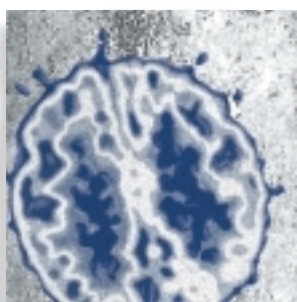


Evolutionary aspects of anxiety disorders

John S. Price, DM



Danger and harm are avoided by strategic decisions made at all three levels of the triune forebrain: rational (neomammalian), emotional (paleomammalian), and instinctive (reptilian). This applies also to potential harm from conspecifics, which leads to a choice between escalating and de-escalating strategies. Anxiety is a component of de-escalating strategies mediated by the paleomammalian and reptilian forebrains. When the neomammalian (rational) brain fails to deal with the threat of conspecific danger, these more primitive de-escalating strategies may be activated and may present as anxiety disorders. The capacity for concealment of anxiety and other forms of negative affect has also evolved, and excessive concealment may lead to psychopathology by breaking the negative feedback loop of excessive motivation, leading to impaired performance, leading to signals of distress, and leading to reduced exhortation to succeed on the part of parents and teachers; this situation is illustrated by a model based on the Yerkes-Dodson law.

© 2003, LLS SAS

Dialogues Clin Neurosci. 2003;5:223-236.

Keywords: agoraphobia; anxiety disorder; behavioral ecology; de-escalating strategy; depressive disorder; evolution; triune brain; Yerkes-Dodson law

Author affiliations: Department of Psychiatry, South Downs Health NHS Trust, Brighton General Hospital, Brighton, UK

Address for correspondence: John S. Price, DM, Odintune Place, Plumpton, BN7 3AN, UK
(e-mail: johnscottprice@hotmail.com)

*I*nside the animal's form sits the brain, its work broadly to increase the animal's grip on the world about it, and hardly less the grip of the external world upon the animal.

Sherrington, *Rede Lecture*, 1933

Modern times are not like the times in which our ancestors evolved. The environment of evolutionary adaptation (EEA) usually refers to the habitat of our immediate ancestors who are thought to have been hunter-gatherers living in bands of about 50 adults, but is really an abstraction which covers all environmental influences going back over three hundred million years to the common ancestor of humans and present-day reptiles. The "mismatch" between now and the EEA is thought to be one cause of psychopathology. "Bad news" is a source of anxiety. We now have daily, or even hourly, access to the bad news of six billion people, more than could be generated by a hunter-gatherer band. Moreover, in the EEA, bad news was probably discussed and so shared with other group members, whereas modern man tends to watch it or listen to it on his own, or at least without comment. Therefore, as a practicing clinician, I advise all my anxious patients to avoid watching TV news, and I find that many of them have learned the lesson for themselves. They realize that each item of bad news raises their background level of anxiety, and, of course, severely depressed patients may believe that they are personally responsible for the disasters that occur daily around the globe. No one, to my knowledge, has done a controlled trial of "news avoidance" as an item of therapy.

Much has been written about the evolution of anxiety and its disorders.¹⁻¹⁰ Here, rather than repeating familiar arguments, I have tried to break some new ground, looking at approaches that may be relevant to research and treatment. I will concentrate on social aspects of anxiety, because nonsocial anxieties have been well covered, whereas there is still something to say about social anxiety, particularly the relation of social anxiety disorder to

Basic research

generalized anxiety disorder (GAD), and the relation of anxiety to depression, and the relation of anxiety and depression to social competition. Evolution is history, and our speculations about how and why certain things evolved cannot be tested directly. As W. H. Auden said, “History is, strictly speaking, the study of questions; the study of answers belongs to anthropology and sociology.” In the case of evolutionary history, answers are also provided by psychology and physiology. Evolutionary speculations are heuristic, in the sense that they may lead to the posing of questions which otherwise would not have been thought of. The proof of the pudding is in the eating.

Generalized anxiety disorder

Here is an example of how contemplation of the EEA may generate ideas. A team from the University of British Columbia construed GAD as an unsuccessful search for safety.¹¹ They addressed “three distinctive features of GAD: the undue persistence of the anxiety and worry; the excessive generality of the anxiety, and the lackluster response of GAD to cognitive therapy procedures [...] People with GAD persist in multiple, persistent searches for safety, but they seldom succeed in achieving lasting satisfaction.” The big question is: where does safety come from? This becomes clear if we imagine that during part of the EEA human beings went through a stage of living in hierarchically organized groups, much as most monkeys and apes do today. In such a group, most rewards are dependent on the animal’s social rank, and the only means of social advancement is to rise in rank. An ambitious chimpanzee challenges the animal who ranks above, who probably resists the challenge, and a ritualized fight ensues. This may go on and off for many months, until either the challenger gives up, or the higher-ranking animal is deposed. The two then undergo what the primatologist de Waal has called “conditional reconciliation”: they kiss and hug and make up, but with the understanding that the deposed animal is now subordinate; this means that the subordinate animal has to behave submissively to an animal he may have dominated for some years.¹²⁻¹⁴ If we consider the state of mind of the deposed animal after he has been beaten, but before he has reconciled, we can see the need for some reorganization of goals and attitudes: we have suggested that depressed mood may help the animal give up the goal of retaining his high rank, and reconcile him to his inferior social position.¹⁵ However, the depression does not help him recon-

cile with his supplanter. Here there is a role for generalized anxiety, with its frantic search for safety. There is only one source of safety in the chimpanzee world, and that is from the victorious animal, and so the deposed animal turns to the victor for reassurance and protection, and is so needful of safety that he accepts the terms of the conditional reconciliation, and his gratitude for the relief of anxiety overcomes his resentment at being deposed. In this hypothetical situation, we can see how depression and anxiety can work together to achieve what has been called “functional agonism.”¹⁶

Such a scenario has been reported in a street-corner gang,¹⁷ which is probably the nearest that human society gets to a chimpanzee group. However, most human social life is infinitely complex and the simple situation of the chimpanzee or the human gang cannot be discerned. From the research point of view, our ideas stress the importance of the work carried out by Gilbert and his colleagues in Derby, UK,¹⁸ and others,¹⁹ into the relation between depressed and anxious mood and submissive behavior. From the treatment point of view, we endorse the approach of interpersonal psychotherapy, which explores current conflicts in the lives of patients.²⁰ Unresolved rebellions against parents and other powerful people should be explored. Also, given that in human society, it is often the group as a whole, rather than individuals, who exercise power, the patient’s relations with “authority” should be examined, and, for instance, any questionable self-assertion should be avoided, such as submitting inflated expense accounts or massaged (false) tax returns. This is similar to the suggestion of Buss²¹ that anxiety helps prevent unattractive, incompetent, or deviant people from being excluded from their group; anxiety may not make people more attractive and competent, but it can make them less deviant, and it can help to reconcile unattractive group members to a more subordinate role in which they may be better tolerated. One cannot help noticing that in a Christian country, many of the population submit to a powerful figure every week, confessing their sins, going through a ritual not unlike the conditional reconciliation of the chimpanzee. One recalls that C. S. Lewis, in *The Problem of Pain*, concluded that the function of mental pain is to reconcile man to God. Lewis, having experienced severe depression, concluded that man is so proud and arrogant that to achieve submission even this degree of mental pain is required. Submission to a cult leader and his beliefs, or to a psychotherapist and his theories, may achieve a similar result.

