

Natural selection and the elusiveness of happiness

Randolph M. Nesse

Department of Psychiatry, Department of Psychology and Institute for Social Research, The University of Michigan, 426 Thompson Street, Room 5261, Ann Arbor, MI 48104, USA (nesse@umich.edu)

The quest for happiness has expanded from a focus on relieving suffering to also considering how to promote happiness. However, both approaches have yet to be conducted in an evolutionary framework based on the situations that shaped the capacities for happiness and sadness. Because of this, the emphasis has almost all been on the disadvantages of negative states and the benefits of positive states, to the nearly total neglect of 'diagonal psychology', which also considers the dangers of unwarranted positive states and the benefits of negative emotions in certain situations. The situations that arise in goal pursuit contain adaptive challenges that have shaped domain-general positive and negative emotions that were partially differentiated by natural selection to cope with the more specific situations that arise in the pursuit of different kinds of goals. In cultures where large social groups give rise to specialized and competitive social roles, depression may be common because regulation systems are pushed far beyond the bounds for which they were designed. Research on the evolutionary origins of the capacities for positive and negative emotions is urgently needed to provide a foundation for sensible decisions about the use of new mood-manipulating technologies.

Keywords: evolution; natural selection; happiness; well-being; depression; goals

1. THE CORE DILEMMA OF MODERNITY

At the beginning of the third millennium, we humans in technological societies are not sure how to proceed. Ever since the Enlightenment, people in the West have pursued happiness by trying to eliminate the causes of suffering, on the sensible belief that this would lead to a world that was, if not utopia for all, at least much happier for most. Subsequent advances in technology have made life easier, safer and more pleasurable and comfortable to a degree that could not have been imagined. The suffering caused by hunger, pain, sickness, boredom, and even the early death of loved ones have been largely eliminated from the experiences of many people. The triumph of technology over most of the specific causes of human suffering is nothing short of miraculous. But the deeper hope that this would lead to general happiness is not only unfulfilled, it is almost a cruel joke. Even among those who have succeeded beyond measure in getting what people always wanted, vast numbers of people remain deeply unhappy, and many of the rest live lives that feel frantic, meaningless or both. This is the core dilemma of modernity. What we have been doing to increase general happiness is no longer working, and there is no consensus about what we should try next.

This quest for happiness is, of course, much more ancient and diverse than just the Western attempt to use rationality to solve problems. Every religion offers its own answers, most of which emphasize the need to act according to duty instead of desire, and the power to change one's own attitudes in an unchangeable world. A related range of

solutions offered by ancient philosophers in the Western world can be arrayed on a continuum from hedonistic pursuits to balanced living to ascetic denial (Nussbaum 1994). In more recent historical times, utilitarian social philosophers offered various schemes for organizing human groups, advocating variations on policies that provide the greater happiness for the greatest number (Mill 1848; Bentham & Mill 1973). The great experiments in communism have foundered spectacularly on the shoals of human nature, leaving the appearance that capitalistic democracies are the stable final condition of human social groups (Fukuyama 1992). In very recent years, attention has shifted from grand social theory to the effectiveness of mood-altering drugs and the beliefs they foster, that severe states of unhappiness are usually the products of brain abnormalities (Andreasen 1984; Valenstein 1998).

This is not the place to review the attempts by priests, philosophers, politicians and physicians to understand and relieve unhappiness. For our purposes, it is essential to note only the diversity, persistence and passion of the quest over the centuries, and the tendency to focus on relieving unhappiness. The strategy at the social level has mainly been to give people more of what they want by promoting economic growth and solving specific problems. Although a reliable method to compare well-being across the centuries is lacking, the remarkable growth in wealth and the technological advances of recent decades have improved human well-being considerably, but we have now reached a point where average life satisfaction is stable at best, and possibly declining rapidly (Kahneman *et al.* 1999). The time is ripe to consider new perspectives on the factors that influence well-being.

One contribution of 12 to a Discussion Meeting Issue 'The science of well-being: integrating neurobiology, psychology and social science'.

(a) Social science tackles well-being

Human subjective well-being has long been a central focus of social science. From Durkheim's attempts to understand the social origins of anomie to Freud's interpretations of an individual's impulses and defences, the ancestors of modern social science have doggedly persisted in the task of finding out why people are unhappy. More modern social science has applied objective methods that provide detailed epidemiological pictures of the correlates not only of anomie, but also of depression, anxiety and other aversive states (Tsuang & Tohen 2002). It examines how developmental experiences influence individual relationships and emotions and the effects of different kinds of therapies (Rutter & Rutter 1993). Increasingly, it explores not only the effects of genetic factors (Bouchard & Loehlin 2001), but also the effects of specific genes (Bouchard & Loehlin 2001; Caspi *et al.* 2002). The vast bulk of this research has been structured as attempts to explain pathology. Although effective interventions have only recently become available, a great deal of work to find the correlates of unhappiness has been accomplished. Because resources for intervention are so much more available than those for prevention, the effects of early abuse and neglect, and the effects of dysfunctional social groups, have been overshadowed by the dominant paradigm of biological psychiatry, with its emphasis on individual differences in brain mechanisms and drug treatments (Valenstein 1998).

In the past decade, the challenge of finding routes to human happiness has taken a new turn, with an explicit focus not only on the causes of suffering, but now also on the origins of positive states of well-being (Kahneman *et al.* 1999). This, in part, reflects a growing recognition that happiness and flourishing do not automatically emerge when the swamps of suffering are drained, and it results also from indications that positive and negative affect are not necessarily opposite ends of one continuum (Watson *et al.* 1988). Furthermore, some people experience states of flow and flourishing that are far more positive than ever appear in the lives of average people (Csikszentmihalyi 1977). If some proportion of their extraordinary well-being could be shared with others, the benefits would be truly wonderful. The Discussion Meeting that gave rise to this paper highlights many of those advances.

Many findings from these research endeavours are increasingly solid. Although most people describe their lives as 'generally happy' (Diener & Diener 1996), 16% of individuals in the USA have experienced episodes of serious depression, and in any given year *ca.* 6% of adults will experience two weeks or more during which depressive symptoms interfere with their ability to function effectively (Kessler *et al.* 2003). Rates of anxiety disorders are of the same order of magnitude, and the comorbidity of anxiety and depression is extraordinary (Maser & Cloninger 1990). The definitions of these severe disorders are quite restrictive, and considerably more people report more mild states of low mood or anxiety. Another major finding is that the comorbidity among many mental disorders is so striking that most of the disorders occur in the small proportion of the population who have many diagnoses, while most people have none. That is not quite true. Almost half of the population has qualified for a lifetime psychiatric diagnosis using the criteria from the American Psychiatric Association's DSM criteria, and *ca.* 30% qualify for a diagnosis in a

given year (Kessler *et al.* 1994). The problem of understanding how such a large proportion of the population can report that they are 'happy', despite so many suffering from a mental disorder, is a complex one whose resolution will require comparison of the quite different methods used to gather these two kinds of data.

Research that moves beyond pathology to measures of well-being has now been conducted with large samples in dozens of countries (Diener & Suh 1999; Prescott-Allen 2001; Helliwell 2002). There is some consistency in the shape of the distribution, with most people reporting general satisfaction with their lives and a fraction saying that they are dissatisfied. The correlates are also consistent and significant. The average well-being for a society increases as the average income increases up to the equivalent of *ca.* \$10 000 per year; above that level additional GNP adds little to the average happiness ratings of the populace (Kahnemann *et al.* 1999). Within societies, the picture is different; increasing income increases ratings of well-being, although the benefits taper off in high income brackets, perhaps in part because of ceiling effects for the scales used.

Dozens of studies have examined demographic correlates of well-being (Argyle 1999). Women, on average, have well-being levels similar to those of men, but men are more likely to report extreme levels. Married people have higher well-being than single or divorced individuals but the differences are small, last only a few years, and the direction of causation is often uncertain. A particularly large and careful study that provided a multivariate analysis including both individual factors within cultures and differences among cultures, found the strongest effect from health, closely followed by unemployment, results that tend to support the old view that happiness is indeed mostly lack of unhappiness (Helliwell 2002). Other effects found in the study were the positive effects of being married, believing in God, having a personal sense that people can be trusted, living in a country where trust is high, and the tendency for negative affect in the prime adult years and for those living in the former Soviet Union. The grand sum of variance explained in this study is 25%. Adding variables for societal differences accounted for an additional 1% of the variance. These estimates are comparable to the estimated 20% of SWB variance explained by demographic factors in other studies (Diener & Lucas 1999).

Although accounting for only 25% of the variance may seem low, it is remarkably high given the profound and disturbing evidence that individual levels of well-being are remarkably stable over time almost irrespective of what happens (Loewenstein & Shane 1999). Even dramatic events such as becoming paralysed or winning the lottery have effects on SWB that are strikingly small and temporary (Brickman *et al.* 1978). While reconsideration of these findings suggests mood changes more congruent with everyday expectations (Easterlin 2003)—the lottery makes most people somewhat happier and serious medical problems leave most people less happy—the stability of SWB remains impressive. Furthermore, studies of twins and adopted children suggest that much of the variation in SWB among individuals, more than half in most estimates, can be attributed to their genetic differences (Tellegen *et al.* 1988; Lykken & Tellegen 1996). Perhaps even more surprising is that little, if any, of the correlations among siblings can be attributed to being raised in the same family,

suggesting that the similarities arise from shared genes (Bouchard & Loehlin 2001). Personality traits, especially extraversion and neuroticism, predict SWB even over and above demographic factors (Diener & Lucas 1999). Variations in these traits arise, like those for SWB, mostly from genetic variation, with considerable similarity for sibs raised in different families, but little similarity among adopted children raised together in the same household (Bouchard & Loehlin 2001).

