance of low and high rank on the other (Price, 1969, Price and Sloman, 1987).

It may seem inconceivable now, but at that time (in the 1970s) it was politically incorrect to write about social hierarchy much less any biology of human behavior. The buzz-word was “equality” and those who wrote about inequality were assumed to approve of it and were labelled fascist. It therefore seemed more tactful to frame our ideas in terms of the behavior which leads to the formation of territories and hierarchies; namely, ritual agonistic behavior. Depression, and neuroticism, could be thought to have evolved as part of the yielding component of ritual agonistic behavior, leading to low rank and loss of territory. There is a ritual quality to depression, which gives the impression to sufferers and observers that it is not “real” in some way, and that all the sufferer needs to do is to “snap out of it” or “pull himself together” and the whole thing would vanish like smoke. In this way we could see depression as being the result of ritual combat, so that the psychological incapacity of depression represents a ritual equivalent of the physical incapacity which may follow unritualised combat, or we could even say that it was a ritual equivalent of death. When this idea was put to some of our depressed patients, they replied that they did indeed feel “dead”.

These ideas depended on the plentiful observations of ethologists on ritual agonistic behavior in a wide variety of species (Huntingford and Turner, 1987, Huntingford, Taylor, Sneddon, and Neat, 2000), and soon they were supported by the mathematical calculations of behavioral ecologists (Krebs and Davies, 1981, 1997; Maynard Smith, 1982), who

showed that in the analysis of pairwise contests it was necessary to have both “hawk” genotypes who always escalated the contest and “dove” genotypes who always capitulated (or you could have mixed genotypes who played hawk on some occasions and dove on others). The idea of mutually incompatible alternative behavioral strategies was becoming popular in ecology, and it seemed appropriate to describe elevation and depression of mood as related, respectively, to escalating and de-escalating strategies, which had evolved in relation to ritual agonistic behavior, but had become relevant to other and more diffuse types of competition, such as competition for prestige.

The match of escalation/de-escalation with elevation/depression of mood

Many of the features of mood disorders could be accounted for by changes in the three variables which are needed to predict winning and losing in pairwise contests: Resource Holding Potential (RHP), Resource Value (RV), and ownership (Krebs and Davies, 1981). RHP is a self-concept representing fighting capacity, and in some complex way animals are able to compare their estimate of their own RHP with that of their rival, so avoiding unevenly matched contests. It seems likely that RHP is one of the forerunners of human self-esteem (Price, 2000), and we know that self-esteem and mood co-vary, so that our manic patients have an elevated sense of their own power and importance, while our depressed patients tend to feel inferior and insignificant. The second variable predicting the outcome of contests is Resource Value, or the value which the contestant attaches to whatever is being fought about; and we know that to manic patients things tend to seem significant and important, while to depressed patients the various prizes of life seem so much dust and ashes – to them, nothing seems worth doing, let alone fighting for. The only other relevant variable is ownership, in that, in most species, the owner of a territory tends to win a fight, while the intruder loses – and here there is a vast difference between manic patients, who tend to think they own the whole world, and depressed patients who may feel they own nothing at all, and do not deserve even the room they take up in space.

Thus, when a person adopts an escalating strategy, he or she undergoes an increase in RHP, Resource Value and sense of entitlement (Ownership), experienced as a surge of elevated mood, and in such a state is likely to win whatever conflict he or she is engaged on (unless the elevation of mood is excessive, as seen in clinical hypomania, in which case the patient becomes too disorganised to win anything). Conversely, an individual adopting a de-escalating strategy undergoes a decrease in self-esteem, Resource Value and Ownership, and these changes are experienced as depressed mood, which makes that person more likely to lose a conflict, and to accept that he or she did not deserve to win and so accept reduced social rank and reduced access to resources.

Contributions from younger colleagues

At this stage we were joined in our efforts by several younger colleagues, who all made important contributions. Daniel Wilson, a psychiatrist who trained in anthropology at Cambridge (UK) and in psychiatry at McLean Hospital and Harvard Medical School, took a genetic epidemiological approach and – encouraged by E.O. Wilson and Ernst Mayr – showed that psychiatric epidemiology (and, indeed, all of medical genetics) could be reformulated in terms of evolutionary population genetics. This new evolutionary epidemiology could begin to clarify whether traits associated with specific forms of epigenetic psychopathology – notably affective disorders – were more prevalent in the

population than would be expected by random mutation. If so, this indicated fitness advantage at least in the environment of evolutionary adaptation (Wilson, 1989, 1993, 1994 a and b, 1998).

The fitness advantage of depressed states is not immediately apparent. In fact, to the extent that genetic success depends on social success, the depressed patient does not appear, and certainly does not feel, destined for success. We should note, however, the high correlation between the features of depression and those qualities which make for social success. The fact that this correlation is negative reflects the fact that failure, losing and submission are essential features of the kind of competitive social life which has evolved in vertebrates, and without a well-developed capacity for submission social life would not be possible (MacLean, 1990). This intuitive view is reinforced by the calculations of behavioral ecologists, who have shown that a mixed strategy of escalators (hawks) and de-escalators (doves) is evolutionarily stable under most conditions, whereas a strategy of pure hawk is not (Maynard Smith, 1982). The ability to select a hawk or dove strategy (probably on a randomized basis) may be adaptive to a degree, but is seen in excess in our bipolar patients.