In summary, I have suggested that depression and anxiety work synergistically together to promote functional agonism, whereby rank differences are maintained and rank reversals are achieved without group disruption. Depression prevents rebellion and generalized anxiety promotes reconciliation, so that a hierarchy based on reassurance, gratitude, and respect can replace either social chaos or a hierarchy based on intimidation. Groups with such “hedonic” hierarchies are likely to outcompete groups with agonistic hierarchies, so that the effect of selection between groups will be added to the individual advantage of the anxious person (avoiding punishment or exclusion by a more powerful person or by the group as a whole) and these advantages have presumably, during the course of evolution, outweighed the disadvantage of giving up the resources that are the rewards of high social rank. This synergistic action of depression and anxiety is compatible with the finding of extensive comorbidity between anxiety states and depressive disorders,²²⁻²⁵ and with the finding that the genetic predisposition to major depression is indistinguishable from the predisposition to GAD.²²

Social anxiety disorder

I have suggested above that GAD plays a part in managing the organization of a social hierarchy, and promotes reconciliation with a successful rival. Thus, it is concerned with social change. Social anxiety disorder is also concerned with avoiding harm from conspecifics, but is concerned with social homeostasis. The difference is one between anxious mood and anxious emotion. An emotion is directed at an object, and is sensitive to changes in the object, whereas a mood is unfocused or self-focused, and is unaffected by changes in the environment.²⁶ It is likely that emotions and moods are mediated by different levels of the brain, and in order to illustrate this I will use MacLean’s model of the triune brain,^{27,28} suggesting that depressed emotion and anxious emotion are mediated by the paleomammalian forebrain, whereas depressed mood and anxious mood are mediated by reptilian forebrain.

A triune mind in a triune brain

In order to comprehend clearly the human response to danger, and to see anxiety in the context of all the mechanisms deployed in the avoidance of danger, it is neces-

sary to invoke the concept of the triune mind.^{29,30} The idea that the mind consists of two or more relatively independent entities has been around at least since the time of Plato.³¹ This 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.³⁰ 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.³¹

The work of the evolutionary neuroanatomist MacLean has given support to the idea of the triune mind by his demonstration of a triune brain.²⁷ 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, and such social matters as were no (or little) part of reptilian social life. This brain is situated in the limbic system. Not only did it deal with mammalian matters, but it also dealt, in a mammalian way, with those problems which had been faced by reptiles and were also faced by mammals, such as the avoidance of danger, the courtship of the opposite sex, and competition with the same sex; however, at the same time, the reptilian brain continued to deal with the same old problems in its old reptilian way. In higher mammals, there developed the neomammalian brain, which subserves what we recognize 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 that are addressed

Basic research

by the reptilian and paleomammalian brains such as avoidance of danger, 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 cooperate, 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 the case of danger avoidance, there is some advantage in speed of reaction, so that avoidance occurs rapidly before the more sophisticated, but slower, neomammalian brain can take action. However, there is also a sense in which the lower brain “knows better,” having sources of information not available to the higher brain. This seems to be particularly true in the case of avoiding danger from conspecifics. 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 (*Table I*).

Since anxiety may be a component of the de-escalation response, it is necessary to say something about escalation and de-escalation, which are familiar concepts in ethology³² and behavioral ecology,³³ but have not yet been clearly formulated in psychology.

Escalation and de-escalation

For over three hundred million years, competition between members of the same sex has taken the form of agonistic behavior, and, from observation of countless species of existing mammals and reptiles, ethologists have pointed out that this behavior is ritualized, in the sense that it obeys certain rules. One of these rules is that each individual has a limit in the punishment he is able to receive before switching from escalation to de-escalation. Another rule is that when one contestant submits, the winner exercises mercy and does not take advantage of any submissive posture adopted by the loser. In a contest, there is usually mutual signaling of resource-holding potential (RHP), which is an estimate of fighting capacity, and if there is a significant difference in RHP

The triune model for escalation/de-escalation: agonistic competition			
	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

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

The triune model for escalation/de-escalation: prestige competition			
	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 and anxious mood

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

between two contestants, the one with less RHP usually backs off before any engagement starts. Or, if the contest occurs on a territory owned by one contestant, there is a convention that the owner of the territory wins. If territory is not an issue, and RHP is equal, a fight ensues, which may escalate through several stages of fighting behavior, such as the roaring of stags,³⁴ which is followed by parallel walking, which is followed by locking horns. Each contestant is giving out punishment to the other, and receiving punishment in return. When does one of them give up? This interesting value has been honed by hundreds of million years of evolution, but for simplicity's sake can be expressed in terms of "punishment units received," a value which is determined partly by the animal's motivation (the value to the animal of what is being fought over, a quantity known as resource value), partly by ontogenetic experience, and partly by heredity.³⁵ Assuming the resource to be of equal value to both contestants, and their life experience to have been equivalent, the deciding factor, according to behavioral ecologists, is either genetically determined or randomized according to a genetically determined schedule, and the contestant with the greater capacity to endure punishment before submitting is said to adopt a hawk strategy, while the contestant with the lesser capacity, and who therefore submits, is said to adopt a dove strategy. Adopting reasonable parameters, a mixture of hawk and dove strategies is evolutionarily stable³⁶ (whether the mixture is between individuals or within individuals on different occasions does not matter). Hawk and dove are graded characters, so that in any contest, an individual is likely to be confronted with an opponent who is either more hawkish or less hawkish than himself, and this is why contests can be resolved without injurious fighting, and why ritual agonistic behavior has become such a widespread means of distributing resources such as territory and social rank between individuals.

Escalation and de-escalation at three brain levels

Decisions to escalate or de-escalate take place either simultaneously or consecutively at all three levels of the triune brain (*Table I*). At the rational, or neomammalian level, the decision is made consciously and voluntarily either to fight harder or to back off; when 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 and the sense of being chastened. Also, since this level involves the rules of group membership and prestige competition, guilt and shame also play roles so the appeasement display typically consists of weeping, blushing, and protestations of repentance (*Table II*). 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, self-confidence, and heightened sociability all of which function to recruit allies. Conversely, de-escalation at the instinctive level takes the form of depressed mood and may include the unfocused anxiety of GAD, the fatigue of chronic fatigue syndrome, and the physical disabilities of somatization disorder.³⁷ 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."³⁸

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. 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 stabilizing 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) 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).³⁹ Related to SAHP is the concept of

Basic research

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.⁴⁰

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 (*Table II*). 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 consists 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, and elevation of mood represents escalation, whereas depression of mood, together with the anxious mood of GAD, represents de-escalation. However, the information that 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 and the likelihood of being found out.