Shared genetic factors could, of course, account for the association of certain personality features, especially extraversion, with SWB. But it is increasingly clear that the observed high heritability estimates for such traits does not mean that they are in any way directly 'encoded in the genes'. Far from it. First of all, there may be many different genetic routes to a trait, some more direct than others. But equally important is recognizing that the crucial inherited factors may be preferences. For instance, an individual's likelihood of experiencing a severe life event in the past 12 months is highly heritable (Saudino *et al.* 1997). There are obviously no genes that directly cause life events, but there certainly are inherited tendencies such as risk-taking or having a short temper, which are likely to lead to life events (Bouchard & Loehlin 2001). Consideration of such possibilities is even more important for conditions such as depression, where there is a pronounced tendency to assume that the influence of genetic factors implies brain defects. An evolutionary functional view of the involved systems suggests many other routes for genetic influences. One person might inherit a tendency for ambition that can never be satisfied, whereas another inherits a tendency to become so attached to a partner that she will not leave despite mistreatment. Perhaps most depressogenic of all, in the model developed here, would be tendencies to undertake huge difficult goals, and to be unwilling to give them up, even when all efforts are obviously in vain.

Another line of research is explicating the brain mechanisms that mediate states of well-being. Progress is coming rapidly in uncovering the neurochemistry of mood, with the role of dopamine in attention and motivation increasingly well understood, and the role of serotonin in anxiety and depression becoming more clear (Nathan *et al.* 1995; Gershon *et al.* 2003). The anatomic correlates of mood are becoming clear, with evidence showing an association of depression with increased activity in a region of the right forebrain (Davidson 1992). Even within-subject manipulations of mood influence activation of this brain region. Trans-cranial magnetic brain stimulation that disrupts neuronal activity in this area seems to relieve depression in some individuals, although the matter of finding adequate control conditions is difficult (Gershon *et al.* 2003).

On a social and political level, it is abundantly clear that certain policies can increase average SWB in a society (Layard 2005). More equitable income distribution is highly correlated with the average level of well-being in a society, and high taxes on high incomes and luxury goods would result in only infinitesimal decrements in the positional pleasures provided by luxury goods (Frank 1999). Most democratic societies seem unable, however, to enact laws based on this knowledge to increase the well-being in their societies. Or is it possible, as Layard and Felicia Huppert have separately suggested, that confirmation and dissemination of these findings may help political groups to

transcend short-term self-interest and to enact policies that would improve well-being for whole societies?

In a parallel phenomenon at the individual level, people often do not act in ways that would bring them happiness. Addiction is obviously a huge cause of misery, but even in domains where people are imagined to make more considered and free choices, they still seem to pursue goals that bring pleasure more reliably than happiness. The human tendency to make decisions with a short-term time horizon has been noted for several millennia, but it is nonetheless a powerful explanation for human behavioural tendencies that limit SWB (Kimball 1993). At least in modern Western societies, people also tend to make disproportionate investments in the pursuit of money, status and attractiveness, domains in which the value of resources is intrinsically relative to what others have, resulting in escalating arms races that sap time and energy from friendships and social engagement that are highly correlated with SWB (Crocker & Wolfe 2001).

Many of the other articles from this Discussion Meeting will further explicate the extraordinary knowledge base we now have on factors that influence SWB. But what are we to do with all this information? We need a model. All the variables studied and their connections need to be incorporated into a path diagram so we can see their interrelationships. Figure 1 summarizes some major pathways.

Taken together, the studies that measure the coefficients for each of these relationships comprise a remarkable achievement. Lest it be thought that figure 1 is just an imaginary exercise, models nearly this complex have been published for depression (Kendler *et al.* 2002). Continuing research is investigating the details and the interaction effects in an attempt to make the model stronger. However, from another perspective, the model vividly illustrates the limits of this paradigm. How exactly are we to use this information? What should we do next? Carry out still more careful studies of these relationships? Add yet more variables? It seems that there is something missing from the picture. Perhaps there is some way to begin to make sense of all this information.

2. WHAT EVOLUTION OFFERS TO THE STUDY OF WELL-BEING

(a) *New questions*

All of the research already described is about proximate mechanisms. It explicates the components and operation of the systems that influence well-being, from the level of neurochemistry to brain loci, life events, relationships, personality, cultural factors and methodological factors that influence how an individual reports SWB. Two things are omitted.

First, the model assumes that different individuals will have the same pathways to SWB. We all know, of course, that a life event such as divorce can devastate one person while rejuvenating another. Recent studies are increasingly investigating how genetic differences interact with different life experiences to generate changes in SWB (Kendler *et al.* 1999; Caspi *et al.* 2003). However, few studies look at differences in individual life goals and strategies to provide an idographic (individualized narrative) context in which innate and acquired differences can be analysed (Brown & Harris 1978). The divorce of idographic and nomothetic

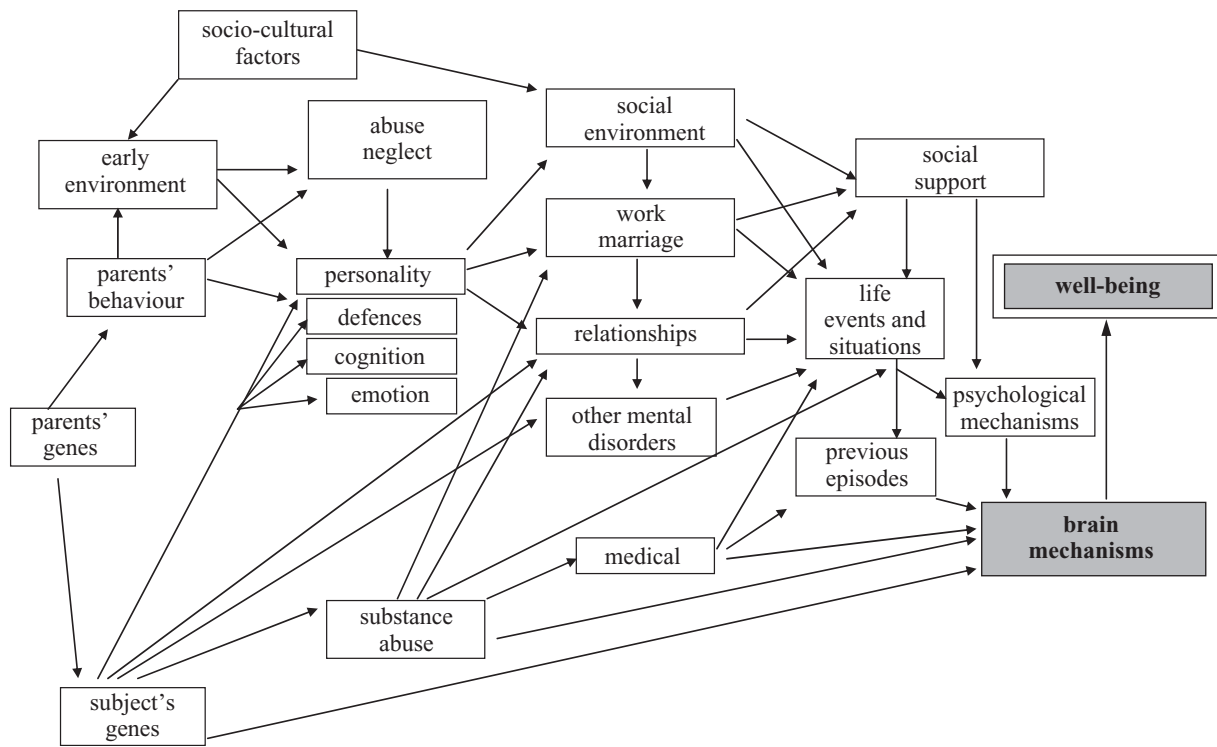


Figure 1. Factors and pathways that influence SWB.

methods poses a very serious problem for social science studies in general and studies of SWB in particular. Everyone knows someone who became depressed because his wife was having an affair, or someone who fell in love and got a new lease on life, but the effects of these powerful individualized factors are not captured in studies that rely on age, sex, social class, education and other demographic variables. One study that has attempted to bridge the gap finds that SWB is influenced mainly by events and resources that influence a person's ability to reach his or her individual goals (Diener & Fujita 1995). This offers an explanation for why levels of resources so poorly predict SWB, and it offers the beginnings of a scientific basis for bringing data on individual situations to bear on the problems of psychology.

Many people assume that an evolutionary approach necessarily treats all humans crudely as if they were all the same. Instead, however, an evolutionary approach offers a theoretical bridge from the richness of idographic data to the solidity of nomothetic understanding. Once you know the core goals that humans tend to pursue and the mechanisms that regulate their pursuit of these goals, you can understand how individuals deal with these desires, and with the exigencies that inevitably keep people from their goals. This section concludes by returning to this issue to argue that natural selection provides a nomothetic framework that can incorporate the effects of individual differences in goals and strategies.

The other gap is the absence, with a few exceptions (Buss 2000), of evolutionary explanations of happiness to complement existing proximate knowledge. Even if we knew every connection of every neuron and the effects of every life event on all levels of the system, we would still only have an explanation of how the mechanisms work. Also needed, and equally important, is knowledge about why those

mechanisms exist at all and if they give a selective advantage (Tinbergen 1963). Such questions about behavioural mechanisms are structurally identical to questions about physical traits such as the shape of a finch's beak or a fish's fin. They are best addressed using the comparative method to determine if differences in the environments encountered match the characteristics of species in different environments. For instance, guppies vary considerably in their degree of bright coloration. The hypothesis that bright colour is a product of sexual selection is supported by strong and consistent female preferences for brightly coloured males across environments. However, in deep water, where predators are common, the bright colour is often fatal; there, natural selection has selected camouflage coloration instead (Endler 1986). Even when the comparative method is not applicable, however, there are other strategies for assessing the viability of evolutionary hypotheses about why behavioural regulation mechanisms are the way they are (Alcock 2001).

