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The Evolutionary Origins of Mood and Its Disorders

Review

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The term 'mood' in its scientific usage refers to relatively enduring affective states that arise when negative or positive experience in one context or time period alters the individual's threshold for responding to potentially negative or positive events in subsequent contexts or time periods. The capacity for mood appears to be phylogenetically widespread and the mechanisms underlying it are highly conserved in diverse animals, suggesting it has an important adaptive function. In this review, we discuss how moods can be classified across species, and what the selective advantages of the capacity for mood are. Core moods can be localised within a two-dimensional continuous space, where one axis represents sensitivity to punishment or threat, and the other, sensitivity to reward. Depressed mood and anxious mood represent two different quadrants of this space. The adaptive function of mood is to integrate information about the recent state of the environment and current physical condition of the organism to fine-tune its decisions about the allocation of behavioural effort. Many empirical observations from both humans and non-human animals are consistent with this model. We discuss the implications of this adaptive approach to mood systems for mood disorders in humans.

Introduction

The word 'mood' is most often used in biology with the word 'disorders' immediately following it. This is not surprising, as conditions in which mood is a primary component are a huge source of suffering in humans. The World Health Organization's 2004 *Global Burden of Disease* report [1] estimates that the mood disorder depression is currently the world's third largest source of morbidity. In middle- and higher-income countries, and amongst women everywhere, it is the largest single source, by some margin. The research literature on mood understandably reflects medical priorities, with a greater emphasis being placed on clinical problems of mood than on the 'normal' psychology of how mood systems work, and, to the extent to which 'normal' mood is studied, a greater emphasis on questions of *proximate mechanism* (how is mood controlled in the brain, or the endocrine system?) than on those of *adaptive function* (what is the survival value of having a mood system, and how does the mood system regulate the individual's behaviour in its natural environment?). As behavioural ecologists, it is these questions of adaptive function that we are drawn to asking. We also believe that taking such an adaptive perspective may provide some insights which are of use to researchers with more mechanistic and therapeutic goals. In this review, then, we sketch an account of what moods are, how they should be classified, and what the adaptive function of mood systems may be. The framework provides us with a clear definition of mood that can be applied across taxa, and we show that much of what we know empirically about mood phenomena both in humans and other species fits naturally into it. We also briefly discuss what light the adaptive perspective on mood *systems* sheds on the origins and distribution of mood *disorders* in humans.

The framework presented here integrates ideas from a number of sources, notably work on emotions as the activity of survival circuits related to reward and punishment [2–4], the dimensional classification of emotions [5–8], signal detection approaches to emotions [9–11], and the human and animal cognitive bias literatures [8,12,13]. It suggests potential relevance to mood phenomena of ideas from behavioural ecology concerning the adaptive tracking of changing environments [14–16], and the sensitivity of adaptive decisions to the individual's current physical condition [17]. These may be promising areas for future work.

Emotions: The Signal Detection Approach

Mood belongs to the class of affective, or emotion-related, phenomena. Emotions are suites of cognitive, motivational and physiological changes that are triggered by appraisal of specific classes of environmental situations [4,18]. Fear, for example, is a suite of responses including increased vigilance, attentional bias to potential sources of danger, and physiological preparation for fight or flight that is activated by the appraisal that there is danger in the environment. The neural and hormonal mechanisms underlying core emotions such as fear appear to be highly conserved across a wide variety of organisms, certainly all vertebrates, and there are important homologues of these mechanisms in invertebrates too [4]. This suggests both ancient origins, and ubiquitous selection maintaining the key features of emotions as organized systems. In humans, emotions are also characterized by a subjective valence. That is, they are experienced as inherently pleasant or unpleasant. This subjective component has been a focus for emotion theorists in human psychology (for example, [19–21]), but clearly cannot be invoked in any definition of emotion applicable across taxa, as we have no direct access to what, if anything, non-human animals subjectively feel [4,22].

There is a long tradition of explaining the design features of emotions from an adaptive point of view; they allocate and marshall the individual's cognitive and behavioural resources towards the most immediately important fitness-relevant priorities given the current state of the world [4,23–26]. Viewing emotions in this way implies that the capacity for negatively-valenced emotions has positive survival value, and there is evidence consistent with this. In humans, for example, people who are unusually low in anxiety-proneness suffer increased long-term mortality risk compared to their more anxiety-prone peers [27,28]. When considering emotions from an adaptive perspective, it is useful to conceptualize them as *detectors* [9–11,29]. That is, they are mechanisms whose function is to identify when some input situation X applies in the world, and deliver the

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suite of cognitive, physiological and motivational changes Y that is useful for dealing with situations of class X. The advantage of thinking about emotions as detectors in this way is that we can draw on a developed body of signal detection theory [30] to make predictions about how emotions should work if optimized by natural selection.