The manifestations of escalation and de-escalation at the three brain levels are shown for agonistic competition in *Table I* and for prestige competition in *Table II*.

The importance of attachment, equality, and cooperation

We have been accused of emphasizing the competitiveness of human life at the expense of cooperation, equality, and affiliation.³⁸ We certainly do not deny the importance of affiliation, and we respect the enormous contribution of

Bowlby who first introduced the idea of attachment and separation into psychiatry,⁴¹⁻⁴⁴ and also his reliance on data from comparative ethology; nor do we deny that a lot of psychopathology derives from the loss of attachments, from death, rejection, infidelity, or boredom.

Even the threat of the death of a spouse may cause both anxiety and depression. Also, it seems likely, both from research and experience in the clinic, that adverse experience with parents in early childhood, leading to insecure attachment, and also failure to integrate successfully with the peer-group in adolescence, can predispose to psychiatric disorder in later life.¹ Basic research on the way these early adversities alter brain function is important.⁴⁵

From the evolutionary point of view, however, we think that the roots of depression and anxiety go back further than the evolution of attachment, at least back to the common human and reptilian ancestor, who very likely shared with most present day reptiles the complete absence of attachment, or family life, or even pair-bonding, and in whom relations with the opposite sex were restricted to courtship and with the same sex to ritual agonistic behavior. When attachment evolved, it had a profound effect on ranking behavior, and even in monkeys, let alone apes, rank depends on kinship and alliances, so that the loss of a powerful patron was probably the best predictor of a fall in rank.^{46,47} Depression and anxiety following loss thus represent a preemptive mood change to adjust the individual to lower status. (This does not apply to the emotion of grief, which is likely to have other functions.)

The Standard Social Science Model portrays human ancestors as independent, egalitarian people, much like present-day hunter-gatherers.¹ The inequalities and competitiveness of the developed world were seen as recent cultural pathologies. It followed from this view that anxiety, depression, and other psychopathologies could not have evolved in the context of social competition. However, this cultural view greatly underestimates the power of culture to transform society. Stevens and I have pointed out that humans have a powerful capacity to undergo a sudden and radical change of belief system, and to indoctrinate others into that new belief.⁴⁸ It only takes a single prophet to look around at his competitive society, in which success is considered good and to be rewarded, and to pronounce "Success is bad and should be punished," for a new society to arise in which, as in present-day Kalahari Bushmen, success and ostentation are ridiculed, and an atmosphere of "counterdomi-

nance” prevails.⁴⁹ Thus, we should expect groups of our ancestors to be wildly culturally divergent, along many dimensions of variation, but the dimension of equality/inequality was likely to be a popular one. It only takes a message of three words (“success is bad” or “success is good”) to transform the entire way of life. But, although the message is short, it is a uniquely human one. There is no way in which a chimpanzee group could switch from one ideology to another (even though environmental conditions such as food supply have a large effect on the competitiveness of chimpanzee groups). In summary, we are saying that our ancestors had the capacity to live in both equality and inequality, and they had available, if needed, the behavioral mechanisms such as depression and anxiety, which made cohesive group life possible in conditions of inequality.

Implications

In painting this evolutionary scenario of affective disorders, I have passed the white light of escalation/de-escalation theory through the prism of triune brain theory, and revealed a triptych of three central processing assemblies operating relatively independently in the forebrain, each of them responding to the fortunes and misfortunes of social competition, subserving what Darwin described as intrasexual selection.⁵⁰ The implication for both research and treatment are fairly clear. Research into defeat in experimental animals has largely been initiated and financed by specialties in general medicine, because defeat, especially when escape is blocked, causes high blood pressure, renal failure, and gastrointestinal ulcers, but now it is at last being realized that these defeated animals, so distressed that their bodily organs are diseased, also suffer from some psychological upset, and that subordinate animals may suffer from depression.^{51,52} It is now nearly 20 years since McGuire and his colleagues,⁵³ reported alterations in blood serotonin associated with hierarchical position in vervet monkeys, a finding which is counterintuitive since the majority of the body’s serotonin resides in the gastrointestinal tract, but in spite of this evident breakthrough, their findings have not to my knowledge been repeated by other laboratories, let alone extended. There is a pressing need for an all-out sociophysiological assault on the mechanisms of hierarchical behavior.^{54,55} In relation to treatment, it is clear that if the rational level of the brain can sort out the problems of social competi-

tion that the individual encounters, there is no need for the more primitive levels to introduce their uncomfortable solutions, any more than it is necessary for a cold individual to shiver when he has the alternatives of putting on more clothes, turning on the central heating, or migrating to the tropics. The object is to replace unconscious behavioral strategies with conscious, rational ones.⁵⁶ This has implications for the time a therapist spends sorting out real life conflicts, as opposed to ventilating emotions and arguing the patient out of depressive thinking. Also, it illustrates to the therapist how he inevitably enters the patient’s hierarchical world, to exercise influence, which may be benign or otherwise.

Depression is more common than elevation of mood, and this reflects the fact that submission has been a more useful evolutionary tool than fighting to the death. Some individuals have easily triggered submissive responses,⁵⁷ on the “smoke detector” principle that several false alarms are better than one burning, and there is likely to be considerable genetic variation in this trait of dysthymia,⁵⁸ which also appears to be sensitized by adverse experience in childhood. This realization is important for parents, educationists, and those concerned with primary prevention.

Concealment of affect

I noted above that the rational brain has little control over the emotional brain (or the instinctive brain), but to some extent it can conceal the manifestations of affect mediated by the emotional brain. This applies to both positive and negative affect.

Concealment of positive affect

The poker player learns to adopt a “poker face,” so that his opponents cannot see his excitement when he picks up and looks at a straight flush in his hand. Players of “quinze” at Almack’s rooms in London in the 18th century used to sit around the table wearing masks; although this reduced the skill and excitement of the game, it reduced the stress of having to maintain the poker face. Likewise, the dealer in jade, so the story goes, knows that his customer will hide his pleasure in seeing a particularly desirable piece, and so he looks at the customer’s pupils, knowing that the pupillary dilation of excitement is one aspect of positive affect over which the rational brain has no control.

Basic research

Concealment of negative affect

In some social situations, concealment of negative affect is not required, for instance, after bereavement. In fact, exaggeration of negative affect may be required in some mourning rituals, in which conspicuous voluntary actions, such as beating the breast, rending garments, and tearing the hair, may be required to accompany loud lamentations. However, as a general rule, people are motivated to hide the manifestations of depression and anxiety from others. Blushing in the context of shame and embarrassment presents in the clinic because it cannot be concealed; indeed, it is considered an “honest signal” and tells the observer that the person blushing is biddable and sensitive to social norms. However, this is a signal that the blusher does not usually wish to send, preferring to present him or herself as someone with poise, confidence, and social success. There is truth in the folk wisdom that, “Laugh and the World laughs with you; weep, and you weep alone.”