Behaviours and associated emotional mechanisms are not shaped directly, but the brain mechanisms that regulate them are (Symons 1990). No mechanism can give rise to the exact optimal action in every circumstance but, on average, ultimately, in the natural environment, we can safely assume that evolved behaviour regulation mechanisms will give rise to actions that tend to maximize reproductive success.

(b) Six reasons why the body is not better designed

Most people like to imagine that normal life is happy and that other states are abnormalities that need explanation. This is a pre-Darwinian view of psychology. We were not designed for happiness. Neither were we designed for unhappiness. Happiness is not a goal left unaccomplished by some bungling designer, it is an aspect of a behavioural regulation mechanism shaped by natural selection. The

utter mindlessness of natural selection is terribly hard to grasp and even harder to accept. Natural selection gradually sifts variations in DNA sequences. Sequences that create phenotypes with a less-than-average reproductive success are displaced in the gene pool by those that give increased success. This process results in organisms that tend to want to stay alive, get resources, have sex and take care of children. But these are not the goals of natural selection. Natural selection has no goals: it just mindlessly shapes mechanisms, including our capacities for happiness and unhappiness, that tend to lead to behaviour that maximizes fitness. Happiness and unhappiness are not ends, they are means. They are aspects of mechanisms that influence us to act in the interests of our genes.

Although the capacities for unhappiness and other aversive states are normal, their expression may be normal or abnormal, useful or harmful. Even after recognizing the utility of affects, we still need to ask why unhappiness is so widespread. Is it a design flaw present in only some individuals? Is it an acquired disease resulting from some kind of damage to the brain? Is it a typical response to an abnormal environment? Or is most such suffering useful even now? The six categories of evolutionary explanations for vulnerability to disease offered by Darwinian medicine (Williams & Nesse 1991; Nesse & Williams 1994) offer a framework that is helpful in attempts to address the question of why so many people find well-being so elusive. They apply to mental conditions just as well as to physical ailments, and the link to physical disease provides a solid grounding for analysis of mental disorders.

One obvious possibility is that natural selection is too slow to adapt us to rapidly changing environments. Our modern world is vastly different from the environments in which we evolved. Much, even most, chronic disease results from this mismatch; atherosclerosis, diabetes, hypertension and the complications of smoking and alcohol are rare in hunter-gatherers even at older ages. In discussing these findings Eaton *et al.* (1988) have described modern people as 'stone-agers in the fast lane'. Many before and after Rousseau have attributed human unhappiness to our separation from a state of nature (Stevens & Price 1996) and most generations imagine that life was more calm and happy in times past, even if not more healthy. One recent book uses growing knowledge about evolution and how our lives differ from those of our ancestors as a guide to authentic happiness (Grinde 2002).

A second reason is that no speed of selection can keep us ahead of other organisms that evolve faster than we can. We can never hope to evolve defences against all pathogens, and our defences and their ways to get past our defences give rise to arms races that yield expensive and dangerous bodily devices. Perhaps even more disturbing is recognition that competition with other humans, especially mate competition (Buss & Schmitt 1993) has shaped similar arms races, including products such as jealousy that help to explain the elusiveness of well-being (Buss *et al.* 1999).

Third and fourth, there are many things that no system can accomplish and some that are impossible for organisms shaped by selection. Design trade-offs leave every aspect of any machine, including the body, somewhat less than optimal. For instance, thicker bones would break less easily, but they would be heavy and unwieldy. Natural selection is

Table 1. Six reasons why the body is not better designed.

Selection is too slow.

1. The body is poorly adapted to modern environments.
2. Arms races with other fast-evolving organisms.

Selection cannot do everything.

3. Constraints.
4. Trade-offs.

What appears to be a defect is actually useful.

5. Trait increases reproduction at the expense of health.
6. The trait is a defence that is useful even if aversive.

subject to additional constraints, especially the requirement that changes can take place only by incremental alterations of existing designs, and the result must work well in every generation. There is some hope that the awkward QWERTY keyboard will be replaced some day, but our eyes will always be an absurdly designed device, with the nerves and vessels running between the light and the retina where they cast shadows and cause an unnecessary blind spot.

Fifth, some traits shaped by natural selection are useful even though they seem like mistakes. A tendency to compete to the death for a mate, for instance, seems like the height of absurdity. However, selection shapes many such traits that benefit the genes at the expense of the individual and of community peace and solidarity. Organisms are designed for maximum reproduction, nothing else (Dawkins 1976). An allele that increases reproductive success will increase in prevalence over the generations, even at the cost of health, longevity and happiness.

Finally, other apparent abnormalities are actually useful defences. Pain, fever, nausea and cough arise when something is wrong, but they themselves are useful responses. Their very aversiveness is a product of selection, almost certainly a component of motivational systems that move organisms out of bad circumstances and that promote future avoidance of harm. Likewise, the aversiveness of anxiety and other negatives is also useful (Marks & Nesse 1994). We would rather live without them, but they are essential for our own welfare; people born without a capacity for pain are dead by the age of 30. Other aversive emotions motivate us to do things that advance the interests of our genes; most people would be better off without envy, jealousy and sudden lust, but we experience them nonetheless.

The six evolutionary explanations in table 1 offer a robust framework for examining the possible origins of lack of well-being. Although the focus on negative states may seem to be the old 'negative psychology' approach that positive psychology is trying to transcend, this evolutionary approach is actually quite novel in that it expands attention from the causes of individual pathologies to the evolutionary explanations for why emotional systems are designed the way they are, and to the benefits of negative as well as positive emotions. For this reason I address the evolutionary origins and functions of negative affects prior to considering positive affects.

(c) *The utility and prevalence of negative emotions and affects*

In seeking evolutionary explanations for emotions and affects, the temptation is to jump directly to hypotheses

about possible functions. This is a mistake. Although emotional states would not exist unless they had been useful, there is no one-to-one correspondence between an emotion and a function. One emotion can serve multiple functions, and one function may be served by several different emotions. Anxiety motivates escape and future avoidance, and it can serve as a warning to others. Disgust also motivates escape, prepares the body to make escape more likely, and motivates future avoidance. Instead of jumping directly to postulated functions, a more explicitly evolutionary approach attends to the situations that shaped each emotion (Nesse 1990; Tooby & Cosmides 1990). It is these situations, with their adaptive challenges recurring over evolutionary time, that shaped special states of the organism that facilitate coping with these challenges. If a situation contains neither threats nor opportunities it will have no influence on fitness. This is why there are few, if any, neutral emotions.

Aversive emotions arise in situations when a loss has occurred or when the risk of loss is high. From the primal capacity of one-celled organisms to move away from excess heat, dryness, acidity or salinity, natural selection has gradually differentiated a host of responses to cope with different kinds of threats. This phylogenetic perspective emphasizes that the differentiation of defensive states will be only partial and that we should expect much messy overlap in both regulatory and effector mechanisms. Our human minds insist on parsing the world into nice neat categories such as fear, sadness, anger and jealousy; our minds rebel at the untidiness of psychological reality. The history of emotions research may be interpreted as a reflection of human attempts to view the mind as a machine with neat components designed by some intelligence (Plutchik 1980). Many attempts have been made to locate the emotions in a two- or three-dimensional space, often with a positive-negative axis and another axis that reflects the level of arousal. Others have tried to pair each emotion with its opposite in circumplex models. Much has been made of the distinction between emotions, with their short duration and specific referents, and affects with their longer duration and relative disconnection from specific stimuli (Morris 1992). All of these descriptions are informative, but match only very roughly the evolutionary origins of emotional states in the specific situations that shaped them.

This is not the place for details about how best to parse the negative emotions, but as an example, consider the subtypes of anxiety disorders. Even the avowedly atheoretical DSM system (American Psychiatric Association 1994) differentiates general anxiety, phobic anxiety (with several subtypes), panic and social anxiety, among others. The observation that excesses of one kind of anxiety predispose to others has spawned a small research industry to examine the origins of this 'comorbidity' (von Hecht *et al.* 1989; Maser & Cloninger 1990). From an evolutionary point of view, however, there is every reason to expect that these states will be only partly differentiated (Marks & Nesse 1994). Note the contrast between this position and the massive modularity sometimes espoused by evolutionary psychologists (Cosmides & Tooby 1994). An evolutionary view certainly does imply that the mind cannot be a blank slate, but it equally strongly implies that the mind's structure consists not of distinct modules, each shaped to carry out a particular task, but of jury-rigged and partly

overlapping mechanisms that one way or another tend to lead to adaptive behaviour most of the time (Nesse 2000b). The mechanisms do process information, but calling them algorithms incorrectly suggests that their mechanisms are like those of a digital computer. Nevertheless, the emotions are closer to modules than anything else is. Each was shaped to cope with the challenges associated with a particular kind of situation.

The prevalence of negative affect seems excessive. As already noted, 15% of the US population has had an episode of severe depression. Many other people just have many bad days when they are too worried, sad or angry to function, or at least nowhere near being full of energy and loving well-being. Most attempts to understand this state of affairs seeks explanations in individual differences, often based on the assumption that there is something wrong with these suffering people. In some cases there is. But an entirely separate question is why we are all designed in ways that leave us likely to experience negative emotions, often for no apparent reason (Gilbert 1989).

Because many defences are inexpensive compared with the harm they protect against, false alarms are both normal and common for many defences. For instance, if successful panic flight costs 200 calories but being clawed by a tiger costs the equivalent of, say, 20 000 calories, then it will be worthwhile to flee in panic whenever the probability of a tiger being present is greater than 1%. This means that the normal system will express 99 false alarms for every time a tiger is actually present; the associated distress is unnecessary in almost all individual instances. Blocking the tendency to panic would be an unalloyed good. Except, that is, for that 1 time in 100. This has been called the 'smoke detector principle' after our willingness to accept false alarms from making toast because we want a smoke detector that will give early warning about any and every actual fire (Nesse 2001).