Organisms do not apprehend the state of their environment directly, but instead are constantly receiving cues that carry some information about it. These cues are probabilistically associated with the presence of important fitness-relevant situations, but there is generally some uncertainty about what they imply. For example, a noise might be caused by a predator approaching, but it might only be the rustling of leaves; a certain colour might indicate obtainable food, but it might just be a trick of the light. In both cases, the fitness-relevant situation produces a signal whose distribution overlaps to some extent with the distribution of background noise. The organism thus has to decide how much information likely to indicate X it has to receive before mobilizing the appropriate response set Y. This amount of information is called the detection threshold. There are four possible outcomes of any detection problem: a true positive (detects X and does Y when X really does obtain); a true negative (does not detect X or do Y when X does not in fact obtain); a false positive (detects X and does Y even though X does not obtain); or a false negative (fails to detect X and do Y even though X really does obtain). If the level of uncertainty is fixed, then in general, lowering the threshold leads to more true positives, but also more false positives, and raising it leads to more true negatives, but also more false negatives.

The optimal detection threshold — that which maximizes the expected value of the decision — is the product of two factors: the probability of the event X, and the relative costs of the four different outcomes [9,31]. If X is very likely under current conditions, then a low threshold should be set; and if X is very unlikely under current conditions, then a high threshold should be set. If a false negative is very costly relative to a false positive, then all else being equal a low threshold should be set, even though it leads to many false positives. Emotions show evidence of these design principles. In particular, negative emotions such as fear and anxiety exhibit the 'smoke detector principle' [11,32]. That is, because the cost of the false negative might be death whilst that of the false positive is just a few calories, the threshold is set in such a way as to produce many false positives, but very few false negatives. Having discussed emotions in general and the way they can be analysed as signal detectors, we now turn to mood more specifically.

What Is Mood?

Moods are differentiated from acute emotional states in that they are longer lasting, and are detached from any immediate triggering stimulus [33]. This does not mean that the state of an individual's mood is unrelated to its environment. Rather, mood state appears to be an integrative function of the organism's acute emotional experiences over time [8,34]. An animal repeatedly experiencing specific threats will gradually develop a more anxious baseline to which it returns even when no threat is present, and a repeatedly rewarded animal will develop a more positive mood state that persists between individual rewards. This temporal 'spillover' of emotional state beyond an individual event or context is a necessary condition for the concept of mood to be invoked. A person who experiences a severe fright or a sad loss is experiencing an acute emotional response. It is when this fright or loss spills over into future activities and contexts that we describe it as an anxious or low mood, and mood *disorder* is invoked when this spillover becomes very prolonged and severe. Thus, the central question of our review concerns the adaptive function of having the capacity for mood over and above the capacity for acute emotion: why would it be advantageous to carry over emotional state from one time or situation to the next? Before we address this question directly, we must first review the ways in which moods can be classified.

A number of different proposals have been made regarding the best classificatory framework for understanding emotional phenomena, including mood. Here, we adopt a framework based on two orthogonal continuous dimensions, one relating to readiness to respond to potential reward, and one relating to readiness to respond to potential punishment (Figure 1). Mood states can be classified by their coordinates in the two-dimensional space. Although this may not capture all of the ways mood states can vary, particularly in humans, it does capture the principal axes of variation. This framework, in slightly different versions, has a venerable history [2,3,5–8], and has several advantages.

First, it is applicable in principle to any organism, regardless of its cognitive complexity or ability (if any) to report subjective feelings. Even bacteria approach rewards and withdraw from punishers [35], and in invertebrate animals, the mechanisms regulating such behaviours are recognisably homologous to those in vertebrates (see [4]). This generality does not mean the framework does not apply well to humans. In fact, there is considerable evidence that the subjectively experienced structure of emotions in humans can be mapped onto the same two axes [7,20]. Second, reward and punishment are fundamental constructs in animal learning theory, and have clear operational definitions. Rewards are stimuli that can be used to increase the frequency of a behaviour, whilst punishments are stimuli that can be used to decrease the frequency of a behaviour. Third, responses to reward and to punishment are subserved by somewhat distinct mechanisms in vertebrates, and so the framework maps on to the underlying neurobiology [36,37]. Fourth, the framework provides a natural link to adaptive questions, since rewards and punishments relate to fitness [3]. Primary rewards tend to be things whose capture covaries positively with fitness over evolutionary time, such as food and mates. Primary punishers tend to be things whose experience covaries negatively with fitness, such as tissue damage, toxins, isolation, and so forth. Thus, natural selection will favour mechanisms that lead, over the set of environments that animals encounter over evolutionary time, to strategies that maximize the capture of reward whilst minimising the exposure to punishment.