Paul Gilbert, a professor of clinical psychology in Derby, UK, carried out surveys on depressed patients documenting that they do indeed show characteristics associated with low hierarchical rank (Gilbert, 1992, 1993, Gilbert and Allan, 1994, Gilbert, Price and Allen, 1995); he also clarified how social competition in mammals evolved beyond agonistic to prestige competition, an important theoretical development to which we will return. Linda Mealey formulated a compelling evolutionary epidemiological explanation of how sociopaths adopt a strategy of freedom from altruism so that they are not bound by affective attachment, reciprocal sociability and devotion to the common good (Mealey, 1997). This strategy works provided there are not too many of them, reflecting a phenomenon called negative frequency-dependent selection, in which a strategy's fitness depends on its rarity. It also applies to hawks and doves, in that the advantage of being a hawk increases as the proportion of hawks in the population falls. This is a powerful mechanism for maintaining genetic variation in the population, and may help to counter the argument that if any traits such as those predisposing to mental illness were adaptive, they would have been selected to fixation, and therefore should not manifest heritability (Price, 2006; Wilson, 2006).

Mark Erickson was impressed by the altruism which occurs between close relatives, and he explored the possibility that this "familial bonding" might occur as a result of close association during early childhood, and might indeed be a part of the incest avoidance mechanism which prevents romantic attachment between individuals brought up in the same household (Erickson, 1993).

Peter Rohde, a psychiatrist working for the NHS in London and also in Harley Street, reported that our hypothesis was useful in his clinical work, and he added the observation that the agonistic encounter important to the patient can be with an element of his or her own mind rather than with an external person; he also pointed to the lack of attention to hierarchy in social science literature (Rohde, 2001).

Catalytic influences during these years were the Birmingham Group which revolved around the late ethopharmacologist Michael Chance, and the ASCAP Society (Across Species Comparisons and Psychopathology). In particular, the ASCAP Newsletter (followed by the ASCAP Bulletin) edited by Russell Gardner, Jr. provided an informal and

hedonic forum for the exchange of ideas (the hedonic mode, contrasted with the agonistic mode, was an idea generated by Michael Chance (Chance, 1996; Price, 1992; Kortmulder and Robbers 2005).

In spite of these contributions, our theory did not gain wide acceptance. In part this was due to an exponential growth in all manner of evolutionary psychological ideas over the past two decades (Mysterud, 2004). Still, the time had come for a critical examination.

Discussion

We realised that there were problems with the hypothesis:

1. A lot of high ranking people are depressed.
2. A lot of low ranking people are happy.
3. Ritual agonistic behavior has been called “inter male aggression” because in most species it is the prerogative of the male, but depression is commoner in human females in a ratio between 2:1 and 3:2.
4. Depression tends to follow what social scientists call “exit events” such as death and desertion by loved ones, rather than by the “entry” of a rival or competitor.
5. Depressed patients can be quite powerful and stubborn. Aaron Beck advised, “Do not lock horns with a depressed patient or you will be pushed right out of the office (consulting room)” (Beck, 1974).
6. Depressed patients do not express submission to individual people, and their skills at appeasement displays such as flattery are impaired (Schelde, 2000).
7. In a different logical category, is it a good thing to classify depressed patients as “losers”, and so possibly stigmatise them (Klerman, 1974)?

There are a number of reasons why there is an imperfect correlation between mood and social rank. One is ambition or “up-hierarchy motivation” – if one has no ambition, then low rank may not be depressing. Another is the existence of multiple hierarchies – for instance, a man who is high-ranking at work may be depressed because is dissatisfied with his low rank at home, and vice-versa.

The human female may be not much less aggressive than the male, but the aggression is expressed in different ways – for instance by social exclusion rather than by fighting, and the weapons used are verbal rather than physical. Also, the female is exposed to situations which the male does not encounter, such as domination by a mother-in-law. Moreover, because of the lesser variation in fertility among females, a de-escalating strategy may be less of a disadvantage.

There is no doubt that depression follows exit events, such as bereavement, separation, rejection and betrayal. Bereavement may lead to loss of rank, especially in widows, but it may lead to a rise in rank, as when a son inherits a title from his father. We

can, at least, say that exit events are likely to lead to rank instability. Even among Old World monkeys, rank is determined by patronage, kinship and alliances as much as, or even more than, by individual qualities. It is not surprising therefore that human should be exquisitely sensitive to the social effects of bereavement and other exit events (Price and Gardner, 1995b).

We dealt at some length with the problem of the power apparently wielded by depressed patients and the fact that they often appear aggressive (Price and Gardner, 1995a). The important thing is the object of the aggression. If we divide the social environment into loving supporters on the one hand and competitors on the other, then there are two categories of people who are the recipients of the aggression of depressed people. One such group is the loving supporters, and the other is lower-ranking competitors. That this simple distinction is not generally understood is revealed by the surprising fact that in all the extensive work that has been carried out on the aggressiveness of depressed patients, the relative rank of the recipient has never been recorded, nor whether that person was a supporter or competitor. For one thing, a contestant in a fight or other conflict is often acting as a representative of a group of allies, who are supporting the contestant and making, as it were, aggressive noises in the background. So that when the protagonist de-escalates he or she must force the supporters to de-escalate too, and this may require some forcefulness – the message is, “Do not force me into the arena to fight on your behalf, and stop making those aggressive noises, otherwise my submission will not be accepted, and moreover, you might like to treat me as sick and succour me.” And thus we are in the common situation of having a patient apparently suffering from a physical disease, and who forcefully insists on a physical diagnosis which will support the de-escalating strategy of being “off sick” or “out of action” (Price, Gardner and Erickson, 2004).