The same principle explains how it is possible for physicians to relieve so much suffering with so few complications. Much of general medicine consists of using drugs to block perfectly normal expressions of cough, fever, vomiting, pain, etc. This is generally safe because the regulation of these defences follows the smoke detector principle and the vast majority of the time the defence is not needed to the degree expressed and because the body has redundant defences that offer good substitutes if one defence is blocked (Nesse & Williams 1994). Attention to the risks of mindlessly blocking defences is, however, gradually growing.

(d) *Positive emotions and affects*

Just as negative emotions give an advantage in situations that pose threats, positive emotions give advantages in situations that offer opportunities (Fredrickson 1998) or when progress towards a goal is faster than expected (Carver 2003). The common notion that positive and negative emotional states are simply opposites has been challenged. Even on questionnaires, scales of positive and negative affect can be remarkably unrelated to each other (Watson *et al.* 1988). Nonetheless, brain research has documented the substantially different pathways and mechanisms for the 'behavioural inhibition system' as contrasted with systems that regulate appetitive behaviour (Gray 1987). These findings are perfectly congruent with an evolutionary view

of emotions. In bacteria, information that feeds in from cell surface receptors for over 30 different substances all gets funnelled into a binary output—continue swimming ahead, or tumble randomly and swim in some other direction. Bacteria are too small to be able to detect chemical gradients over the length of their bodies, but they can compare the concentration of a substance now with the concentration half a second previously. This rudimentary memory allows extraordinarily adaptive behaviour, movement towards food and away from dangers (Dusenbery 1996). Our positive and negative emotions are mere elaborations, albeit vastly more complex after at least an additional 600 Myr of evolution.

It is, however, somewhat harder to specify the situations that arouse positive as compared with negative emotions. Although it is fairly easy to see the advantage negative emotions offer by facilitating escape from threats, it is harder to see exactly why someone with a capacity for joy would have a selective advantage over someone who lacked the capacity. Why not just move towards opportunities and take advantage of them, why get all emotional about it? One answer involves the social functions of emotions. These we will save for consideration later. Even for an organism that is simply foraging, however, states of positive arousal can be useful and are quite distinct, even neurologically, from incentive motivation (Berridge 1996). In the simplest possible terms, an organism needs to do only three things well for its behaviour to maximize fitness. First, it must exert the right amount of energy in the current task, walking versus running, for instance. Second, it must stop its current activity at the point when some other activity offers a greater pay-off per minute. Third, it must choose what subsequent activity would most advance fitness. All of these may be usefully regulated by affective states.

If a major opportunity suddenly becomes temporarily available, say the appearance of a tree full of fruit that is also being harvested by birds, then an intense burst of effort will be worthwhile to take advantage of the opportunity. When nearly all the fruit is gone, continuing to spend hours to get the last small bits at the top will not be worthwhile; it is better to quit and do something else. Whether that something else involves looking for another tree, going back to camp, or something else, depends on the detailed characteristics of the available alternatives and inner states.

Different kinds of positive experiences seem to be somewhat differentiated according to domain, from the generic differences between physical pleasure versus social joy, to the more distinct differences in positive feelings from being praised versus the pleasure from vanquishing an enemy (Ellsworth & Smith 1988*b*). Nonetheless, much about positive feelings fits nicely into a larger framework based on the situations that arise in the pursuit of generic goals. If an organism is pursuing a goal and encounters an obstacle, it becomes aroused, even aggressive (Klinger 1975). The increased effort and risk taking soon determine if the obstacle is surmountable or not. If it is, or if other circumstances make approach to the goal more rapid than expected, the resulting positive emotions facilitate investing yet more effort. If, however, increasing efforts lead to positions further and further from the goal, then low mood tends to disengage effort from the goal, or at least from the specific strategy. This prevents wasted effort and tends to allocate

Table 2. A simple model of emotions for goal pursuit.

	before	after
opportunity	desire	pleasure
threat	fear	pain

effort efficiently among various possible enterprises and strategies.

This model has been elaborated in two decades of work by a score of psychologists (Klinger 1975; Janoff-Bulman & Brickman 1982; Pyszczynski & Greenberg 1987; Cantor 1990; Carver & Scheier 1990; Emmons 1996; Martin & Tesser 1996; McGregor & Little 1998; Mackey & Immerman 2000). Together, they offer a sophisticated description of a domain general mechanism for regulating effort allocation. Surprisingly, it has hardly been recognized by psychiatry, and it is only now being mapped to the behavioural ecology equivalent, foraging theory (Charnov 1976). At the core of foraging theory is the principle that organisms should stay in the same feeding patch until the rate of return per unit time decreases to the average rate of return over all patches including the search time needed to find a new patch.

Organisms do not need to calculate differential equations to behave optimally: they just need to have a mechanism that disengages effort from the current patch whenever the rate of return falls below the average recent rate of return. They also need to monitor the magnitude and trajectory of the average rate of return. As the evening cools, flying costs a bumble-bee more and more calories per minute. When the rate of expenditure is greater than the rate of return, it is best to give up foraging for that day (Heinrich 1979).

Whether the bumble-bee experiences anything like joy or sadness is of little consequence here. What is important is that people experience positive affect when they are reaching their goals more quickly than expected, and they experience negative affect and decreased motivation when goals seem to be unavoidably slipping away (Carver & Scheier 1990). As many psychologists have noted, opposing this normal emotional blockade of motivation only makes the negative affect stronger, and an inability to disengage from a major unreachable life goal is a recipe for serious depression. Although this effect has been documented for subjects in experimental and cross-sectional designs (Martin & Tesser 1996; Carver & Scheier 1998; Wrosch *et al.* 2003), it has yet to be applied to clinical or community samples to see how well it can explain episodes of mild and more severe depression (Nesse 2000*a*).

This view suggests locating positive affect not as a response to a domain-specific situation but as a response to the various situations that arise in pursuit of individual goals. The simplest framework incorporates the distinctions between opportunities and threats, and between the time before and after the outcome to yield four core emotions that regulate motivation (see table 2). The earliest reference to such a model is from Plato, but the basic model was elaborated by Cicero and the Stoics, then endorsed by Virgil and other leading Romans. Later it was slightly modified by the replacement of desire by hope in Hume's simplest formulation (Fiesler 1992).

Table 3. Emotions for situations that arise in the pursuit of social and physical goals.

situation	before	usual progress	fast progress	specific obstacle	slow/no progress	success	failure
physical opportunity	desire	productive effort	flow	frustration	resignation	pleasure	disappointment
social opportunity	excitement	friendship engagement	gratitude	anger	low mood	happiness	disappointment
physical threat or loss	fear	defensive behaviour	confidence	despair	despair	relief	pain
social threat or loss	anxiety	defensive behaviour	confidence	anger or helplessness	helplessness	relief	sadness

The model can be elaborated further, however, by distinguishing physical from social domains, and by expanding the sequence of situations that are routinely encountered in the course of goal pursuit (see table 3). The word 'goal' can be problematic both because some goals are things people want to avoid (e.g. the goal of avoiding sickness) and also because many goals are very personal or even spiritual quests (such as trying to be good, or seeking a state of transcendence) that are far removed from the competitive tone of the word 'goal' (Emmons 1999). Nonetheless, as things or states that people want, they can be described usefully as goals, and this construct makes important links with work on motivation (Gollwitzer & Moskowitz 1996), efficacy (Costa *et al.* 1985), possible selves (Oyserman & Markus 1993) and control theories (Wrosch & Heckhausen 2002), in addition to the burgeoning literature on goal pursuit and mood (Klinger 1975; Carver & Scheier 1990; Cantor 1994; Emmons 1996; Little 1999; Wrosch *et al.* 2003).

It appears that generic emotions for coping with the situations that arise in pursuit of all goals have been differentiated by natural selection and experience to deal with specific kinds of opportunity or threat. For instance, the threat that involves the possible loss of a mate's fidelity arouses emotions that are aspects of jealousy (Buss *et al.* 1999). If the threat involves a risk of loss of social position, the specific emotions are humiliation, pride, etc. (Gilbert & Andrews 1998). The important point is that emotional states were shaped to deal with the situations that arise in the pursuit of goals, and they were subsequently partially differentiated to deal more effectively with the situations that arise in the pursuit of certain specific goals. Social goals are of particular importance (Kenrick *et al.* 2002). There is no attempt here to suggest that all of the differentiation is a result of natural selection. Life experience, including the richness of human language and forethought, elaborate and further differentiate variations on the basic themes to yield the complexities we observe and experience.

3. A PHYLOGENY OF EMOTIONS

The tendency in emotions research has been to attempt, in the best traditions of science, to describe as many data as possible with the simplest and smallest number of concepts and relationships. This has given rise to three main traditions. One posits two or more dimensions and tries to locate emotions in the space described (Larsen & Diener 1992). Usually one dimension is positive versus negative affect and another is aroused versus non-aroused. A related

approach orients each emotion directly opposite from its paired converse emotion in a circumplex (Plutchik 1980). A second main approach tries to define a few basic emotions, usually starting with joy, sadness, fear, anger, surprise and disgust (Izard 1992). Finally, appraisal theories explain emotions more explicitly in the framework of how events change an individual's perception of his or her ability to reach personal goals, and thus take us further towards a functional evolutionary view (Ellsworth & Smith 1988a; Ortony *et al.* 1988).