Every point in the two-dimensional space of Figure 1 represents a possible mood state. But what exactly do the coordinates represent? Here we can employ the signal detection framework discussed in the previous section. The position on the horizontal axis gives the individual's current threshold for responding to cues of reward. The further to the right one goes, the lower the threshold. Thus, individuals toward the right-hand end will readily initiate reward-approach behaviour when given only minimal cues that a reward may be available. In humans, these states are associated with subjective feelings of optimism [38], with

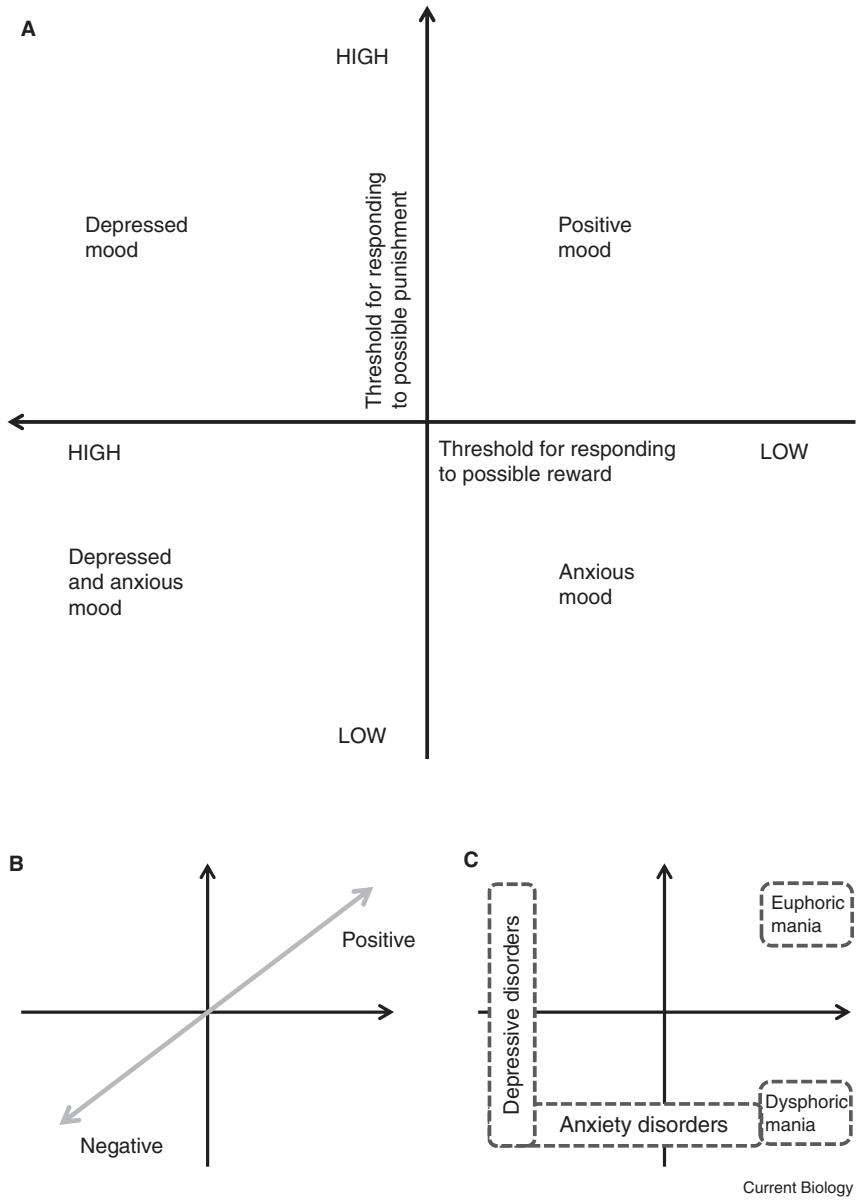

Figure 1. Biaxial framework for classifying moods across species.

(A) The axes represent the individual's detection thresholds for responding to potential rewards and punishments, respectively. (B) Subjective valence of human moods on the same axes. (C) Locations of some disorders of mood in humans on the same axes.

attentional biases towards, or salience of, reward-related stimuli [39,40], and with willingness to try out novel reward-oriented strategies [41,42]. The left-hand end of the horizontal axis represents a high threshold for the initiation of reward-approach behaviour (henceforth, we refer to this end of the horizontal axis as the depressed mood end, though note no implication of disorder or pathology is intended). In humans, the depressed mood end of the axis is characterized phenomenologically by the trio of anhedonia, pessimism and fatigue [43]. These subjective features reflect the person's reluctance to initiate reward-approach behaviour: they feel that it won't be pleasurable, that they probably won't succeed and that they don't have the energy to try. (There are also other features of depressed mood specific to humans that plausibly reflect adaptive function, but we do not discuss these here: see [44–46]). In non-human animals, there is also evidence that repeated reward moves individuals towards a state of high expectation of reward, whilst repeated non-reward moves them to a state of low expectation of reward [8].