Another reason for the aggressiveness of depressed patients is that the de-escalating strategy applies to those who are higher-ranking and/or have just defeated them, and not to those lower in the hierarchy. If alpha falls to beta, then gamma may hope to get in on the action and rise to beta, so the new beta may be aggressive to gamma in order to prevent a further fall. Thus lower-ranking competitors may experience an increase in aggression from depressed patients.

Regarding the lack of focussed submissive behavior in depressed patients, we consulted with Tyge Schelde in Denmark, who has spent many years carrying out ethological studies of depressed patients (personal communication; see also Schelde, 2000). He told us that when he divides appeasement into active and passive, he finds that the depressed patients are low on active submission but high on passive submission: they showed a lot of involuntary submissive behaviors but not a single voluntary submissive behavior. We developed the idea that the submission of depressed patients is a passive, involuntary process, which we variously called the “yielding subroutine” or “the Involuntary Subordinate Strategy (ISS)”. Then we read about Paul MacLean’s triune brain theory. It was like shining the white light of escalation/de-escalation theory through the prism of triune brain theory, revealing a double triptych in which the escalatory and de-escalatory behaviors at the three brain levels were revealed in their primary colors (Table 1).

A triune mind in a triune brain

The idea that the mind consists of two or more relatively independent entities has been around at least since the time of Plato. It has been most pithily expressed by Pascal in his aphorism, “The heart has its reasons which the Reason knows nothing of.” Ancient Eastern philosophers, whose ideas were largely promulgated in the West by Gurdjieff, used the metaphor of the cart, horse and driver. The driver represented Reason, or the rational mind, but he had only limited control over the horse, who represented the emotional mind (located in the heart), who in turn had limited control of the cart, representing the instinctive mind, located by some in the gut. Plato likened the three minds to different organs of state.

Table 1. Escalating and de-escalating strategies at three brain levels: agonistic competition.

The Triune Model for Escalation/De-escalation			
	Escalate		De-escalate
Rational level (isocortex)	Decide to fight on (stubbornness or courage)	or	Decide to back off (submission or escape)
Emotional level (limbic system)	Feel assertive, angry or hostile	or	Feel inferior (anxiety, depressed emotion)
Instinctive level (basal ganglia)	Elevated mood	or	Depressed mood Anxious mood

The work of the evolutionary neuroanatomist Paul MacLean has given support to the idea of the triune mind by his demonstration of a triune brain (MacLean 1985, 1990). Prior to MacLean, it was thought that over the course of evolution the brain had gradually grown in size, with the later additions on the whole controlling the earlier parts, largely by inhibition. MacLean pointed out that the forebrain had grown in three distinct stages, leaving three “central processing assemblies” which relatively independently respond to changes in the environment. Firstly, the reptilian forebrain evolved from the fish and amphibian brains and concerned itself, as far as social relations went, with the courtship of the opposite sex, and competition with the same sex by means of agonistic behavior. This brain is present in all reptiles, birds and mammals, and in humans it occupies the basal ganglia or corpus striatum. Then, instead of a homogeneous accretion of additional brain volume, there developed a “paleomammalian brain” which dealt with mammalian social life, the family, the parent/offspring bond, play, and such social matters as were not part of reptilian social life. This brain is situated in the limbic system. And not only did it deal with mammalian matters, but it also dealt with those problems which had been faced by reptiles and were also faced by mammals, such as the courtship of the opposite sex and competition with the same sex. In higher mammals there developed the neomammalian brain which subserves what we recognise as rational thought and decision-making, and it brings these capacities to bear not only on modern problems such as technology and litigation, but also on the older problems which are addressed by the reptilian and paleomammalian brains such as courtship and competition. This neomammalian brain is situated in the neocortex.

Thus we have three brains dealing with the same problems, and to some extent they co-operate, but also to some extent they act independently. They have different sources of information, they make different executive decisions, and they have different representations in awareness. This is quite a surprising situation, one that would not have been predicted, say, by an engineer accustomed to designing robots. The most surprising thing is that the rational brain, which appears to be the most sophisticated thinking machine ever to have evolved, has so little control over the two lower brains. The driver is not in control of the horse or the cart. It would have been easy for such control to have evolved, so the fact that it has not evolved suggests that there is some advantage in having one or more relatively independent lower “central processing assemblies”. In competitive relations with conspecifics, a decision frequently has to be made between escalation (fighting harder) and de-escalation (fleeing or submitting) and this decision appears to be made, relatively independently, by each of the three brains, sometimes sequentially, sometimes simultaneously. Possibly the rational brain, in order to maximise fighting ability, has abandoned the contemplation of possible defeat to fail-safe mechanisms at the lower brain levels.

Agonistic competition at three brain levels

As we have said, decisions to escalate or de-escalate take place either simultaneously or consecutively at all three levels of the triune brain (Table 1).