A further step in that direction is to consider the phylogeny of emotions. The behavioural repertoire of bacteria is limited to moving forward in the same direction, or tumbling randomly to some new direction (Dusenbery 1996). This allows them to move towards food and away from danger, a dichotomy that matches the neurologically instantiated differentiation between behavioural approach and behavioural avoidance systems in mammalian brains (Gray 1987; Davidson 1992). After the fundamental division of affect into positive and negative, selection seems to have gradually further differentiated responses to increase the ability of organisms to cope with the vicissitudes that arise in efforts to obtain the three main kinds of life resources recognized by behavioural ecologists: personal, reproductive and social effort. Further differentiation would facilitate coping with opportunities and threats involving more specific kinds of resources in each domain. The illustration of these relationships in figure 2 is not intended as a definitive proposal for how selection actually shaped the emotions, but it offers a framework for thinking about the origins of emotions that is rooted in biology. It suggests that some long-standing debates about emotions may arise from our human cognitive tendency to try to organize reality into crisp simple categories that may not match what selection has shaped. Furthermore, the diagram intentionally shows overlap between emotions. The key concept is that emotions are *partly differentiated* from precursor states. They are neither fully distinct nor areas in a dimensional space; instead, they are states that are simultaneously both overlapping and somewhat separate. Note that observing this phylogenetic tree from above would give the appearance of separate emotions, possibly even in an arrangement something like a circumplex model.

4. DIAGONAL PSYCHOLOGY

The costs of negative emotions are obvious enough, but neglect of their benefits is so prevalent it has been called

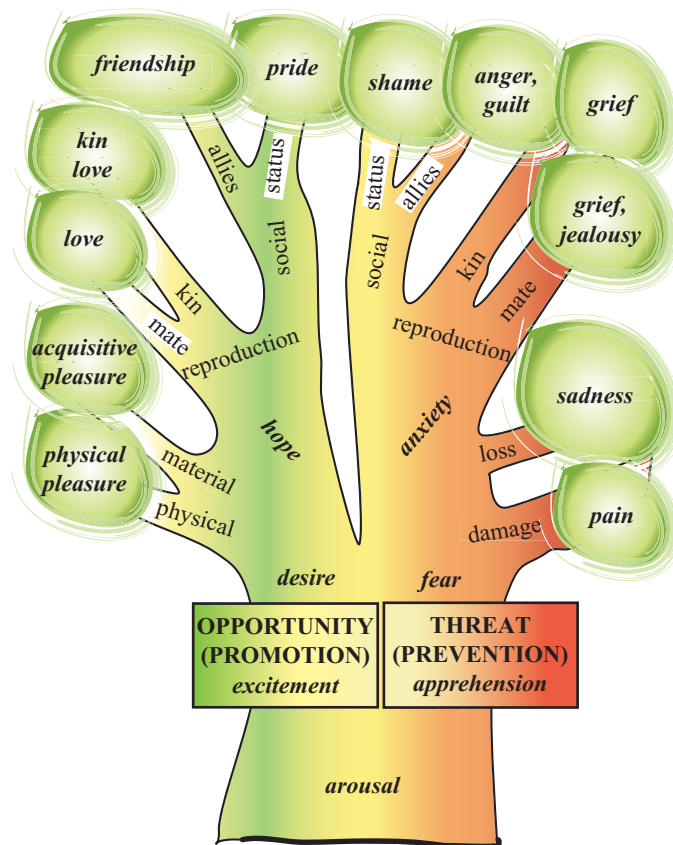


Figure 2. A phylogeny of emotions. Resources are in upright font, emotions in italic font and situations in capitals.

'The Clinician's Illusion' (Nesse & Williams 1998). Clinicians are especially prone to being unable to recognize the utility of defences because negative states are aroused when something is wrong, because they are aversive, and because they can usually be blocked without adverse consequences. A parallel illusion, perhaps even stronger, is prevalent in considerations of positive emotions. Only rarely are the dangers of positive emotions considered, except in the context of drug abuse. However, the utility of any emotion depends entirely on whether it is expressed in the situation in which it is useful. In other situations, it can be expected to be harmful. The case for the dangers of positive emotions is made most straightforwardly by individuals with mania. Their joy is infectious, their optimism and self-confidence unbounded. However, they usually lack the ability to stick with one thing long enough to accomplish anything, they often are incensed by the least criticism, and their respect for other people diminishes to the vanishing point. One manic may give away his life's savings on a whim, while another joyfully drives 100 m.p.h. to a sexual liaison with a potentially dangerous stranger.

Much milder is hypomania. This state of high mood without justification often leads to substantial accomplishments and its charisma may bring an expanding network of admirers. It is hard to see any down-side without very carefully looking for life problems that are being neglected and dangers that are unprepared for. Enquiries of several chronically happy people revealed that two had stayed for years in untenable marriages that, in retrospect, should have ended much sooner. Others continued without much dissatisfaction in jobs that did not begin to use their potentials. Another admitted that she knew cognitively that her

spontaneous and exuberant affairs were dangerous to her health and her marriage, but lack of anxiety left her to continue until catastrophe occurred. These anecdotes offer only a few examples of some costs of high mood. They do not mean that most individuals with hypomania would be better off with more average states of mood; that is an open empirical question. If higher than average mood were shown to be useful for most people, an evolutionary perspective suggests the need to look hard for explanations in aspects of the modern novel environment.

One of the main questions facing happiness research is whether most people would be better off if they experienced more positive affect, and if that proves to be the case, how it can be accounted for given that mood regulation mechanisms were shaped by natural selection. Much happiness research starts with the folk psychology notion that happiness is good for you and proceeds to demonstrate correlations between positive affect and a variety of other indicators of well-being including friendships, achievement, health and longevity. The confounding factor here is, of course, that people who are in good circumstances or are otherwise doing well can be expected to experience positive affect as a result of these circumstances. The solution is to conduct longitudinal studies that either look at changes in well-being or that experimentally induce positive affect to examine the effects on other variables. Studies of both kinds have been conducted, and both show that changes towards positive affect are associated with other positive changes.

Aside from the quite plausible possibility that file drawers are full of unpublished negative studies, this conclusion combines with the documented heritability of positive

affect to pose a serious question. If positive affect is strongly heritable and improves function, and presumably reproduction, then why did natural selection not long ago shape a higher average level of positive affect? More directly, why are there so many very successful people with many friends and resources who remain in states of chronically low mood? They may, of course, have a disorder. However, determining what is and is not a disorder will be secure only when we have an understanding, so far elusive, of the origins, functions and normal regulation of the mood system.

(a) *Affect and goal pursuit*

Our brains could have been wired so that good food, sex, being the object of admiration, and observing the success of one's children were all aversive experiences. However, any ancestor whose brain was so wired would probably not have contributed much to the gene pool that makes human nature what it is now. Similarly, if there were someone who experienced no upset at failure, no anxiety in the face of danger and no grief at the death of a child, his or her life might be free of suffering but also would probably be without much accomplishment, including having offspring. These evolved preferences for pursuing certain resources and avoiding their loss are at the very centre of human experience. It is not surprising that bad feelings are reliably aroused by losses, threats of losses, and inability to reach important goals (Emmons 1996).

This has led thinkers over several millennia to a common prescription for happiness. Just adjust your goals to what is possible, be satisfied with who you are and what you have, and happiness will be yours. It is wise advice with an increasingly strong scientific foundation. Occasionally someone is able to follow it, usually with good effect. Some follow the established middle way of Buddhism, striving to transcend the tangles of desire that are seen as the origins of all suffering. However, most of us muddle on, trying to do things in life, some feasible, some grand, others mundane, some successful, others sources of constant frustration, and some that lead to abject failure after huge efforts. The effects of discrete successes or failures on mood are strong, but not as strong as efforts that are steadily productive or increasingly ineffective despite great effort. It is important to recognize that only some of the goals in question are tangible, such as getting a job or buying a house. Success for many other goals, such as winning the golf tournament, being chosen as the beauty queen or the valedictorian, or having higher social status than others in a group, depends on winning a zero-sum game with escalating competition. Other goals that influence our states of mind are more elusive yet. How may people spend their lives trying to get their mothers finally to love them, to get a spouse to want to have sex again, to stop a child from taking drugs, or trying to control their own habits? In such desperate enterprises that cannot be given up are the seeds of intense dissatisfaction that often precede serious depression.

5. THE MOTIVATIONAL STRUCTURE OF INDIVIDUAL LIVES

The actual situation is often even more challenging. The task is not just to choose sensible goals; individuals must at every juncture make decisions that allocate effort to the pursuit of one goal and not another. This is not just a human problem. As noted in figure 2, behaviour ecologists

Table 4. Categories of effort.

somatic	effort to get external resources such as food and shelter effort to get and keep personal resources such as health and staying alive
reproductive	mating effort parenting effort
social effort	effort to make alliances effort to gain status and social power

routinely categorize effort into one of several domains. Somatic effort gets material resources and preserves health. Reproductive effort is spent finding and wooing mates, and caring for offspring. Social effort is divided between helping others and otherwise making alliances, and striving for status, recognition and power in a group (table 4).

Most animals must allocate their effort carefully between feeding and watching for predators (Krebs & Davies 1997). Without adequate monitoring, sudden death will come soon, but too much time looking about will result in starvation. The amount of time an animal spends feeding takes away from time guarding its nestlings. With too little guarding they will probably become victims, but with too little time feeding they will starve. For males especially, there is a major trade-off between effort displaying to attract mates, and the effort that can go into foraging, and protecting offspring and the existing mate. In species that have hierarchies, such as most primates, yet another major trade-off requires allocating the optimal amount of effort and risk-taking to competing for position in the group, and every bit of this effort takes away from effort available for protection, foraging, mating and parenting. Reproductive success depends on managing these trade-offs effectively. Many of the decisions made by the brain, usually at an intuitive and automatic level, involve allocation of resources. And many of the difficulties that we call 'stress' arise from conflicts among the demands for pursuing multiple resources. These conflicts are not pathological, or found only in extreme circumstances, they are the substance of everyday decisions.