The vertical axis of Figure 1 represents the individual's current threshold for responding to cues of potential punishment. At the bottom end of the axis (the anxious mood end), this threshold is low. This means that the individual readily interrupts other activities to focus on potential dangers. Concomitant with this are vigilance, sleeplessness, hyperarousal, and attentional biases towards threat cues [47–50]. The top end of the axis represents a relaxed state where the threshold for mounting a punishment-oriented response is high, and the hallmark features of the bottom end are absent.

Note that the two axes of Figure 1 represent two independent thresholds. At any particular moment an individual could have a high threshold for reward-approach and a low threshold for punishment-avoidance, in which case they will be both depressed and anxiety-prone, but they could also have a low threshold for reward-approach and a low threshold for punishment avoidance (anxiety-prone but not depressed), or a high threshold for reward-approach and a high threshold for punishment-avoidance (depressed but not anxiety-prone). Thus, the axes are genuinely orthogonal, although for the human case, the overall subjective valence of the mood is captured by the line y = x, with unpleasant moods towards the bottom left, and pleasant ones towards the top right.

Why Should Animals Have Mood States?

Having defined and classified moods, we are now in a position to return to our core question of why organisms have evolved the capacity for mood. To recall, mood integrates acute emotional experiences, such that an individual who experiences a punishment sets a lower threshold for the detection of punishments in the next period of time, and an individual experiencing reward sets a lower threshold for the detection of reward in the next period of time. This means that a run of many non-rewards will lead to depressed mood (move the individual to the left of Figure 1), and many punishments will lead to anxious mood (move the individual downwards on Figure 1). Why would it be adaptive to adjust

thresholds in this way? When posing such evolutionary questions, it is worth considering what the alternative might be. In this case, the alternative would be an emotional system where there are fixed thresholds for reward-detection and for punishment-detection, and the individual returns to these at the end of each bout of experience, regardless of what happened during that bout. We will call this a fixed-emotion architecture, to be contrasted with the mood architecture animals actually possess.

As discussed above, the optimal threshold for a detector depends on two factors: the probability of the event to be detected, and the relative payoffs to the four possible outcomes of detection. Let us take the probability of the event first. Environments are so variable in space and time that evolution cannot build-in detailed information about the probabilities of particular events. Instead, individuals use their life experience to derive estimates of these quantities in the context into which they happen to be operating. The world is generally an autocorrelated place: if a certain food type was too difficult for me to capture today, then other things being equal, it would be appropriate to infer that this will also be the case tomorrow. If the environment above ground was full of hostile predators today, then it is likely, given that predators are continuous in space and time, that this will also be the case tomorrow. Thus, given that the environment of tomorrow is usually statistically predicted by the environment of today, it makes sense that the architecture of emotion should exploit this information rather than throwing it away. That is, a negative experience should provoke an acute response, but also an adjustment of expectations about future experiences. One advantage of a mood system over a fixed-emotion architecture is that it does exactly this.

A second source of continuity between successive bouts of behaviour is that it is the same individual performing them. This is important, because the payoffs of the four different outcomes of signal detection should not be thought of as absolute, but rather dependent on the physical condition of the individual doing the detecting. The cost of a false negative in the domain of predation is higher for an individual who is lame than one who is sound. The cost of a false positive in the domain of foraging may be lower for an individual with abundant energy reserves than for an individual who has little spare energy [51,52]. In behavioural ecology, such examples would be captured by modelling adaptive strategies as a function of 'state', where 'state' encompasses current attributes of the individual such as lameness or energy reserves [17]. Here, we continue to refer to such attributes as physical condition, to avoid confusion with emotional states. Physical condition is another source of autocorrelation, as an individual who is lame today will tend to be lame tomorrow, and an individual who is poorly nourished today will tend to be poorly nourished tomorrow. An optimal emotional architecture needs to capture such persistence of physical condition across bouts of behaviour, and a fixed-emotion architecture where thresholds are always fixed fails to do so.