At the rational, or neomammalian level, the decision is made consciously and voluntarily either to escalate by fighting harder or to back off; escalation may take many forms, such as insulting or attacking the opponent, obtaining a weapon or recruiting allies; when de-escalating or backing off, the appeasement display may take the form of a graciously worded apology, or a flowery speech of submission. At the emotional or limbic level, escalation takes the form of anger, indignation and the exhilaration of combat, with its associated bodily changes; de-escalation at this level may recruit the dysphoric emotions of anxiety, depression and the sense of being chastened. At the instinctive level, we hypothesize that escalation in the reptilian brain takes the form of elevated mood, giving the individual a prolonged increase in energy, optimism and self-confidence; since mood is pervasive and, from its origin in the reptilian brain, affects all the higher levels of the brain, in the human (and probably the chimpanzee) it will increase sociability with which to recruit allies. Conversely, de-escalation at the instinctive level takes the form of depressed mood and may include unfocused anxiety, fatigue and a sense of physical disability. The appeasement display at this level communicates this impairment and disability to any rival or to society as a whole. Parenthetically, when directed at friends and allies, the appeasement display takes the form of a distress signal, sending the message, “I am sick, care for me, and do not send me into the arena to fight on your behalf”. We have suggested that the submission of the depressed patient is often communicated by the metaphor of physical illness (Price, Gardner and Erickson, 2004) in the way that the submission of animals may be communicated by the male/female metaphor (monkeys) or the parent/child metaphor (wolves). If this metaphorical communication is denied by the doctor who refuses to give a physical diagnosis, the patient may feel frustrated, and this may account for the search for alternative diagnoses such as myalgic encephalomyelitis (ME).

Prestige competition overtakes agonistic competition

Methods of competition have become more complex over the course of evolution. Group living lengthened the duration of contests, so that even in apes a struggle for dominance may take several months to be resolved. And, instead of fleeing, as happens in territorial species, the loser could remain in the group with the winner of the contest, and this gave rise to appeasement or submissive behavior, which reflects the capacity to live in a subordinate social role. Anxiety and fear of the dominant individual, together with relatively low self-esteem and lowered mood, enabled the social hierarchy to maintain stability, and prevent rebellion. At some stage in evolution, this stabilising anxiety gave rise to a new way of relating to a higher-ranking individual: respect. The leaders of the group made themselves attractive to the group members instead of (or in addition to) intimidating them. Social rank was then determined by the choice of the group rather than by agonistic dyadic encounters. The new self-concept of Social Attention Holding Power (SAHP) (Gilbert, 2006) began to replace RHP, as group members evaluated themselves according to their power to attract interest and investment (such as votes or other forms of political support). Related to SAHP is the concept of prestige, which is the extent to which the group is prepared to invest in the individual. Prestige competition was added to, but did not entirely replace, agonistic competition (Barkow, 1991).

The capacity for escalation and de-escalation appears to have survived the switch to prestige competition, but takes different forms, at least at the upper two forebrain levels. At the highest level, pursuit of goals replaces the decision to attack, so that escalation consists in the adoption of new goals, and de-escalation consist of giving up goals. The goals are usually ones that lead to prestige, if achieved. Also, on social occasions, escalation takes the form of self-assertion, such as standing up to speak, and promoting one's own goals, whereas de-escalation takes the form of self-effacement, and allowing other people's goals to take precedence in the group.

At the emotional level, escalation is less dramatic than the anger of agonistic competition; it takes the form of exhilaration, enthusiasm and self-confidence. De-escalation reflects the fact that punishment comes from the group rather than from a dominant individual, so there is social anxiety, guilt and shame. This is an appeasement display to the group, expressing contrition for breaking group rules, or for failing to come up to group standards.

At the instinctive, reptilian level of the forebrain, little seems to have changed: elevation of mood represents escalation, and depression of mood de-escalation. However, the information which leads to the activation of the strategy set is clearly different. Instead of measuring punishment received from the rival, the reptilian brain in some way monitors social standing in the group, and is sensitive to group approbation and disapprobation, to comparison of self with other group members, and with one's own aspirations, and to the knowledge of having failed the group in some way by not living up to its standards, or, having broken the group's rules, to the likelihood of being found out. Note that depressed and elevated mood are "all or none" things; whereas at the higher levels it is possible to escalate in some areas of life and de-escalate in others, in the reptilian brain the mood change is pervasive and affects all aspects of life – it is not situation dependent. This may reflect the pervasive change in the defeated reptile, who often loses his gaudy adult coloring and reverts to the dull brown or green of the adolescent coloration.

The manifestation of escalation and de-escalation at the three brain levels are shown for agonistic competition in Table 1 and for prestige competition in Table 2.

Table 2. Escalating and de-escalating strategies at three brain levels: prestige competition.

The Triune Model for Escalation/De-escalation			
	Escalate		De-escalate
Rational level (isocortex)	Adopt new goals, actively pursue existing goals, assert oneself	or	Give up goals, efface oneself
Emotional level (limbic system)	Feel assertive, exhilarated and enthusiastic	or	Feel inferior (shame/guilt/sense of failure, social anxiety)
Instinctive level (basal ganglia)	Elevated mood	or	Depressed mood Anxious mood

Different decisions at the three levels

Normally a “resource challenge” will activate only one or two of the three levels, and then, if anger accompanies rational escalation, the individual is likely to win the conflict and the resource challenge is dealt with. Or, if chastened mood accompanies rational submission, the individual loses the conflict and becomes reconciled to the loss of whatever was at stake.