The evolutionary origin of the concealment of negative affect derives from the behavioral ecology of pairwise contests, and probably goes back hundreds of millions of years. In a confrontation between two equally matched rivals, there is a lot of signaling of size and strength and determination to win.³² Clearly, it is in the interest of each contestant to know the determination of the other, because if he were able to say to himself, “If only I can hold out for 10 more minutes without giving in, I know that my opponent will then give in,” this knowledge will give him enormous advantage in the fight. Therefore, each contestant will be motivated to hide any suggestion of being about to give in until the actual moment of doing so. Since negative affect is the result of punishment, and associated with the appeasement display of giving in, the capacity to conceal negative affect is likely to be selected for. This evolved capacity is augmented by training, and even by surgery as when the nerves and muscles of the upper lip are incised to prevent the tell-tale lip quivering of fear, and so to maintain a “stiff upper lip.”

The same applies to the social aspects of prestige competition, when individuals try to present themselves as competent and in charge of the social situation. In most cultures, in order to promote their own social advantage, people like to associate with successful others, and avoid those who show signs of failure. Indeed, in our own culture it has been found that depressed and anxious indi-

viduals are found to be socially aversive and are avoided by others.^{59,60} On the other hand, there are cultures in which the demonstration of fearfulness is encouraged; among the Chewong,⁶¹ an aboriginal tribe in Malaya, the gods and ancestors are characterized by “fearfulness, timidity, and retreat in the face of perceived danger,” and these supernatural beings act as role models for the living Chewong, who are proud of their timidity, and among whom the old men tell tales of occasions when they have run away. Unfortunately, epidemiological psychiatry has not yet reached the Chewong, so we do not know whether this cultural endorsement of fearfulness is associated with an increase or decrease in clinical anxiety disorders. However, the Chewong are an exception to the social rule of concealment of negative affect, and it seems likely that, on the whole, culture has facilitated the evolution of the capacity for concealment.

Communication of negative affect to friends and allies

Even among nonhuman primates, and more so among humans, the result of social competition depends on friends and allies, usually close kin. The signals of submission directed at rivals are not directed to allies. On the contrary, the signal to allies is one of distress, sending the message, “Do not push me into the arena to fight on our joint behalf, I am unwell (off games), so please comfort and succor me.” We have pointed out that submitting people can be quite firm with friends and allies in getting this message across.³⁸

When we come to prestige competition, the situation is more complex. People are motivated to encourage their allies to perform as well as possible, and in particular parents are motivated to push their children to optimal performance. Female macaques strive to maintain their daughters in a social rank immediately below themselves,⁶² but humans go one better, and parents are notorious for trying to launch their children into social orbits higher than their own station; this parental boosting of children must have evolved in the human lineage because of a correlation between social and reproductive success during the EEA. We can speculate that the parental boosting continues until it is switched off by a signal of distress from the child, indicating to the parent that it has passed its optimal performance and is now overmotivated. How can we conceptualize the signal of distress in this situation? One possible answer is to make use of the Yerkes-Dodson Law, which relates performance to motivation.

The Yerkes-Dodson Law

This law states that, as motivation increases, performance rises to a peak and then falls (*Figure 1*).⁶³ In other words, the curve is an inverted U. This means that, for any given level of performance (except for the peak), there are two possible readings for motivation, one below the peak, and one above it. The law also states that the peak for easy tasks is at a higher level of motivation than the peak for difficult tasks. Yerkes and Dodson⁶⁴ worked with mice and taught them to avoid a compartment of the cage in which they received electric shocks: the mice learned better with moderate shocks than with either slight or severe shocks. Also, when task difficulty was varied by changing the relative brightness of the safe and shocked compartments, the mice learned faster with smaller shocks when the brightness difference was less, making the task more difficult. More recently, the law has been confirmed in human beings⁶⁵; using baseball scores as a measure of performance, and the size of the audience (and the importance of the game) as a measure of motivation, researchers found that performance improved as motivation increased; however, in very vital games with a huge audience, performance was reduced, when presumably the players were beyond the peak and on the descending limb of the curve.

If we imagine our ambitious parents promoting their children's success, we can see them tracking their children's

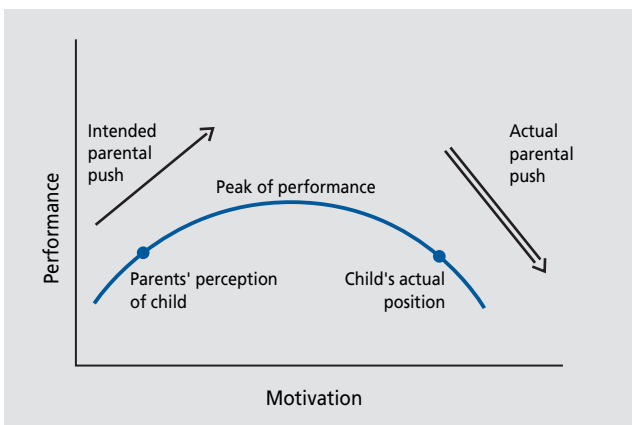


Figure 1. The inverted U-shaped curve of the Yerkes-Dodson Law. The single-shafted arrow represents the parents' attempt to push the child up toward the peak of performance. The double-shafted arrow represents the actual effect of the parental pushing.

Reproduced from reference 63: Curtin LL. The Yerkes-Dodson law. *Nurs Manage.* 1984;15:7-8. Copyright © 1984: Lippincott, Williams and Wilkins.

progress on the Yerkes-Dodson curve, trying to push them up to peak performance. If they see the children on the ascending limb of the curve, they know they are under-motivated and they push the children harder. If they see that they are on the descending limb, they restrain them and encourage them to ease off. But how do they tell which limb of the curve the children are on? One source of information to the parents is the signal of distress given out by the children who are being pushed too hard, and sense themselves slipping down the descending limb of the curve. This signal of distress is a display of negative affect. What if the children are highly skilled in the concealment of negative affect? Then the parents may not realize that they are on the descending limb, but attribute poor performance to lack of motivation. As a result, they may push their children even harder, and the children, already beginning to slide down the descending limb of the curve, are pushed further down by increased parental pressure.

The Ydler causation

In the clinic, we meet cases in which the children's distress has been magnified to the level of illness. I have described two such cases,⁶⁶ both suffering from many years of anxiety and depression, one complicated by eating disorder, and the other by repeated self-harm. They had the following features in common:

- They were well-turned out in dress and self-care.
- Their social manner was poised and concealed their underlying distress.
- They were conscientious.
- Their parents were ambitious for them.
- The families were close.
- There was no history of childhood ill-treatment, adolescent bullying, or major environmental stress, such as we usually find in our patients' histories.