Not only are there two sources of autocorrelation affecting animals' optimal signal detection thresholds — the spatio-temporal autocorrelation of the environment, and the persistence of the individual's physical condition — but there is also an interaction between the state of the environment and the physical condition of the individual. A world containing few rewards today not only predicts a world with few rewards tomorrow, but also leaves the individual in worse condition to cope without reward tomorrow. A day of many attacks by predators not only increases the individual's best estimate of predator prevalence tomorrow, but also leaves the individual with less energy for coping with attacks tomorrow. Through such 'double effects', optimal detection thresholds in the current bout of behaviour can be quite strongly affected by experience in the previous bout (see Box 1 for a very simple illustrative model). Mood systems deliver the ongoing adjustments in thresholds for detecting rewards and punishment required for adaptive behaviour in such situations, whereas fixed emotion architectures would not.

To summarise, having a mood system, which adjusts thresholds for responding to cues of reward and punishment in the light of each emotional experience, rather than an architecture where those thresholds are fixed, is advantageous where there is autocorrelated variation in the prevalence of events in the environment, and/or in the individual's physical condition. The higher these autocorrelations are, the more detection thresholds should show temporal persistence. The adaptive benefit of the capacity for dynamically changing but persistent mood will be highest where the degrees of autocorrelation of environment and physical condition are intermediate. If they are close to zero, then there should be no persistence of thresholds from one time period to the next, whilst if they are close to one, then individuals can set lifelong thresholds and there should be no need for mood to update in the light of recent experience. These ideas link the study of mood to a mature theoretical literature on how animals should optimally track changing environments more generally (for example, [14–16]).

Adaptive Interpretation of Mood Phenomena

To what extent does the adaptive framework described in the previous section capture empirically observed mood phenomena? It predicts that recent experience of non-reward should raise the threshold for initiation of reward-orientation behaviour, which will manifest as depressed mood. On the other hand, repeated punishment should make individuals more and more ready to initiate punishment-avoidance behaviour, manifest as anxiety. The human evidence on the distinct life-event triggers of depression and anxiety — typically loss or humiliation versus danger, respectively — are consistent with these predictions [53]. Rewarding life events such as marriage and re-employment also have the predicted antidepressant effect on mood [54]. In non-human animals too, changing the distribution of rewards and punishments in the environment alters response thresholds as predicted [8].

The framework also predicts that any changes in an individual's physical condition that influence the relative payoffs of the four possible outcomes of detection are likely to alter thresholds, and hence mood. Physical infirmity or limitation will usually mean that individuals are less able to cope with undetected threats if they should arise, and may be less able to risk the energy of trying and failing at reward capture. Thus, we should predict that physical infirmity or limitation will be associated with both anxious mood and depressed mood. In humans, there is considerable epidemiological evidence that this is indeed the case [9,55]. Other circumstances that deplete an individual's condition, such as poverty and social isolation in humans, should be expected to be depressogenic and anxiogenic for similar

Box 1

An illustrative model of mood effects.

How much information should a detector whose function is to detect a dangerous situation of class X require before outputting that X has occurred? Signal detection theory gives the optimal threshold as:

$$\lambda > \frac{(1-p)}{p} \cdot \frac{(w_{TN} + w_{FP})}{(w_{TP} + w_{FN})} \quad (1)$$

Here, λ is the likelihood ratio of the currently received information being generated when X does obtain compared to when it does not, p is the probability for the current environment that X does obtain, and the ws are the long-term expected fitness payoffs of the four possible outcomes of detection, the true positive (*TP*), the true negative (*TN*), the false positive (*FP*), and the false negative (*FN*). From (1), we see that as X becomes more prevalent in the environment (p is higher), the optimal threshold gets lower, and if the false negative is very costly compared to the false positive, the threshold should also be low (the 'smoke detector principle' [11,32]).

If the environment was dangerous today, how does this affect the optimal threshold for detecting threats tomorrow? Assume a world where the prevalence of threats has a long-term mean μ, and today's threat level, p_t, is partly predicted by the prevalence of threats yesterday p_{t-1}. We can thus write the expected deviation of p_t from μ as $\beta(p_{t-1} - \mu)$, where β is the temporal autoregression coefficient of the environment. Also, it could be the case that more threats yesterday, by depleting an individual's physical condition, makes undetected threats today more difficult to cope with, whilst few threats yesterday leads to an improvement in physical condition meaning undetected threats today are easier to cope with. We capture this by changing w_{FN} for today by an amount proportional to yesterday's threat prevalence ($\delta(p_{t-1} - \mu)$, where δ is a scaling factor). The optimal threshold for detecting a threat today is thus:

$$\lambda_t > \frac{(1 - \mu - \beta(p_{t-1} - \mu))}{(\mu + \beta(p_{t-1} - \mu))} \cdot \frac{(w_{TN} + w_{FP})}{(w_{TP} + (1 + \delta(p_{t-1} - \mu))w_{FN})} \quad (2)$$