However, two very human tendencies may lead to trouble. Our often implacable ambition and stubbornness may lead to prolonged escalation at the rational level in situations in which victory is extremely unlikely, and then the anticipation of losing may activate the reptilian level strategy set and select for de-escalation at that level. The resulting incapacitating depression makes winning even less likely, and a chronic situation results in which there is continued escalation at the rational level and continued de-escalation at the instinctive level. This is a common manifestation of depressed mood as seen in the clinic, as first pointed out by Edward Bibring (1953) who noted that his depressed patients were often clinging on to unrealisable goals. Of course success may be achieved in spite of depression, and this may have been the case with Milton and Darwin, both very brave and dedicated men, but who had to battle to achieve their goals, Milton incurring the wrath of the Royalists, and Darwin the wrath of the Church (Price, 1999).

The other human tendency is our desire to see fair play and our intolerance of injustice – this manifests at the emotional, limbic level, which seems finely tuned to evaluate the fairness of events and particularly of other people’s actions. If we feel we have been treated unfairly we feel angry, and if this anger is ineffective in righting the situation, our reptilian strategy set may be activated and we have a mood change. If elevation of mood is selected, we may then have enough energy to right the wrong, but if depression is selected, the depressive incapacity then makes effective action even more impossible. Then, again, we get chronic reptilian de-escalation which presents in the clinic as depressive illness.

Case examples

In order to give an idea of how these things appear in the clinic, we will give some case examples, disguised to maintain confidentiality.

Case A: Rational escalation and instinctive de-escalation. A highly moral lady had a job taking classified ads for a magazine. The magazine started losing money and the manager was desperate to increase the advertisement revenue. He required the patient to take ads from call girls. She refused to do this and received a lot of negative signals from the manager and other staff and eventually went off sick with depression. In the treatment of such a patient, we do not direct attention to the depressive symptoms, but rather ask the patient why they have not dealt with the problem at a higher brain level. We say to them, “If you came to us complaining of shivering, we would not rub ointment on your shivering muscles, but rather we would ask why you had not turned on the central heating.” One treatment option for her is to forget the magazine and get another job. But she was too angry with the manager (escalating at the emotional level too) to let it go, and she instructed a lawyer to take action against the magazine.

This patient had refused to submit to her manager because of high moral standards. We have seen a case of depression in a health service clerk who refused to “fiddle” waiting list data in order to make the waiting time appear to be getting shorter. Sometimes the required submission is not to management but to colleagues. We have seen depression in workers who refused to take part in systematic theft. Stevens and Price (2000) described a hospital porter who became depressed because he refused to take sick leave when he was not sick (and so allow his colleagues to claim overtime pay). These are all cases in which adherence to moral values prevents voluntary submission. Other blocks to voluntary submission are pride, stubbornness, sense of fair play, and in general the sort of mental state which made Job say, “I will never submit” and Garibaldi to say, “Rome or death!” (Pick, 2005). In these cases, while voluntary submission is blocked, the involuntary submission of depression may take over the direction of behavior.

Table 3. Case A. Blocked de-escalation at the rational level due to moral standards.

The Triune Model for Escalation/De-escalation			
	Escalate		De-escalate
Rational level (isocortex)	Refused to obey manager’s instructions	or	
Emotional level (limbic system)	Angry with manager	or	
Instinctive level (basal ganglia)		or	Depressed mood Anxious mood

Case B: Emotional escalation and instinctive de-escalation. A couple had a daughter who at the age of nine developed a pituitary tumor. This led to premature puberty and menstrual bleeding. The parents took the girl to hospital, where the father was

detained by social services, aided by the police, for twenty four hours, accused of sexually assaulting his daughter, and he was not allowed to return to the family home until the diagnosis of pituitary tumor was made some weeks later. The parents were overwhelmingly angry at the treatment of the father, but they did not have the social skills to seek redress – it was the mother who came to the clinic some years later suffering from depressive illness.

Common causes of emotional escalation (anger) are mistreatment by management or official bodies, or by fate, as when parents suffer the death of a child at the hands of a drunken driver. In Palestine depression may be due to punishment by the occupying power (Costin, 2005). In these cases it is helpful for the patient to join a group of those who are similarly afflicted. Then the anger can become group anger, and the depression may remit as depression is part of ritual agonistic behavior and not of inter-group conflict. Also the anger may be directed into useful channels, such as lobbying for stricter drink/driving laws. In Palestine, the groups organised by the health service also reduce the chances that victims will join groups for training suicide bombers.

Table 4. Case B. Has given up trying but still feels angry

The Triune Model for Escalation/De-escalation			
	Escalate		De-escalate
Rational level (isocortex)		or	Gave up making formal complaint
Emotional level (limbic system)	Still feels extremely angry	or	
Instinctive level (basal ganglia)		or	Depressed mood Anxious mood

Case C: Triune de-escalation but submission not accepted. A morbidly jealous man had financial difficulties and so his wife went out to work, and the husband fantasised that she was meeting other men. He would not admit to these feelings, but criticised his wife for being stupid, ugly and slovenly. Although the wife submitted totally, she did not know that the submission he required was for her to give up work. Eventually he got his way when she went off sick with depression.

Submission may also be blocked by a third party. We remember a patient who tried to submit to her husband but was prevented by an even more dominant mother, who insisted that her daughter visit her (and do housework) at a time when the husband wanted her at home (in this case the patient recovered when her mother died).

Table 5. Case C. Submission not accepted by dominant other. This distribution also applies to people who are hypersensitive to threat and criticism (e.g., Case D).