In one case, the patient refused to allow me to meet her family, and this refusal was a part of her concealment of negative affect from her parents, who did not know she was having psychiatric treatment; her illness began shortly after she went to university, when her parents were not able to monitor her day-to-day affect. In the other case, I held a meeting with the parents and siblings, and it was the siblings who immediately realized the plausibility of the interpretation, and said that they themselves had felt the pressure to perform. Even the parents accepted that they had been bamboozled by their daughter's apparent self-control.

Basic research

I felt that the acronym Ydler was appropriate for this situation, standing for Yerkes-Dodson limb erroneous recognition, to be pronounced “idler,” to emphasize that idlers was something that these young ladies certainly were not (but seemed to be).

Apart from a suggestion that car accidents should be classified according to whether the driver was on the ascending or descending limb,⁶⁷ I do not think the descending limb of the Yerkes-Dodson curve has ever been analyzed from a diagnostic point of view, but if it were, then it would probably be found to consist, in its milder forms, of the appearance of tiredness and tearfulness, and in its severer forms, of anxiety and depression, probably manifesting as physical symptoms. For some reason, our Ydler patient is failing to make the appropriate display. As a result, the parents attribute the poor performance to undermotivation, and mistakenly think that the child is on the ascending limb of the curve, and so they keep on pushing, which drives the child further down the descending limb, which causes the parents to push even harder, which drives the child even further down the descending limb, and so on.

The Yerkes-Dodson law has been criticized because it assumes a unitary variable of arousal.⁶⁸ However, it has been supported independently and, I think, unknowingly, by Hans Selye’s work on stress. Selye related strain to stressor,⁶⁹ and found a U-shaped curve, so that too little stress caused strain, a middling amount caused less strain, and too much stress caused more strain. If we identify Selye’s strain as negative performance, and Selye’s stress as motivation, then Selye’s curve is the Yerkes-Dodson curve upside down.

Social sharing of nonsocial anxiety

Social anxiety, caused by fellow group members, is usually a solitary thing, endured by an individual bullied by a dominant, or by a scapegoat punished by the group. But anxiety to nonsocial sources of harm is often shared with other group members, and so becomes a social experience, modulated by social customs. In some cases, the group comes together to reduce anxiety, as when chimpanzees cuddle each other when presented with a stuffed leopard, and so presumably revive the safety sensations of the child being cuddled by its mother; in other cases, the group allocates to an individual the responsibility for sensing danger, allowing the remainder of the group to carry out foraging and other activities free from anxiety.

Alarm calls

The alarm calls given by an allocated “sentry” are specializations of calls given by ordinary individuals in the group:

“In 1967, T. T. Struhsaker reported that East African vervet monkeys gave different-sounding alarm calls to at least three different predators: leopards, eagles and snakes [...] and, in play-back experiments of tape-recorded alarm calls [...] monkeys responded to play-back of leopard alarm calls by running into trees, to eagle alarms by looking up in the air or running into bushes, and to snake alarms by looking down in the grass around them.”⁷⁰

Vervets were later shown to have, in addition to the above, specific alarm calls eliciting specific responses to baboons, small carnivores, and unfamiliar humans.⁷¹ Other monkey species also have specific alarm calls, but apes apparently do not, and human alarm calls would appear to be as nonspecific as apes, perhaps because apes and humans are under lesser predation pressure than monkeys. Giving an alarm call is clearly a disadvantage to the individual who gives it, and the adaptive advantage accrues to close kin, and how this might evolve has been a concern of evolutionary biology.³³ The misuse of alarm calls has also received attention, in that animals may give them out of context to manipulate others; for instance, New World monkeys have been seen to give the alarm call when an aggressive subordinate was making a challenge, with the result that the subordinate had to abandon the challenge and take his place guarding the periphery of the group; and subordinate great tits may give an alarm call to dislodge dominant birds from a feeding perch.⁷² Alarm calls do not appear to play any part in the symptomatology of anxiety disorders; for instance, patients having panic attacks may turn to others for comfort, but they do not call “Look out!” or even “Help!”; nevertheless, the importance of alarm calls in other primates should alert the clinician to be on the lookout for them.

The role of sentry

In some groups of social animals (meerkats, dwarf mongooses), the role of anxious individual is allocated to a single group member, who sits on a high perch and scans the surrounding countryside for predators and the air for birds of prey. The rest of the group can forage without anxiety

until they hear the alarm call from the sentry, when they dash for cover. A meerkat who did not trust the sentry, or was not aware of the sentry's existence, might be considered to be suffering from an anxiety disorder. Akiskal⁷³ has pointed out that asking an anxious patient to relax may be like asking a sentry to desert his post. In treating anxiety disorders, it is important to clarify where responsibility for safety lies. Perhaps through bad experiences in childhood, the patient may not trust other people to take on the role of sentry. Group exercises in which patients are encouraged to fall and allow themselves to be caught by other group members may be helpful in developing an attitude of trust. In obsessive disorder, the responsibility for cleaning and checking should be clearly allocated, and the therapeutic problem may revolve around getting the patient to trust whoever is responsible.

Avoidance of nonterritory

In the classical case of agoraphobia, the patient feels perfectly safe in her own house, but feels extreme panic when he or she goes out of the front door. Some patients describe a "glass wall," which prevents them going out. In this experience, the agoraphobic patient is similar to the vast majority of terrestrial mammals, who all lose confidence and tend to run away from conflict when they leave what they regard as their home territory. Even ferocious baboons were seen to fall to the ground in paroxysms of anxiety when driven across the border of their group's territory by primatologist Irven DeVore.⁷⁴ Nonagoraphobic humans share with elephants the capacity to wander wherever they will over the globe. The other exception to the agoraphobic rule is the dispersal of individuals during puberty, when it is common for one sex to leave the group and join other groups; for instance, in macaques and baboons the males leave at puberty, whereas in chimpanzees the females leave at that time.⁷⁵

In many agoraphobics, the inhibition is in the form of a ring around the house, which, if broken through, allows nonanxious travel. One of my severely agoraphobic patients happily traveled around Europe on the back of her boyfriend's motor cycle. This reflects our possible nomadic existence during the EEA, when the restriction to the summer quarters must be broken for the migration to the winter quarters. For men, it must be broken during hunting expeditions, whereas the female role may be exercised nearer the home base, and many writers

have pointed out that this protects women from attack by predators, head-hunting neighbors, rape, and gossip,¹⁷ and may even protect the marital bond.⁷⁶

The literal ownership of territory may be important. One sufferer recovered when she moved from her own house into a rented flat, but her agoraphobia returned when she bought the flat. The knowledge of ownership may also aggravate obsessional cleaning.

Conclusion

On the face of it, anxiety seems easier than other forms of psychopathology to tackle from the functional point of view, because its function in avoidance of harm is clear for all to see. Parents try to train their children to be anxious about traffic, strange men, drugs, and other dangers, which did not appear in the EEA, and so have no built-in avoidance mechanism. In one unusual case, a child suffering from congenital indifference to pain was trained to experience anxiety in situations that normal children avoid because of pain.⁷⁷ However, in other ways anxiety is more difficult to analyze than, say, depression, which we have portrayed as a simple, primitive defeated or submissive strategy. Anxiety is a complex mixture of cognitive, affective, behavioral, and somatic components, and it has complex relations to other aspects of motivation such as arousal. Moreover, there are the following interesting polarities.