Under these assumptions, then, events yesterday affect the optimal threat-detection threshold for today in two ways: via the autoregression coefficient of the environment (the more autocorrelated the environment, the more a bad yesterday should lower the optimal threat-detection threshold for today, and a good yesterday raise it) but also by the degree to which events yesterday affect the individual's capacity to cope with undetected threats today (the stronger the spillover effect δ, the more a bad yesterday should lower the optimal threshold today, and a good yesterday raise it). We can see how these forces interact by plotting the optimal threat-detection threshold for today against the prevalence of threats in the environment yesterday for representative values of the parameters of the model (Figure 2). Very similar models could be constructed for reward-approach rather than threat-avoidance, where positive experiences or an improvement in physical condition yesterday would affect the optimal threshold for responding to potential cues of reward today.

reasons [56–58]. There are analogous non-human examples. For example, in European starlings, not having access to bathing water causes individuals to become more sensitive to potential cues of danger (a conspecific alarm call) [59]. This is presumably because their ability to escape a predator is compromised by the worse condition of their flight feathers, meaning that their optimal threshold for threat-detection is lowered.

Interestingly, when researchers want to create analogous states to human mood disorders in laboratory rodents, for example in pharmacological research, they do this either by increasing the frequency of negative fitness-relevant events in the animal's daily experience, as in the social defeat stress [60,61] and chronic mild stress [62] paradigms, or else by manipulating the animal's physical condition in ways that may make it less able to cope with adversity, as in the olfactory bulbectomy paradigm [63]. The behavioural changes produced by these interventions are similar to symptoms of human mood disorders, and are reversed by antidepressant medication. Thus, there is at least an implicit understanding within neurobiological research into mood disorders that mood is a normal response to changes in the probability of negative events in the environment, or changes the animal's ability to cope with them if they do occur. However, this understanding is not usually expressed explicitly in this way.

The framework presented here may be helpful for explaining why depressed mood and anxious mood so often co-occur. As we have stressed, the reward and punishment thresholds are logically and mechanistically distinct, so there is no reason why an individual experiencing anxious mood should be any more likely to experience depressed mood than anyone else. In humans, however, depression and anxiety are very often comorbid, and share many epidemiological predictors [64,65]. A possible reason for this is that, rather generally, deteriorations in physical condition make both false-negative threat detections *and* false-positive reward-approaches more costly. Thus, anything with a negative impact on physical condition might be expected to entrain both anxious and depressed mood simultaneously. The current approach might also help account for the developmental origins of proneness to anxiety and depression. Adverse developmental conditions, both pre- and post-birth, have been found to increase the likelihood of lifetime depression and anxiety in humans [66–69], and there are analogous findings in non-human animals [70–73]. It may be that such developmental insults cause permanent constraints on the individual's physical condition that mean that they are less able to deal with threats and non-rewards as adults. In this case, it would make adaptive sense that they calibrate their threat-detection threshold lower, and their reward-approach threshold higher, accordingly.

'Cognitive Bias' as Central to Mood

In the framework described here, the defining features of any particular mood state within the space illustrated in Figure 1 are the individual's current thresholds for detecting possible

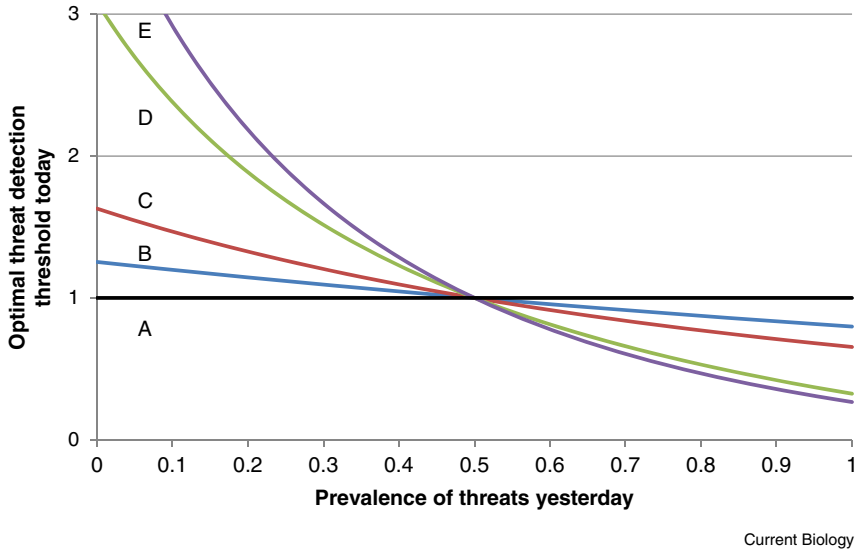

Figure 2. The optimal threat-detection threshold for today as a function of the prevalence of threats in the environment yesterday, for different combinations of model parameters.