The Triune Model for Escalation/De-escalation			
	Escalate		De-escalate
Rational level (isocortex)		or	Tried to appease husband
Emotional level (limbic system)		or	Felt inferior
Instinctive level (basal ganglia)		or	Depressed mood Anxious mood

Case D: Inappropriate triune de-escalation. A female patient had been told by her mother that she was unwanted, and would have been aborted if the mother could have afforded it. Then she was badly bullied by her peers in adolescence. As a result she had very low self-esteem, and became depressed as a result of trivial setbacks. She required individual psychotherapy to give her a successful “rerun” of the parent child relationship, and group therapy to give her a successful rerun of the peer-group relationship.

In these cases the agonist/investor strategy set (of escalation and de-escalation) is too easily accessed or triggered, a problem well described by Sloman (2000).

Principles of treatment

The depressive de-escalating strategy not only inhibits retaliation and signals appeasement, but it also induces depressive thinking which influences the highest processing assembly, making it more prone to switch from escalation to de-escalation. This enables the person to abandon what is now seen to be a failing enterprise, and make a voluntary submission, and this appears to allow the depression to clear. Depression and anxiety have complementary roles here: the depression reduces expectation, while the anxiety promotes safety- and comfort-seeking, which may lead to reconciliation with a former rival (Price, 2003; Sloman, Farvolden, Gilbert, and Price, 2006), although regrettably chimpanzees are rather better at reconciliation than humans. The therapist can also encourage the patient to give up unrealisable goals, and this may be better done while the depression is creating a giving up frame of mind. The therapist may also guide the patient away from conflict towards negotiation, compromise, reframing and if necessary leaving the arena. Therapists of many persuasions do this, but our theory is especially attuned to Interpersonal Psychotherapy (IPT) which addresses issues of conflict resolution, and which has been shown to be effective in randomised trials (Markowitz, 2004; Morris, 2002; Weissman and Markovitz, 1994).

Our ideas support the practice of helping the patient to sort out the causes of the problem, rather than dealing with symptoms or trying to argue the patient out of depressive thinking. We may say to the patient, “If you came to us complaining of shivering, we

would not waste time rubbing ointment on your shivering muscles, rather we would ask you why you have not turned on the central heating.” Then the challenge is to find out what represents central heating for that particular patient.

Conceptual issues – accessing the strategy set

In behavioral ecology, variation in behavior is sometimes seen as mutually incompatible alternative strategies, two or more of which comprise a strategy set (Krebs and Davies, 1997, 1981). For example, in partially migrating bird species, in which some birds migrate while others overwinter in the summer location, the stimulus of shortening day length accesses the strategy set, whereupon some of the birds migrate and others stay (Gauthreaux, 1982). There is no in-between strategy; if one doesn't stay, one must go all the way. Some birds migrate one year and stay the next. It is not certain what determines the choice, but it could relate to the possession of a territory. There might be a third strategy in the set, such as hibernation; but, whereas there are species in which only a proportion of the animals hibernate, we do not know of a species which has the threefold choice of migrating, hibernating and staying. The variation is thought to be maintained by negative frequency dependent selection, in that the fewer birds stay, the more food there is, and presumably the advantages of migration increase the less birds migrate.

In this paper, we are talking about an inherited strategy set which evolved for dealing with agonistic situations and now relates more generally to social competition. We called it the agonistic strategy set, but this seems inappropriate in view of the non-agonistic nature of most human competition, and we would suggest the term Agonist/Investor Strategy Set, which contains the escalating strategy of “invest more” and the de-escalating strategy of “invest less”. This fits with Nesse's view that mood change is related to investment (Nesse, 2000). The fact that it is a strategy set rather than a response or sequence of behavior makes it a little different from what Gilbert (1992) refers to as a “psychobiological response pattern”, but it is basically similar. Troisi (2005) has recommended the use of strategy sets in psychiatry, suggesting an attachment strategy set which includes a strategy of secure attachment in childhood leading to monogamy with good parental behavior, and a strategy of insecure attachment leading to a promiscuous sexual behavior. This is a lifetime strategy set. A lifetime Agonist/Investor Strategy Set might contain strategies such as “always de-escalate” or “select escalation with a probability of 0.3”, but here we are talking about a strategy set which may be accessed on more than one occasion in a person's life, and a different strategy may be chosen on different occasions.

There must be at least four components:

1. The strategies in the strategy set. These are escalation and de-escalation (at each of the three brain levels). Escalation is behavior which increases the chance of winning but also increases the costs of losing; de-escalation is behavior which reduces the chances of winning and also reduces the costs of losing. But we cannot rule out the possibility of a third strategy in the set.
2. The situation which causes the strategy set to be “accessed”. We have called this “ranking stress”, and clearly people vary greatly in the ease with which the set is

accessed. This variation may be partly genetic, partly ontogenetic (e.g., secure vs. insecure attachment) and partly due to current personal or environmental factors (e.g., physical illness or lack of intimate relationship)

3. The choice between the two strategies:

At the rational level, this is a conscious decision, and must obey the rules of decision-making theory.

At the emotional level, the choice appears to be determined by expectations of fairness and entitlement; as Aristotle put it, if someone hurts you it causes pain, and if the pain is caused by a lower ranking person, it makes you angry, but if it is caused by a higher ranking person, it makes you feel chastened. With non-agonistic competition, there are expectations of fairness and being “right” or “in the right” which if thwarted lead to anger (escalation), whereas the sense of being “in the wrong” is likely to lead to depressed emotion.

At the instinctive level, we do not know what decides between escalation and de-escalation. Possibly it is randomised. This would fit with the apparently random distribution of mania and depression in bipolar patients.