When there are sufficient time, energy and resources to successfully pursue current goals, life is good. Recent survey research has made it clear that a simple level of resources is not a strong predictor of well-being; both theory and laboratory studies suggest that rate of approach to goals is much more closely correlated with affect (Carver & Scheier 1990). However, an evolutionary assessment suggests considering a still broader view of what is important to the organism. What really counts is the viability of the overall motivational structure, that is, the degree to which all major goals can be pursued successfully without unduly compromising others. If this is correct, it means that survey studies of well-being will overlook most of what is important (Diener & Fujita 1995). Not only do individuals differ in their values, they also have different commitments to pursuing certain goals at different times in life (Heckhausen & Schultz 1995; McGregor & Little 1998). Furthermore, a person with substantial resources in every area may nonetheless be faced with impossible dilemmas. The

ambitious executive who is climbing nicely, and who has a wonderful spouse and child at home, may be faced with demands from a spouse to participate more in caring for the children at the very time when promotion in the company requires accepting more assignments out of town. This is no different, in principle, from the dilemma of a hunter-gatherer who has to choose to forage far afield or to stay at home and protect his family.

The implications for methodology are severe. To better predict positive affect, not only must multiple efforts in different domains be considered, but also individual differences in commitment to idiosyncratic goals and how much progress can be made towards these goals in the current context, which includes the effects of all other efforts to reach other goals. This takes us close to the perspective of those who argue that only narrative includes information detailed and idographic enough to allow a real understanding of an individual's life (Oatley 1999). However, instead of giving up on trying to find nomothetic generalities, this evolutionary approach to affect anticipates which goals people will typically pursue at each life stage. It also maps generic emotional responses onto the nomothetic framework of situations that arise during goal pursuit, and it provides a strong expectation that affects will reflect an individual's assessment of their ability to make progress towards important life goals. In this perspective, the distress of people who seem to be successful in every area need not be automatically attributed to autonomous brain processes or deep unconscious complexes, but instead may arise from the necessity of coping with impossible trade-offs and other threats to the stability of the whole system.

6. IN THE GRIP OF OUR GENES

The systems that regulate our emotions were shaped not to benefit individuals or the species, but only to maximize the transmission of the genes themselves. Thus, every species experiences a tension between efforts to maintain individual welfare and efforts to maximize reproductive success. An oyster allocates substantial effort to making the usual 10–20 million eggs; an oyster that makes 100 million eggs will probably compromise its ability to survive. We humans experience the situation much more acutely, feeling ourselves drawn into status competitions, driven to pursue sexual partners, and subject to envy despite our very best intentions. Many of these tendencies benefit our genes but not our individual selves. The dissatisfactions arising from these unending pursuits drain our capacities for happiness; however, even many people who know this still find themselves unable to enjoy what they have because of their efforts to get what their genes motivate them to want. The very same dynamic, however, plays out in taking care of children. Here, too, people spend effort and take risks that assist their reproductive success. The difference is that the investment is in quality and success of offspring, something that is often achievable, in contrast to the unending struggle for positional goods such as status and relative wealth and recognition. This said, many people spend years distressed because they cannot recover from an illness, help a child cope with drug abuse, or reform an abusive spouse.

7. MODERN GOALS

The mechanisms that regulate behaviour were shaped for an environment considerably different from the one we live in now. The size and duration of personal goals may be a major difference that accounts for much pathology. Just a few thousand years ago, most individuals allocated their effort among a limited variety of tasks: gathering food, taking care of kin, participating in the group, etc. But as social groups enlarged and roles became more specialized, the requirements for success have escalated so that the big rewards now go to those who allocate a huge proportion of their life's effort to one domain, and sometimes even just to one goal. The Olympic athlete, for instance, has to devote him or herself so completely to the goal of gold that a balanced life is impossible. Likewise, someone who wants to be a music star, a top academic or a CEO will almost always have to sacrifice much to strive for the goal. What is worse, the goal may take years of specialized effort, it may not be reached, and if failure occurs, no satisfactory alternative may be available. Our brain regulation systems were never designed to cope with efforts so long in duration, towards goals so large, with all-or-none outcomes that offer few alternatives. It is relatively easy to give up on looking for nuts when several days of foraging have proved fruitless. Giving up on a PhD programme after 5 years, or a marriage after 10 years, are decisions orders of magnitude larger, decisions whose costs often lead individuals to persist in the pursuit of hopeless or unwanted goals, creating the exact situations that disengage motivation and cause depression.

The competition for scarce elite social roles requires not only extreme efforts, but also extravagant displays whose significance is proportional to their expense (Veblen 1899). Once Rolex watches are no longer a reliable indicator, status display moves on to extravagant cars and homes (Frank 1999). Once the pool of available spouses expands to thousands of people, simple attractiveness is overlooked in favour of exaggerated sexual characteristics. Many bemoan the human costs of such competitions, but when employers seek a worker, the Harvard graduate gets the edge, and when people with options decide who to marry, the drop-dead good-looking partner is rarely resisted.

In short, the connections between modern life and compromised well-being may be far more complex than simple increased exposure to situations that foster upwards social comparison (Gilbert *et al.* 1995). Instead, modern social structures often seem to induce motivational structures that leave individuals sacrificing much in life to pursue major efforts to reach huge goals, whose attainment is uncertain and whose alternatives are few and unsatisfactory. Furthermore, these pursuits may foster personal relationships based on exchange, and even exploitation, instead of the commitment that characterizes small kinship groups (Fiske 1992).

8. INDIVIDUAL DIFFERENCES

Although some variation in happiness arises from life circumstances, most is a subject characteristic that remains remarkably stable despite changing life circumstances. Twin studies find that half of the variance in SWB in most modern populations can be attributed to genetic differences between individuals (Bouchard & Loehlin 2001;

Lykken & Tellegen 1996). This poses an evolutionary question entirely separate from the questions addressed so far. Instead of asking why the capacities for mood exist and how they are regulated, it asks instead why natural selection would leave such wide variation in baseline mood, and in the responsiveness of the mood system. A full answer depends on a better understanding than we now have about the evolutionary origins and functions of mood and mood regulation systems. However, some general principles nonetheless apply.

There are good reasons to expect that selection should leave baseline mood and its responsiveness with parameters somewhere in the vicinity of those that maximized reproductive success in the ancestral environment. How selection acts on a trait such as mood depends, of course, on the relative fitness of individuals with different phenotypes. Consider baseline mood first. We have already addressed the illusion that steady levels of very positive mood are optimal. If they were, we would expect that selection would quickly shift mood for most people to a steady high positive level. Of course, the data on depressive realism do suggest that the average person is more optimistic than is justified, at least about his or her own abilities (Alloy & Abramson 1988; Taylor & Brown 1988). One can readily imagine how social factors could shape such a tendency. People prefer to associate with others who are happy and successful, so an advantage might well accrue to those with a tendency towards optimistic distortion. Whether natural selection, life experience, or both would shape such a proposed distortion is unanswered. Nonetheless, as with other traits, fitness should be highest at some intermediate level of baseline mood with selection acting against genes that foster extremes of high or low baseline mood. It might well be that the distribution is skewed, perhaps with fitness falling off much faster on the side of low baseline mood than high baseline mood. More important is the width of the distribution. It might well be that the average fitness difference between someone with a chronic moderate low mood and a steady high mood would be small, especially since the fitness value of such moods depends mainly on the circumstance.

A previous section emphasized that the fitness value of emotions depends on whether their expression occurs in the situations in which they are adaptive. Baseline levels of mood might well be less important than whether mood changes in response to cues that accurately indicate situations in which high and low mood are useful, and if changes are appropriately intense, and for the right duration. Lowered fitness should be characteristic of individuals whose moods swing too readily to extremes, and of individuals whose mood does not change in situations where it should.

If it is correct that affect reflects rates of progress towards goals, then the baseline mood may matter little so long as its changes adjust future behaviour in ways that allocate effort efficiently. While we attend to, and care very much about, steady levels of mood, they may have little effect on fitness, compared with the importance of changes in mood. Furthermore, what seem to us to be substantial variations in mood and mood regulation may have such small and erratic effects on fitness that the resulting systems are left quite variable. We keep looking for the exact cues and mechanisms that regulate mood. However, because the mind was not designed by an engineer, but was instead

shaped by natural selection, the mood system may be far more irregular than we can imagine.

9. IMPLICATIONS OF EVOLUTIONARY INSIGHTS ABOUT HAPPINESS

An evolutionary view of well-being shifts most people's perspectives substantially. It is disturbing to recognize that negative emotions exist because they have been useful in certain situations, and that positive emotions can be maladaptive. It is harder yet to recognize that the apparent superiority of positive emotions arises mainly because they feel good and they are associated with beneficial situations. More difficult still is recognition that selection does not shape emotion regulation systems for our benefit, and that the motives we experience often benefit our genes at the expense of the quality of our lives. Much easier to accept is the recognition that our brains were designed to function in a vastly different environment, with the resulting mismatch accounting for many malfunctions. In addition, there are the many unnecessary expressions of aversive states whose normality is accounted for by the smoke detector principle.

These insights should promote neither despair nor resignation. Just because a negative emotion is normal and useful in the natural environment, or even in our environment, does not mean that we should just accept it. Instead, an understanding of its normal regulation and functions provides crucial information for deciding if it is or is not safe to block a negative emotion in a particular instance. The pursuit of strategies to increase happiness will get farther faster if we understand the origins and functions of positive emotions (Johnson 2003). An evolutionary view suggests, however, that an excessively direct pursuit of happiness is likely to lead to frustration and, paradoxically, unhappiness, because happiness is not a reachable goal, but a state that emerges when an individual is making good progress towards his or her individual life goals.