(A) Non-autocorrelated environment with no spillover effect of threatening experiences yesterday on physical condition today (β = 0 and δ = 0). (B) A weakly autocorrelated environment (β = 0.1) with small spillover effects of threatening experiences on condition (δ = 0.1). (C) A weakly autocorrelated environment (β = 0.1) with large spillover effects of threatening experiences on condition (δ = 1). (D) A strongly autocorrelated environment (β = 0.5) with small spillover effects of threatening experiences on condition (δ = 0.1). (E) A strongly autocorrelated environment (β = 0.5) with large spillover effects of threatening experiences on condition (δ = 1). The optimal threshold is expressed in terms of the likelihood ratio of current evidence being generated when a threat is and is not present. Other model parameters are μ = 0.5, w_{ALL} = 1, in all cases.

reward and punishment. Thus, it predicts that changing the mood of a person or animal would change the set of ambiguous stimuli judged to fall into the classes of 'threat' and 'reward'. Empirical evidence supports this prediction. In humans, depressed and anxious individuals are more likely to interpret an ambiguous stimulus in accordance with its negative possible meaning than non-depressed non-anxious controls are [13,74]. This phenomenon came to be termed *cognitive bias*, which is in many ways unfortunate now that it has been documented in so many taxa (see below). The *cognitive* is unfortunate because such effects minimally involve the adjustment of a detection threshold, and thus do not necessarily require complex cognitive abilities. The *bias* is unfortunate because it implies that the phenomena involve some kind of distortion or erroneous representation of reality. In fact, in the paradigmatic tasks used to probe the phenomenon, there is no objectively correct answer, and hence there is no possibility of error. Thus, the phenomenon would be better described as condition-dependent adjustment of detection thresholds. However, the terminology is now established in the field.

Harding, Paul and Mendl [75] were the first to demonstrate the cognitive bias phenomenon in a non-human system. They trained rats to respond to one tone (the food tone) by pressing a lever to obtain food, and to a different tone (the noise tone) by not pressing the lever to avoid aversive white noise. The animals were then assigned to either normal housing, or unpredictable housing, which is a source of chronic mild stress. Individuals were then tested with tones that were intermediate between the training stimuli, and hence ambiguous. Rats in the unpredictable housing group were less likely to respond to the original food tone, but also treated more of the intermediates between the food and white noise tones as being like the white noise tone (by not pressing the lever) than the animals from the normal housing did. This basic effect, whereby the threshold for treating an ambiguous stimulus as heralding a negative event is affected by the environment the individual has experienced, or covaries with other markers of mood, has been confirmed with different experimental paradigms in rats [76–78], and also been demonstrated in many other systems, including sheep [79], dogs [80], pigs [81], rhesus macaques [82], starlings [83,84], chickens [85] and even honeybees [86]. The changed thresholds are returned to normal by antidepressant treatments in chickens [85,87], just as they are in humans [88]. This suggests that altered thresholds for detecting rewards and punishment are central to mood across taxa. As well as validating the signal detection approach, this raises the possibility of being able to assess mood in a way that is readily transferable from one species to another, with important implications for the science of animal welfare [8,12].

Implications for Mood Disorders

Everything we have discussed so far concerns the normal functioning of the mood system, which we have argued is an adaptation for allocating the individual's behaviour in ways most appropriate for their current condition and environment. We have claimed that the key features of moods, the anhedonia, pessimism and fatigue in depression, and the vigilance, threat-bias and physiological response of anxiety, represent means by which they fulfil their evolved function. We have also argued that certain epidemiological patterns of depressed and anxious mood, such as their triggering by losses and dangers, and their relationships with infirmity, isolation and poverty, make adaptive sense. How then should we interpret mood *disorders*, which are after all the main clinical concern? The very use of the word disorder implies that something in the system has gone wrong, and that the set of symptoms is the set of downstream consequences of this malfunction. This appears to be the assumption in work in the neurobiological bases of mood disorders. Yet it is also widely recognised that depressive and anxious disorders are often triggered by life events to which depressed and anxious mood would be a normal (healthy) response.

The proper boundary between a normal mood response and a pathological one is extremely hard to identify. There is no statistical point of rarity in the population distribution of current anxious or depressed symptoms that offers an

Box 2

Open questions in the evolution of mood.