4. The intensity of the escalation and de-escalation. We do not know what determines this. Possibly it is affected by the intensity of the ranking stress. In the case of instinctive escalation and de-escalation, small or even moderate levels of elevation and depression of mood may be effective, elevation of mood leading to success and achievement, and depression of mood enabling the individual to give up. However, extreme levels are clearly maladaptive, taking the form of the disorganization of clinical mania and the incapacity of psychotic depression.

In putting forward these ideas we are clearly on uncertain ground, but they represent a primitive form of map which is the best we can do from our clinical experience and our understanding of the basic disciplines of psychology, comparative ethology and behavioral ecology. There are a lot of unknowns; for example, how often is the strategy set accessed by any given person, and how long does the altered behavior last? We have found it to be relatively uncharted territory, and either it will be validated by others or seen to be some sort of fantasy fairy-land. If it receives any sort of validation, it is clearly of relevance to a number of fields of psychology, such as the variation of self-esteem and positive (and negative) affect over time, and the classification of the emotions (escalating and de-escalating emotions, as opposed to positive and negative emotions). To relate our three levels to neuroanatomy and neurophysiology would be desirable, but is beyond our competence.

Research

A lot of animal research is going on concerning the biology of social rank change (Wilson and Price, 2006), using particularly the resident/intruder paradigm in rats. It would be nice to think that our evolutionary speculations had given impetus to this research, but this is not the case. In the 1970's research was funded by departments of internal medicine, because it was noted that defeated and low-ranking animals developed stomach ulcers and hypertension. More recently the researchers realised that the defeated animals were also

depressed, and so the models have been specifically used to study depression in animals (Huhman, 2006).

However, our theorising has stimulated some research on both animals and humans. Jones, Stoddart and Mallick (1995) carried out studies on social rank and mood in the sugar glider, a marsupial native to Tasmania. Paul Gilbert and his team in Derby, England, have shown clearly how depressed patients are high on measures of subordination and entrapment (Gilbert, 2006). Wilson and colleagues have also identified key sequences in the phylogeny of neurotransmission that mediate the sociophysiology of rank hierarchy (Wilson, Stanton, and Wilson, 1999, Wilson, 2006). Akiskal and colleagues have published empirical data that support a significant role of rank sociophysiology in the phenotype of mood and temperament (2003, 2005; Niculescu and Akiskal, 2001).

Researchers have reported depressive-type behavior in low-ranking monkeys and those who fall in rank. Shively et al. (2005) observed conspicuous depressive behavior in low-ranking female cynomolgous monkeys. Those subordinates who did not appear depressed were attacked by the higher ranking monkeys, but the depressed subordinates were not attacked, suggesting that the depressive behavior was acting as an effective appeasement display.

One of the most promising animal models of depression is the vervet monkey, *Cercopithecus aethiops pygerythrus*. This animal was reported to become depressed when it fell in rank, while at the same time its bright blue scrotal skin turned white (Brain, 1965). Apart, possibly, from the reduction of facial red color in the mandrill, and possible color change in the mane of the lion and the hair of the silver-back gorilla, this is the only physical signal of loss of rank known to occur in mammals (Gerald, 2003). Blue skin is common in Cercopithecine monkeys; it is a structural blue caused by the selective scattering of short wavelengths of light by bundles of collagen of a diameter near to the wavelength of blue light, lying over a deep dermal deposit of melanin which absorbs the transmitted red light (Price, Burton, Shuster, and Wolff, 1976, Prum and Torres, 2004). The blue scrotal skin is a dominance signal, and is attended to closely by other males. When the monkey loses rank, the scrotal skin turns white over the course of about two weeks, probably due to hydration of the dermis with resulting change in the diameter of the collagen bundles. Pallor of the scrotal skin was found to be associated with low CSF 5-HIAA, suggesting reduced serotonergic activity in the brain (Gerald and McGuire, 2007). Genital skin hydration is common in Cercopithecine females at oestrus, but the vervet females do not show this. It seems possible that a mechanism of genital skin swelling which subserves the sexual changes in many monkey females has been taken over in this particular vervet to subservise dominance changes in the males (Price, 1989). Much excellent work has been done on the vervet monkey by McGuire and his colleagues (McGuire, 1988), but unfortunately the strain they used (the St Kitts vervet) does not have the blue scrotal skin (which can be readily seen in wild vervets in East Africa). The mechanism of dermal hydration causing the color change in the vervet skin has not been elucidated, but might provide a path leading to the mechanism of mood change.

One of us (JSP) was working with the vervet monkey in the 1970s, but funding was withdrawn by the Medical Research Council on the grounds that the underlying hypothesis (of depression due to loss of social rank) was “out of line with current thinking”, i.e., that depression was due to bereavement and separation. A proposed study of groups of vervets at the African Institute of Primatology (director Sandy Richards) at Limuru in Kenya had to

be abandoned. We now think that the very evident clinical association between depression and loss, separation, rejection and betrayal is a secondary evolutionary development due to the widespread dependence (in many primates) of social rank on alliances and patronage, so that loss of an ally becomes a reliable predictor of loss of rank and the subsequent depression is a pre-emptive move to avoid conflict (Price and Gardner, 1995b). This episode illustrates the importance of evolutionary theorizing for such practical matters as the allocation of research funds.