Social versus nonsocial

One does not submit to a predator, and so, to the extent that one looks on depression as a submissive display, the function of depression is entirely social, whereas anxiety has to keep the individual safe from countless nonsocial dangers in addition to threats from conspecifics. It is difficult to say, in the case of agoraphobia, for instance, how much the anxiety saved our ancestors from people rather than from predators.

Energizer versus paralyzer

Anxiety motivates the individual to escape danger and work hard to avoid social disgrace. On the other hand, too much anxiety impairs performance, and may actually impede attempts to escape or avoid danger. This is illustrated by the two limbs of the Yerkes-Dodson curve (*Figure 1*).

Basic research

Action versus training

Anxiety is concerned with the active avoidance of immediate danger, but it also acts as an unconditioned stimulus in the learning of avoidance of dangerous situations. Certain stimuli appear to have been “primed” by evolution to be favored as predictors of anxious situations.^{9,78}

Emotion versus mood

Like depression, anxiety can be mediated by both the limbic and the striatal central processing assemblies of the triune brain, and we think these two processes reflect the difference between emotion (anxious about something, and feel better when that something ceases to be threatening) and anxious mood (unfocused or self-focused, and indifferent to environmental change) (*Table 1*).

Response to outside versus internal events

Because the human mind can plan ahead, it can predict that something it is going to do is dangerous. If it is planning an aggressive or sexual initiative, it can predict that this may elicit a dangerous response from a more powerful person or the group as a whole. Moreover, because, due to the repression required for socialization, the early planning stage of such an initiative may be unconscious, we may not know what the anxiety is due to. This is the well-known “signal anxiety,” which is used to good effect by psychoanalysts.⁷⁹

Modular versus nonmodular

Because, famously, evolution is a tinkerer rather than an engineer, there is no clear separation between different anxiety responses or the situations that cause them.

Danger may give rise to fight or flight or freezing or jealousy or washing or checking or to the construction of fall-out shelters, and all of these activities are accompanied by the dysphoric affect of anxiety. Whereas GAD is genetically linked to depression and the trait of neuroticism,²² panic disorder and agoraphobia are more mixed in their inheritance, while specific phobias such as those of blood, insects, and heights are relatively independent. In the case of avoidance of aspects of the habitat such as cliffs and caves, one must suspect that anxiety

may have had a function in the splitting of early human groups, as acrophobics abandoned communities living on cliff tops and claustrophobics abandoned communities living in caves; rate of group splitting is an important variable in behavioral ecology, having implications for the evolution of natural selection at the group level.⁸⁰

Basic concepts

Psychiatry sadly lacks a coherent science of normal behavior on which to base our study of the pathological.⁸¹ Sociophysiology has been suggested as a suitable title for such a science,⁸² and I hope it can be seen from the above that certain areas of knowledge are necessary for the appreciation of evolutionary psychiatry. These include:

- The neuroethology of Paul MacLean’s triune brain.²⁷
- The changes in social competition (and so sexual selection) that have occurred since the common reptilian and human ancestor.⁵⁰
- The idea of alternative behavioral strategies (particularly escalation and de-escalation) that has been found useful in behavioral ecology.^{32,33}
- Fundamental psychological concepts such as the Yerkes-Dodson law, which relates performance to motivation.^{64,65}

I hope that I have shown how these ideas illuminate the possible evolution of the anxiety disorders. I am also confident that these basically untestable ideas are not just giving an understanding of the human predicament in a philosophical sense, but are also informing current research^{83,84} and developments in treatment.⁵⁷ There is a pattern there to be seen. As William James⁸⁵ put it, anticipating the words of Sir Charles Sherrington with which I started this paper:

“... *Our inner faculties are adapted in advance to the features of the world in which we dwell, adapted I mean, so as to secure our safety and prosperity in its midst [...]* Mind and world in short have evolved together, and in consequence are something of a mutual fit.” □

I thank my fellow members of the ASCAP Society for exchange of ideas over many years. The ASCAP Society (ASCAP stands for Across Species Comparisons and Psychopathology) is an international organization of people from various disciplines interested in evolutionary aspects of psychopathology (see www.theascapsociety.net).

Aspectos evolucionistas de los trastornos de ansiedad

El daño y el peligro se evitan a través de decisiones estratégicas que se producen en los tres niveles de la triada del prosencéfalo: nivel racional (proveniente de los neomamíferos), nivel emocional (proveniente de los paleomamíferos) y nivel instintivo (proveniente de los reptiles). El peligro potencial de los congéneres, sigue este mismo tipo de decisión estratégica con un posible elección entre una escalada de agresividad o de sumisión. La ansiedad es un componente de la estrategia de sumisión que se produce en la parte del prosencéfalo proveniente de los paleomamíferos y de los reptiles. Cuando la parte del cerebro proveniente de los neomamíferos (racional) no es capaz de afrontar con éxito una situación de amenaza de congéneres, otras estrategias de sumisión más primitivas pueden activarse y se presentan como trastornos de ansiedad. La capacidad de disimular la ansiedad y otras formas de afecto negativo también ha evolucionado. El disimulo excesivo puede conducir a fenómenos psicopatológicos al interrumpir el feed back negativo de la motivación excesiva, lo que conduce a un deterioro del rendimiento, signos de distrés y reducción de la incitación al éxito de parte de padres y profesores; esta situación se ilustra mediante un modelo que se basa en la ley de Yerkes-Dodson.

Aspects évolutifs des troubles de l'anxiété

L'évitement du danger et des risques de préjudice s'effectue au travers de décisions stratégiques prises aux trois niveaux du prosencéphale triun : niveaux rationnel (néomammalien), émotionnel (paléomammalien) et instinctif (reptilien). Ceci s'applique aussi à l'agression potentielle venant des congénères, ce qui conduit à un choix entre une stratégie d'escalade de violence ou de soumission. L'anxiété est une composante des stratégies de soumission médiée par les prosencéphales paléomammalien et reptilien. Quand le cerveau néomammalien (rationnel) ne réussit pas à circonscrire la menace issue d'un congénère, ces stratégies de soumission plus primitives peuvent être activées et se présenter comme des troubles anxieux. La capacité de dissimulation de l'anxiété et d'autres formes de sentiments négatifs a aussi évolué, et une dissimulation excessive peut conduire à une psychologie pathologique en interrompant la boucle du rétrocontrôle négatif d'une motivation excessive, conduisant à des performances altérées, à des signaux de détresse, à une diminution de l'incitation à réussir de la part des parents et des professeurs ; cette situation est illustrée par un modèle basé sur la loi de Yerkes-Dodson.