An evolutionary perspective does not come down definitively on the side of one of the traditional prescriptions for pursuing well-being. It recognizes the pleasures of hedonism and the reasons for satiation and adaptation that limit that approach to happiness. It acknowledges the success of ascetic avoidance of temptations in preventing unhappiness, and the reasons why so few people are able to give up, or even control, their desires. It appreciates the good sense in the golden mean, and the reasons why so many who pursue it nonetheless lurch from unbridled desire to restraint and back again. Although it is disappointing to recognize that there is no formula for happiness, at least not one that applies to everyone, it is reassuring to understand the origins of the emotions in whose loops we dance. It may be so hard to control our emotions, so difficult to foster happiness, and to damp down sadness and envy, because those who could do that were deprived of crucial tools for adaptation, while those whose emotional experiences mapped accurately onto the situations in which they were useful had a selective advantage.

We are entering the period of history when technology will allow us to control our emotions, if not at will, at least far more easily. For now, the techniques are mostly chemical manipulations in the form of psychotropic drugs. Electrical brain influences via trans-cranial magnetic stimulations are developing quickly and implanted brain

electrodes are already being used to influence mood. Within the lifetime of most readers, we will identify the genetic differences that leave some people morose throughout life and provide a fortunate few others with a steady sunny disposition. These advances will lead to profitable technologies for manipulating mood that will be widely used. Governments will no doubt worry initially that such interventions will sap the strength of their citizens, but they will also recognize the benefits of a happier populace who may well demand such interventions. The rich will certainly take advantage of these advances first, but the less fortunate, who have less happiness and disproportionate suffering, may get even greater benefits. The effects of such technologies on social and political structures will be substantial. If we are to make sensible decisions about these issues, we need major efforts now to reach deeper understandings about how our capacities for happiness were shaped by natural selection.

Our growing knowledge about the evolutionary functions of happiness and the situations in which it gives advantages also provides a scientific foundation for individual and social interventions. People imagine that because acquiring things causes joy, having things will cause happiness. Although most people will be unable to use such insights, it is possible that some people will make good use of them, in the same way that some people now use information to modify their diets in ways that decrease immediate pleasure but increase long-term health and vigour. Perhaps most hopeful of all is the possibility that these findings can be used to structure human organizations, or perhaps even societies, in ways that offer people achievable goals that satisfy our deep human needs. We have used science and technology to protect ourselves from want and many diseases. It seems quite possible that we will be able to use our growing knowledge to make similar advances in promoting human happiness.

REFERENCES

- Alcock, J. 2001 *The triumph of sociobiology*. New York: Oxford University Press.
- Alloy, L. B. & Abramson, L. 1988 Depressive realism: four theoretical perspectives. In *Cognitive processes in depression* (ed. L. Alloy), pp. 223–265. New York: Guilford.
- American Psychiatric Association 1994 *Diagnostic and statistical manual of mental disorders (-IV)*, 4th edn. Washington, DC: APA Press.
- Andreasen, N. C. 1984 *The broken brain: the biological revolution in psychiatry*. New York: Harper & Row.
- Argyle, M. 1999 Causes and correlates of happiness. In *Well-being* (ed. D. Kahneman, E. Diener & N. Schwartz), pp. 353–373. New York: Russell Sage Foundation.
- Bentham, J. & Mill, J. S. 1973 *The utilitarians: an introduction to the principles of morals and legislation*. Garden City, NY: Anchor Press/Doubleday.
- Berridge, K. C. 1996 Food reward: brain substrates of wanting and liking. *Neurosci. Biobehav. Rev.* **20**, 1–25.
- Bouchard, J. T. J. & Loehlin, J. C. 2001 Genes, evolution, and personality. *Behav. Genet.* **31**, 243–273.
- Brickman, P., Coates, D. & Janoff-Bulman, R. 1978 Lottery winners and accident victims: is happiness relative? *J. Person. Soc. Psychol.* **36**, 917–927.
- Brown, G. W. & Harris, T. 1978 *Social origins of depression*. New York: Free Press.
- Buss, D. M. 2000 The evolution of happiness. *Am. Psychol.* **55**, 15–23.
- Buss, D. M. & Schmitt, D. P. 1993 Sexual strategies theory: an evolutionary perspective on human mating. *Psychol. Rev.* **100**, 204–232.
- Buss, D. M., Shackelford, T. K., Kirkpatrick, L. A., Choe, J., Hasegawa, M., Hasegawa, T. & Bennett, K. 1999 Jealousy and beliefs about infidelity: tests of competing hypotheses in the United States, Korea, and Japan. *Person. Rel.* **6**, 125–150.
- Cantor, N. 1990 From thought to behavior: ‘having’ and ‘doing’ in the study of personality and cognition. *Am. Psychol.* **45**, 735–750.
- Cantor, N. 1994 Life task problem solving: situational affordances and personal needs. *Person. Soc. Psychol. Bull.* **20**, 235–243.
- Carver, C. S. 2003 Pleasure as a sign you can attend to something else: placing positive feeling within a general model of affect. *Cogn. Emotion* **17**, 241–261.
- Carver, C. S. & Scheier, M. F. 1990 Origins and functions of positive and negative affect: a control-process view. *Psychol. Rev.* **97**, 19–35.
- Carver, C. S. & Scheier, M. 1998 *On the self-regulation of behavior*. Cambridge University Press.
- Caspi, A., McClay, J., Moffitt, T. E., Mill, J., Martin, J., Craig, I. W., Taylor, A. & Poulton, R. 2002 Role of genotype in the cycle of violence in maltreated children. *Science* **297**, 851–854.
- Caspi, A. (and 11 others) 2003 Influence of life stress on depression: moderation by a polymorphism in the 5-HTT gene. *Science* **301**, 386–389.
- Charnov, E. L. 1976 Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.
- Cosmides, L. & Tooby, J. 1994 Origins of domain specificity: the evolution of functional organization. In *Mapping the mind: domain specificity in cognition and culture* (ed. L. A. Hirschfeld & S. A. Gelman), pp. 85–116. Cambridge University Press.
- Costa, D., Mogos, I. & Toma, T. 1985 Efficacy and safety of mianserin in the treatment of depression of women with cancer. *Acta Psychiat. Scand.* **320**(Suppl.), 85–92.
- Crocker, J. & Wolfe, C. T. 2001 Contingencies of self-worth. *Psychol. Rev.* **108**, 593–623.
- Csikszentmihalyi, M. 1977 *Finding flow: the psychology of engagement with everyday life*. New York: Basic Books.
- Davidson, R. 1992 Emotion and affective style: hemispheric substrates. *Psychol. Sci.* **3**, 39–43.
- Dawkins, R. 1976 *The selfish gene*. Oxford University Press.
- Diener, E. & Diener, C. 1996 Most people are happy. *Psychol. Res.* **7**, 181–185.
- Diener, E. & Fujita, F. 1995 Resources, personal strivings, and subjective well-being: a nomothetic idiographic approach. *J. Person. Soc. Psychol.* **68**, 926–935.
- Diener, E. & Lucas, R. E. 1999 Personality and subjective well-being. In *Well-being: the foundations of hedonic psychology* (ed. D. Kahneman, E. Diener & N. Schwartz), pp. 213–229. New York: Russell Sage Foundation.
- Diener, E. & Suh, E. M. 1999 National differences in subjective well-being. In *Well-being* (ed. D. Kahneman, E. Diener & N. Schwartz), pp. 434–450. New York: Russell Sage Foundation.
- Dusenbery, D. B. 1996 *Life at small scale: the behavior of microbes*. New York: Scientific American Library.
- Easterlin, R. A. 2003 Inaugural article: explaining happiness. *Proc. Natl Acad. Sci. USA* **100**, 11 176–11 183.
- Eaton, S. B., Shostak, M. & Konner, M. 1988 *The paleolithic prescription*. New York: Harper & Row.
- Ellsworth, P. C. & Smith, C. A. 1988a From appraisal to emotion: differences among unpleasant feelings. *Motiv. Emotion* **12**, 271–302.