Our theorizing also indicates the possible use of reptiles as animal models of depression. Reptiles who lose rank or territory may show behavioral inhibition suggestive of depression (MacLean, 1990) and in these circumstances they may change color; for instance, the lizard *Anolis carolinensis* loses its bright adult coloring when it loses rank, and reverts to the dull brown adolescent coloring; “When pairs...were placed in neutral habitats, aggressive interactions occurred within 30 minutes...Over a period of several days, the color of one individual remained relatively stable (green) while the other became darker (more brown). In concert with this, the darker individual was often less active, usually adopted a lower body posture, and invariably selected lower perching sites than the lighter lizard. When a dominant-subordinate pair of *A. carolinensis* is broken up, the subordinate animal’s color often becomes lighter again. In certain cases, however, color change is *not* reversible and may reflect pathological processes that attend status change. In such animals, color becomes progressively darker and the animals eventually die” (Greenberg and Crews, 1983, p.489). Reptiles are simpler to study than mammals, having mainly visual rather than olfactory signalling, and lacking the two higher levels of the triune brain. And yet PubMed cites no papers reporting research on depression in reptiles, while there are over 600 reports of depression research in rodents. What we need is work on depression similar to Baxter’s work on OCD patients, in whom activation was found in the ventromedial aspects of the basal ganglia, an area which is activated during submissive displays in the lizard *Anolis carolinensis* (Baxter, 2003).

There is another more theoretical reason why reptiles might make better subjects than rodents for depression research. Rodents are unusual mammals in that they can see by ultraviolet light (Parker, 2005, p. 53). Also they have a greater problem with predation than other mammals, and they are more affected by extremes of weather. Many rodents have developed the capacity to hibernate, and since there are very few switches available for evolution to act on, it is possible that rodents have used the reptilian escalation/de-escalation switch to manage the change from waking to hibernation and back again, leaving possibly the paleomammalian escalation/de-escalation switch (or some newly evolved mechanism) to subserve their agonistic behavior. Therefore to study depression in rodents we should perhaps look not at their agonistic behavior but at the mechanism of hibernation. If we are right in thinking that the depressive mechanism evolved in the reptilian brain, reptiles would seem the obvious choice for research into depression.

Conclusions

Perhaps the musings of Demaret, Gardner, Price and Sloman, supplemented by those of Wilson, Gilbert, Erickson and Rohde, have borne fruit. We should like to think that they have solved two puzzles, which in their solution have cancelled each other out. One puzzle was the biological function of those mood changes from elation to

depression and back again which we see exaggerated and out of context in our bipolar patients. The other puzzle was the behaviors which have evolved to deal with the much contrasted roles of high ranking territory-owners and low-ranking non-territory owners, and the transitions between these roles. Proof that the mood changes evolved to subserve the rank changes is difficult to come by, but we hope that our discussion has illuminated the relation between mood and social competition to such an extent that it will help in the treatment of afflicted individuals. Whereas the concepts of escalation and de-escalation in pairwise contests have been elaborated by behavioral ecologists, these ideas and their possible relation to mood change have not been integrated into individual or social psychology, or even evolutionary psychology (e.g., Van Vugt, 2006).

Other evolutionary functions of depressed mood have been suggested, but it would not be appropriate to consider them here. They have been well reviewed by Nesse (2000), Nettle (2004) and by Allen and Badcock (2006). These writers do not distinguish clearly between depressed emotion at the paleomammalian level and depressed mood at the reptilian level, so that comparison is difficult. Moreover, it has been pointed out there is considerable overlap across many approaches even with varying degrees of systematic rigor and/or other particular points of emphasis (Mysterud, 2004; Wilson and Price, 2006). We should make special mention of the depressive realism hypothesis (Alloy and Abramson, 1979) because, although not advanced as an evolutionary theory, it does suggest an advantage for depressed mood in that it takes away from the depressed person the over-confidence of the non-depressed person. However, in a prospective study, Dunning and Story (1991) found that depressed college students were no more realistic in predicting future events, and this was because, although they predicted more aversive events and less pleasant events, they actually experienced even less positive events and more aversive events, presumably due to their depression. However, this interesting hypothesis continues to stimulate research (Moore and Fresco, 2007).

Fighting to the death, winning at all costs, taking one's case to the highest court in the land, these are escalating strategies which serve to obtain resources for the individual. But everyone cannot win. Giving in, submission and appeasement are vital social behaviors, without which social life would be impossible. They are manifestations of a de-escalating strategy, in which the chances of winning are much reduced but the costs of losing are also reduced. In the course of its evolution from reptiles through mammals to primates, the human forebrain has developed three "central processing assemblies", each of which makes a decision between escalation and de-escalation when confronted by challenge or stress. If the higher assembly does not deal with the problem, the lower assemblies are activated and select more primitive forms of escalation and de-escalation, which in the case of the lowest of the three assemblies may well take the form of elevation and depression of mood, respectively. The appeasement display of the reptilian de-escalating strategy is a sophisticated message which says, in effect, "I am too incapacitated to put on an appeasement display." This is the ultimate in reassurance.

Perhaps it might not be hubristic to envisage a wider application of our ideas. The notion that depression may be a magnifier of small genetic differences is surely relevant to the speed of evolutionary change. And, in addition, the mechanisms here described may have facilitated group living, by promoting the smooth functioning of hierarchies within groups, with depressed mood in particular helping to reconcile low-ranking individuals to forego the rewards of high rank such as food, shelter and mates; and without group living,

if our ancestors had been as solitary as the orang-utan, we might not be in possession of the faculties required to write this article.

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