REFERENCES

1. Stevens A, Price J. *Evolutionary Psychiatry: A New Beginning*. 2nd ed. London, UK: Routledge; 2000.
2. McGuire MT, Troisi A. *Darwinian Psychiatry*. New York, NY: Oxford University Press; 1998.
3. Marks IM. *Fears, Phobias and Rituals*. New York, NY: Oxford University Press; 1987.
4. Marks IM, Nesse RM. Fear and fitness: an evolutionary analysis of anxiety disorders. *Ethol Sociobiol*. 1994;15:247-261.
5. Gilbert P, Trower P. The evolution and manifestation of social anxiety. In: Crozier WR, ed. *Shyness and Embarrassment: Perspectives from Social Psychology*. Cambridge, UK: Cambridge University Press; 1990:144-177.
6. Nesse RM. An evolutionary perspective on panic disorder and agoraphobia. *Ethol Sociobiol*. 1987;8:73s-85s.
7. Nesse RM. Proximate and evolutionary studies of anxiety, stress and depression: synergy at the interface. *Neurosci Biobehav Rev*. 1999;23:895-903.
8. Stein DJ, Bouwer C. A neuro-evolutionary approach to the anxiety disorders. *J Anxiety Disord*. 1997;11:409-429.
9. Ohman A, Mineka S. Fears, phobias and preparedness: toward an evolved module of fear and fear learning. *Psychol Rev*. 2001;108:483-522.
10. Hofer MA. An evolutionary perspective on anxiety. In: Roose SP, Glick RA, eds. *Anxiety as Symptom and Signal*. Hillsdale, NJ: Analytic Press; 1995:17-38.
11. Woody S, Rachman S. Generalised anxiety disorder (GAD) as an unsuccessful search for safety. *Clin Psychol Rev*. 1994;14:743-753.
12. de Waal F. The reconciled hierarchy. In: Chance MRA, ed. *Social Fabrics of the Mind*. Hove, UK: Lawrence Erlbaum; 1988:297-312.
13. de Waal F. *Peacemaking Among Primates*. Cambridge, Mass: Harvard University Press; 1989.
14. Aureli F, de Waal FMB. Why natural conflict resolution? In: Aureli F, de Waal FMB, eds. *Natural Conflict Resolution*. Berkeley, Calif: University of California Press; 2000:1-10.
15. Price JS, Sloman L, Gardner R, et al. The social competition hypothesis of depression. *Br J Psychiatry*. 1994;164:309-135. Reprinted in: Baron-Cohen S, ed. *The Maladapted Mind: Classic Readings in Evolutionary Psychopathology*. Hove, UK: Psychology Press; 1997:241-253.
16. Gardner R, Price J. Sociophysiology and depression. In: Joiner T, Coyne JD, eds. *Recent Advances in Interpersonal Approaches to Depression*. Washington, DC: American Psychological Association; 1996:247-268.
17. Whyte FW. *Street Corner Society*. 2nd ed. Chicago, Ill: University of Chicago Press; 1955.
18. Gilbert P, Allan S, Brough S, Melley S, Miles JNV. Relationship of anhedonia and anxiety to social rank, defeat and entrapment. *J Affect Disord*. 2002;71:141-151.
19. Fournier MA, Moskowitz DS, Zuroff DC. Social rank strategies in hierarchical relationships. *J Pers Soc Psychol*. 2002;83:425-433.
20. Weissman MM, Markowitz JC, Klerman GI. *Comprehensive Guide to Interpersonal Psychotherapy*. New York, NY: Basic Books; 2000.
21. Buss DM. The evolution of anxiety and social exclusion. *J Soc Clin Psychol*. 1990;9:196-201.