- Ellsworth, P. C. & Smith, C. A. 1988b Shades of joy: patterns of appraisal differentiating pleasant emotions. *Cogn. Emotion* **2**, 301–331.
- Emmons, R. A. 1996 Striving and feeling: personal goals and subjective well-being. In *The psychology of action: linking cognition and motivation to behavior* (ed. P. M. Gollwitzer), pp. 313–337. New York: Guilford Press.
- Emmons, R. A. 1999 *The psychology of ultimate concerns: motivation and spirituality in personality*. New York: Guilford Press.
- Endler, J. A. 1986 *Natural selection in the wild*. Monographs in Population Biology. Princeton University Press.
- Fiesler, J. 1992 Hume's classification of the passions and its precursors. *Hume Stud.* **18**, 1–17.
- Fiske, A. P. 1992 The four elementary forms of sociality: framework for a unified theory of social relations. *Psychol. Rev.* **99**, 689–723.
- Frank, R. H. 1999 *Luxury fever: why money fails to satisfy in an era of excess*. New York, NY: Free Press.
- Fredrickson, B. L. 1998 What good are positive emotions? *Rev. Gen. Psychol.* **2**, 300–319.
- Fukuyama, F. 1992 *The end of history and the last man*. New York: Free Press.
- Gershon, A., Dannon, P. & Grunhaus, L. 2003 Transcranial magnetic stimulation in the treatment of depression. *Am. J. Psychiat.* **160**, 835–845.
- Gilbert, P. 1989 *Human nature and suffering*. Hove, UK: Lawrence Erlbaum.
- Gilbert, P. & Andrews, B. 1998 *Shame: interpersonal behavior, psychopathology, and culture*. Series in Affective Science. New York: Oxford University Press.
- Gilbert, P., Price, J. & Allen, S. 1995 Social comparison, social attractiveness and evolution: how might they be related? *New Ideas Psychol.* **13**, 149–165.
- Gollwitzer, P. M. & Moskowitz, G. B. 1996 Goal effects on action and cognition. In *Social psychology: handbook of basic principles* (ed. E. T. Higgins & A. W. Kruglanski), pp. 361–399. New York: Guilford Press.
- Gray, J. A. 1987 *Fear and stress*. Cambridge University Press.
- Grinde, B. 2002 *Darwinian happiness: evolution as a guide for living and understanding human behavior*. Princeton, NJ: Darwin Press.
- Heckhausen, J. & Schultz, R. 1995 A life-span theory of control. *Psychiat. Rev.* **102**, 284–304.
- Heinrich, B. 1979 *Bumblebee economics*. Cambridge, MA: Harvard University Press.
- Helliwell, J. F. 2002 How's life? Combining individual and national variables to explain subjective well-being. National Bureau of Economic Research working papers, paper 9065.
- Izard, C. E. 1992 Basic emotions, relations among emotions, and emotion–cognition relations. *Psychol. Rev.* **99**, 561–565.
- Janoff-Bulman, R. & Brickman, P. 1982 Expectations and what people learn from failure. In *Expectations and action* (ed. N. T. Feather), pp. 207–237. Hillsdale, NJ: Lawrence Erlbaum.
- Johnson, V. S. 2003 The origins and functions of pleasure. *Cogn. Emotion* **17**, 167–179.
- Kahneman, D., Diener, E. & Schwarz, N. 1999 *Well-being: the foundations of hedonic psychology*. New York: Russell Sage Foundation.
- Kendler, K. S., Gardner, C. O. & Prescott, C. A. 2002 Toward a comprehensive developmental model for major depression in women. *Am. J. Psychiat.* **159**, 1133–1145.
- Kendler, K. S., Karkowski, L. M. & Prescott, C. A. 1999 Causal relationship between stressful life events and the onset of major depression. *Am. J. Psychiat.* **156**, 837–841.
- Kenrick, D. T., Maner, J. K., Butner, J., Li, N. P. & Becker, D. V. 2002 Dynamical evolutionary psychology: mapping the domains of the new interactionist paradigm. *Person. Soc. Psychol. Rev.* **6**, 347–356.
- Kessler, R. C., Berglund, P., Demler, O., Jin, R., Koretz, D., Merikangas, K. R., Rush, A. J., Walters, E. E. & Wang, P. S. 2003 The epidemiology of major depressive disorder results from the National Comorbidity Survey Replication (NCS-R). *J. Am. Med. Assoc.* **289**, 3095–3105.
- Kessler, R. C., McGonagle, K. A., Zhao, S., Nelson, C. B., Hughes, M., Eshelman, S., Willchen, H. U. & Kendler, K. S. 1994 Lifetime and 12-month prevalence of DSM-III-R psychiatric disorders in the United States: results from the national comorbidity survey. *Arch. Gen. Psychiat.* **51**, 8–19.
- Kimball, M. S. 1993 Standard risk aversion. *Econometrica* **61**, 589–611.
- Klinger, E. 1975 Consequences of commitment to and disengagement from incentives. *Psychol. Rev.* **82**, 1–25.
- Krebs, J. R. & Davies, N. B. 1997 *Behavioral ecology: an evolutionary approach*. Oxford: Blackwell Science.
- Larsen, R. J. & Diener, E. 1992 Problems and promises with the circumplex model of emotion. *Rev. Person. Soc. Psychol.* **13**, 25–59.
- Layard, R. 2005 *Happiness—lessons from a new science*. London: Penguin.
- Little, B. R. 1999 Personal projects and social ecology: themes and variation across the life span. In *Action & self development: theory and research through the life span* (ed. J. Brandtstadter & R. M. Lerner), pp. 197–221. Thousand Oaks, CA: Sage.
- Loewenstein, G. & Shane, F. 1999 Hedonic adaptation. In *Well-being: the foundations of hedonic psychology* (ed. E. Diener, D. Kahnemann & N. Schwartz), pp. 302–329. New York: Russell Sage Foundation Press.
- Lykken, D. & Tellegen, A. 1996 Happiness is a stochastic phenomenon. *Psychol. Sci.* **7**, 186–189.
- McGregor, I. & Little, B. R. 1998 Personal projects, happiness, and meaning: on doing well and being yourself. *J. Person. Soc. Psychol.* **74**, 494–512.
- Mackey, W. C. & Immerman, R. S. 2000 Depression as a counter for women against men who renege on the sex contract. *Psychol. Evol. Gender* **2**, 47–71.
- Marks, I. M. & Nesse, R. M. 1994 Fear and fitness: an evolutionary analysis of anxiety disorders. *Ethol. Sociobiol.* **15**, 247–261.
- Martin, L. L. & Tesser, A. 1996 *Striving and feeling: interactions among goals, affect, and self-regulation*. Hillsdale, NJ: Lawrence Erlbaum.
- Maser, J. & Cloninger, R. (eds) 1990 *Comorbidity of mood and anxiety disorders*. Washington, DC: American Psychiatric Press.
- Mill, J. S. 1848 *Principles of political economy*. London: John W. Parker.
- Morris, W. N. 1992 A functional analysis of the role of mood in affective systems. *Rev. Person. Soc. Psychol.* **21**, 736–746.
- Nathan, K. I., Musselman, D. L., Schatzberg, A. F. & Nemeroff, C. B. 1995 Biology of mood disorders. In *Textbook of psychopharmacology* (ed. A. F. Schatzberg & C. B. Nemeroff), pp. 439–477. Washington, DC: APA Press.
- Nesse, R. M. 1990 Evolutionary explanations of emotions. *Hum. Nature* **1**, 261–289.
- Nesse, R. M. 2000a Is depression an adaptation? *Arch. Gen. Psychiat.* **57**, 14–20.
- Nesse, R. M. 2000b Natural selection, mental modules and intelligence. In *The nature of intelligence* (ed. G. R. Bock & J. A. Goode), pp. 96–115. Chichester: Wiley.
- Nesse, R. M. 2001 The smoke detector principle. Natural selection and the regulation of defensive responses. *Ann. N. Y. Acad. Sci.* **935**, 75–85.
- Nesse, R. M. & Williams, G. C. 1994 *Why we get sick: the new science of Darwinian medicine*. New York: Vintage.
- Nesse, R. M. & Williams, G. C. 1998 Evolution and the origins of disease. *Sci. Am.* **289**(5), 86–93.

- Nussbaum, M. C. 1994 *The therapy of desire: theory and practice in Hellenistic ethics*. Princeton University Press.
- Oatley, K. 1999 Why fiction may be twice as true as fact: fiction as cognitive and emotional simulation. *Rev. Gen. Psychol.* **3**, 101–117.
- Ortony, A., Clore, G. L. & Collins, A. 1988 *The cognitive structure of emotions*. Cambridge, NY: Cambridge University Press.
- Oyserman, D. & Markus, H. 1993 The sociocultural self. In *Psychological perspectives on the self*, vol. 4 (ed. J. Suls & A. G. Greenwald), pp. 187–220. Hillsdale, NJ: Lawrence Erlbaum.
- Plutchik, R. 1980 *Emotion: a psychoevolutionary synthesis*. New York: Harper & Row.
- Prescott-Allen, R. 2001 *The wellbeing of nations: a country-by-country index of quality of life and the environment*. Washington, DC: Island Press.
- Pyszczynski, T. & Greenberg, J. 1987 Self-regulatory perseveration and the depressive self-focusing style: a self-awareness theory of reactive depression. *Psychol. Bull.* **102**, 122–138.
- Rutter, M. & Rutter, M. 1993 *Developing minds: challenge and continuity across the life span*. New York: Basic Books.
- Saudino, K. J., Pederson, N. L., Lichtenstein, P., McClearn, G. E. & Plomin, R. 1997 Can personality explain genetic influences on life events? *J. Person. Soc. Psychol.* **72**, 196–206.
- Stevens, A. & Price, J. 1996 *Evolutionary psychiatry: a new beginning*. London: Routledge.
- Symons, D. 1990 Adaptiveness and adaptation. *Ethol. Sociobiol.* **44**, 427–444.
- Taylor, S. E. & Brown, J. D. 1988 Illusion and well-being: a social psychological perspective on mental health. *Psychol. Bull.* **103**, 193–210.
- Tellegen, A., Lykken, D. T., Bouchard, T. J., Wilcox, K. J., Segal, N. L. & Rich, S. 1988 Personality similarity in twins reared apart and together. *J. Person. Soc. Psychol.* **54**, 1031–1039.
- Tinbergen, N. 1963 On the aims and methods of ethology. *Z. Tierpsychol.* **20**, 410–463.
- Tooby, J. & Cosmides, L. 1990 The past explains the present: emotional adaptations and the structure of ancestral environments. *Ethol. Sociobiol.* **11**, 375–424.
- Tsuang, M. T. & Tohen, M. 2002 *Textbook in psychiatric epidemiology*. New York: Wiley-Liss.
- Valenstein, E. S. 1998 *Blaming the brain: the truth about drugs and mental health*. New York: Free Press.
- Veblen, T. 1899 *The theory of the leisure class: an economic study in the evolution of institutions*. New York: Macmillan.
- von Hecht, H. Z. D., Krieg, C., Posselt, J. & Wittchen, H. U. 1989 Anxiety and depression: comorbidity, psychopathology, and social functioning. *Comp. Psychiat.* **30**, 420–433.
- Watson, D., Clark, L. A. & Carey, G. 1988 Positive and negative affect and their relation to anxiety and depressive disorders. *J. Abnorm. Psychol.* **97**, 346–353.
- Williams, G. W. & Nesse, R. M. 1991 The dawn of Darwinian medicine. *Q. Rev. Biol.* **66**, 1–22.
- Wrosch, C. & Heckhausen, J. 2002 Perceived control of life regrets: good for young and bad for old adults. *Psychol. Aging* **17**, 340–350.
- Wrosch, C., Scheier, M. F. & Carver, C. S. 2003 The importance of goal disengagement in adaptive self-regulation: when giving up is beneficial. *Self Ident.* **2**, 1–20.

GLOSSARY

- DSM: Diagnostic and Statistical Manual
 SWB: subjective well-being