Basic research

22. Mineka S, Watson D, Clark LA. Comorbidity of anxiety and unipolar mood disorders. *Am Rev Psychol.* 1998;49:377-412.
23. Kaufman J, Charney D. Comorbidity of mood and anxiety disorders. *Depress Anxiety.* 2000;12:69-76.
24. Tyrer P. The case for cothymia: mixed anxiety and depression as a single diagnosis. *Br J Psychiatry.* 2001;179:191-193.
25. Nemeroff CB. Comorbidity of mood and anxiety disorders: the rule, not the exception. *Am J Psychiatry.* 2001;159:3-4.
26. Davidson RJ, Ekman P. Afterword: how are emotions distinguished from moods, temperament and other related affective constructs. In: Eckman P, Davidson RJ, eds. *The Nature of Emotion: Fundamental Questions.* New York, NY: Oxford University Press; 1994:94-96.
27. MacLean PD. *The Triune Brain in Evolution.* New York, NY: Plenum Press; 1990.
28. Cory G, Gardner R, eds. *The Neuroethology of Paul MacLean: Convergences and Frontiers.* Westport, Conn: Greenwood-Praeger; 2002.
29. Price JS. Gurdjieff and the triune brain. *ASCAP Newsletter.* 1998;11:19-21.
30. Price JS. The triune brain, escalation de-escalation strategies, and mood disorders. In: Cory G, Gardner R, eds. *The Neuroethology of Paul MacLean: Convergences and Frontiers.* Westport, Conn: Greenwood-Praeger; 2002.
31. Cornford FM. *The Republic of Plato.* Translated with introduction and notes. London, UK: Turnstone Books; 1976.
32. Huntingford FA, Taylor AC, Sneddon LU, Neat FC. Prowess and the resolution of animal fights. In: Espmark Y, Amundsen T, Rosenqvist G, eds. *Animal Signals: Signalling and Signal Design in Animal Communication.* Trondheim, Norway: Tapir Academic Press; 2000:259-276.
33. Krebs JR, Davies NB. *An Introduction to Behavioural Ecology, 3rd ed.* Oxford, UK: Blackwell Scientific Publications; 1993.
34. Clutton-Brock TH, Guinness FE, Albob SD. *Red Deer: Behaviour and Ecology of Two Sexes.* Edinburgh, UK: Edinburgh University Press; 1982.
35. Maynard Smith J, Harper DG. The evolution of aggression: can selection generate variability? *Philos Trans R Soc Lond B Biol Sci.* 1988;319:557-570.
36. Maynard Smith J. *Evolution and the Theory of Games.* Cambridge, UK: Cambridge University Press; 1982.
37. Price JS, Gardner R, Erickson M. Can depression, anxiety and somatisation be understood as appeasement displays. *J Affect Disord.* 2003. In press.
38. Price JS, Gardner R. The paradoxical power of the depressed patient: a problem for the ranking theory of depression. *Br J Med Psychol.* 1995; 68:193-206.
39. Gilbert P. *Depression: The Evolution of Powerlessness.* Hove, UK: Lawrence Erlbaum; 1992.
40. Barkow JH. *Precis of Darwin, Sex and Status: biological approaches to mind and culture.* *Behav Brain Sci.* 1991;14:295-334.
41. Bowlby J. *Attachment and Loss. Vol 1. Attachment.* London, UK: Hogarth Press; 1969.
42. Bowlby J. *Attachment and Loss. Vol 2. Separation, Anxiety and Anger.* London, UK: Hogarth Press; 1973
43. Bowlby J. *Attachment and Loss. Vol 3. Loss: Sadness and Depression.* London, UK: Hogarth Press; 1980.
44. Holmes J. Attachment theory: a biological basis for psychotherapy? *Br J Psychiatry.* 1993;163:430-438.
45. Clement Y, Calatayud F, Belzung C. Genetic basis of anxiety-like behaviour: a critical review. *Brain Res Bull.* 2002;57:57-71.
46. Price JS, Gardner R. Humans are superhuman animals: a reply to commentaries by J. Birtchnell and P. Gilbert. *Br J Med Psychol.* 1995;68:217-222.
47. De Waal FBM, Harcourt AH. Coalitions and alliances: a history of ethological research. In: Harcourt AH, de Waal FBM, eds. *Coalitions and Alliances in Humans and Other Animals.* Oxford, UK: Oxford University Press; 1992:1-19.
48. Stevens A, Price JS. *Prophets, Cults and Madness.* London, UK: Duckworth; 2000.
49. Boehm C. Egalitarian behaviour and reverse dominance hierarchy. *Curr Anthropol.* 1993;34:227-254.
50. Price JS. Implications of sexual selection for variation in human personality and behavior. In: van der Dennen J, Smillie D, eds. *The Darwinian Heritage and Sociobiology.* Westport, Conn: Greenwood Publishing Group; 1999:295-308.
51. Shively CA. Social subordination stress, behaviour, and central monoamine function in female cynomolgous monkeys. *Biol Psychiatry.* 1998;44:882-891.
52. Shively CA, Laber-Laird K, Anton RF. Behavior and physiology of social stress and depression in female cynomolgous monkeys. *Biol Psychiatry.* 1997;41:871-882.
53. McGuire MT, Raleigh MJ. Serotonin-behavior interactions in vervet monkeys. *Psychopharmacol Bull.* 1985;21:458-463.
54. Gardner R. Evolutionary perspectives on stress and affective disorders. *Sem Neuropsychiatry.* 2001;6:32-42.
55. Gardner R: Psychiatry needs a basic science titled sociophysiology. *Biol Psychiatry.* 1996;39:833-834.
56. Price JS. The adaptive function of mood change. *Br J Med Psychol.* 1998;71:465-477.
57. Sloman L, Atkinson L, Milligan K, Liotti G. Attachment, social rank and affect regulation: speculations on an ethological approach to family interaction. *Fam Process.* 2002;41:479-493.
58. Nicolescu AB, Akiskal HS. Proposed endophenotypes of dysthymia: evolutionary, clinical and pharmacogenomic considerations. *Mol Psychiatry.* 2001;6:363-366.
59. Coyne JC. Studying depressed persons' interactions with strangers and spouses. *J Abnorm Psychol.* 1985;94:231-232.
60. Klerman GL. Depression and adaptation. In: Friedman RJ, Katz MM, eds. *The Psychology of Depression.* Washington, DC: V. H. Winston; 1974:127-145.
61. Howell S. "To be angry is not to be human, but to be fearful is": Chewong concepts of human nature. In: Howell S, Willis R, eds. *Societies at Peace: Anthropological Perspectives.* London, UK: Routledge; 1989:45-59.
62. Datta S. The acquisition of dominance among free-ranging rhesus monkeys. *Anim Behav.* 1988;36:754-772.
63. Curtin LL. The Yerkes-Dodson law. *Nurs Manage.* 1984;15:7-8.
64. Yerkes RM, Dodson JD. The relation of strength of stimulus to rapidity of habit-formation. *J Comp Neurol Psychol.* 1908;18:459-482.
65. Gray P. *Psychology.* New York, NY: Worth Publishers; 1991.
66. Price JS. Developmental features of depression. *ASCAP Bull.* 2002;3:16-20.
67. James B. Why do people have accidents? *BMJ.* 1991;84:382-383.
68. Smith A. Stress and information processing. In: Johnston M, Wallace L, eds. *Stress and Medical Procedures.* Oxford, UK: Oxford University Press; 1990:58-80.
69. Selye H. *Stress Without Distress.* London, UK: Hodder & Stoughton; 1974.
70. Seyfarth RM. Vocal communication and its relation to language. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds. *Primate Societies.* Chicago, Ill: University of Chicago Press; 1986:440-451.
71. Cheney DL, Wrangham W. Predation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds. *Primate Societies.* Chicago, Ill: University of Chicago Press; 1986:227-239.
72. Cheney DL, Seyfarth RM. *How Monkeys See the World: Inside the Mind of Another Species.* Chicago, Ill: University of Chicago Press, 1990.
73. Akiskal HS. Toward a definition of generalised anxiety disorder as an anxious temperament type. *Acta Psychiatr Scand Suppl.* 1998;393:66-73.
74. DeVore I, Hall KRL. Baboon ecology. In: DeVore I, ed. *Primate Behavior: Field Studies of Monkeys and Apes.* New York, NY: Hold, Reinhart & Winston; 1965:20-52.
75. Pusey AE. The primate perspective on dispersal. In: Stenseth NC, Lidicker WZ, eds. *Animal Dispersal: Small Mammals as a Model.* London, UK: Chapman & Hall; 1992:243-259.
76. Lange A, van Dyck R. The function of agoraphobia in the marital relationship. *Acta Psychiatr Scand.* 1992;85:89-93.
77. Dowling S. The ontogeny and dynamics of anxiety in childhood. In: Roose SP, Glick RA, eds. *Anxiety as Symptom and Signal.* Hillsdale, NJ: Analytic Press; 1995:75-86.
78. Menzies RG, Harris LM. Mode of onset in evolutionarily relevant and evolutionarily-neutral phobias: evidence from a clinical sample. *Depress Anxiety.* 1997;5:134-136.
79. Glick RA. Freudian and post-Freudian theories of anxiety. In: Roose SP, Glick RA, eds. *Anxiety as Symptom and Signal.* Hillsdale, NJ: Analytic Press; 1995:1-16.
80. Sober E, Wilson DS. *Unto Others: The Evolution and Psychology of Unselfish Behavior.* Cambridge, Mass: Harvard University Press; 1998.
81. Nesse RM. Evolutionary biology: a basic science for psychiatry. *World Med.* 2002;1:7-9.
82. Gardner R. Sociophysiology as the basic science of psychiatry. *Theor Med.* 1997;18:335-356.
83. Gilbert P. Depression and stress: a biopsychosocial exploration of evolved functions and mechanisms. *Stress Int J Biol Stress.* 2001;4:121-135.
84. Gilbert P. Evolution and social anxiety: the role of social competition and social hierarchies. In: Schnieder F, ed. *Social Anxiety: Psychiatric Clinics of North America.* 2001;24:723-751.
85. James W. *Principles of Psychology.* Vol 1. New York, NY: Henry Holt; 1890.