Our analysis in the main text is simple but leaves unaddressed a number of issues likely to be important in understanding mood phenomena from an evolutionary perspective. We argue that mood involves an integrative function of acute emotional experiences over time. However, we imply that this function is simple accumulation or averaging. In reality, organisms may be sensitive to the local rate of change in their environment (or indeed in their physical condition) as well. This makes different predictions from a simple averaging model; for example, that the mood implications of two poor outcomes followed by a good one would be different from those of a good outcome followed by two poor ones. Such contrast effects have indeed been widely documented in humans and in non-human animals [34,100–102]. They can lead to apparently irrational preferences, such as people preferring a procedure that involves more pain overall, but an improving pain gradient, to one with less pain [103]. However, they may arise from decision rules that are generally adaptive in environments that have marked trajectories of deterioration or improvement. It would be interesting to investigate how much of the seasonal variation documented in human mood [104] arises from the fact that the direction of change of the environment is negative in autumn but positive in spring, even if the averages are not much different.

Another issue for future investigation is how and why mood generalizes across different domains of life. For example, providing cover in birds' housing, which might be expected to reduce perception of hazard in the domain of predation, has an effect on the birds' thresholds for responding to cues of toxins in their prey [100]. Why this generalization across domains should occur is not immediately clear; although environments tend to be autocorrelated within a domain, there is no reason to think that the prevalence of toxins in prey is in general predicted by the prevalence of predators. Thus, it seems that there ought to be separate mood systems for each domain of fitness-relevant activity, rather than a 'general' level of mood. One possible explanation for the generalization of mood across domains is that the individual's current physical condition is the determinant of their ability to cope with negative outcomes across all domains. Thus, just as we argued for the comorbidity of anxious and depressed mood, any change in physical condition should have a pervasive impact (see also [29] on related issues).

Finally, we have not addressed the origins or function of the subjective experience of mood in humans. By defining mood in terms of thresholds for responding to reward and punishment, our formulation allows for mood to be phylogenetically widespread without implying anything about subjective consciousness in non-human animals. However, this does not mean that subjective content is not an important component of mood in the human case. It is clearly the aspect of mood that matters most to people. Why exactly there should be phenomenally experienced components of mood and emotion, and how these evolved from mechanisms we share with other vertebrates is — as the philosophers say — a hard problem, and well beyond the scope of our review. However, this does not mean it cannot be addressed [105].

easy division into the normal and the disordered [89]. The *Diagnostic and Statistical Manual* of the American Psychiatric Association, 4th edition, uses the arbitrary cut-off of two weeks' duration of symptoms for diagnosis of depressive disorder, but the extent to which two weeks of depressed mood is abnormal depends on what is happening in the individual's life. Indeed, the Manual recognizes that the two weeks of symptoms that would usually be taken to indicate pathology constitute a normal response in the recently bereaved. Thus, any purely symptomatic boundary between normality and disorder is inevitably somewhat arbitrary, and must recognise a gradation of severity blending into the range of normal but unhappy.

Evolutionary thinking has been used to propose alternative criteria for what constitutes disorder as opposed to healthy function: disorder is present when a biological system is not producing the effects that led to its evolutionary selection, and the consequences of this are harmful [90]. This leaves unanswered the question of how harmful the consequences have to be (and what the metric of harm is), so arbitrary boundary decisions are still required. Moreover, it is very hard — except in extreme cases — to show that a particular person's mood response is inappropriate to their current environment and state, as we rarely have exhaustive and objective enough information about their lives to be able to determine this. This difficulty is exacerbated by the fact that there is considerable genetic variation affecting the responsiveness of mood systems [91–94]. Such variation may have been maintained in part by variable selection pressures acting on these systems across different environmental conditions [95,96]. A consequence is that some people are prone to more extreme mood reactions than others when faced with the same environmental triggers, even in the absence of any pathology of the system. Given such polymorphism, it is hard to make much progress on the question of what level of mood-responsiveness is normal in an evolutionary sense.

Mood systems are no different from any other biological mechanism in that they can go wrong sometimes, becoming hypersensitive or dysregulated. Horwitz and Wakefield [97] are probably correct to argue that what we currently diagnose as disordered mood represents a mixture of cases where individuals have had adverse life experiences, but their mood system is itself functioning exactly as it should, and cases where the neurobiological mechanisms subserving mood are dysregulated or diseased. There is unlikely to ever be any simple way of demarcating the boundary between these two sources of mood problems with precision (see [45,98] for further discussion). Note, however, that the criteria for therapeutic concern and medical intervention do not need to depend on being able to distinguish evolved function from dysfunction. In physical pain, for example, administration of analgesia is almost universal, and it is implausible that in all cases this is because of malfunction in people's pain systems. Rather, we now have technologies to slightly dampen systems that are in fact fulfilling their evolved function, and the justification for doing this is based on suffering, rather than demonstrable dysfunction in the

evolutionary sense [99]. This does, however, raise largely unexplored questions about whether pharmacologically manipulating adaptive systems, though producing immediate relief, might lead to adverse consequences in the long run. Given the evidence that moderate anxiety is associated with a slightly reduced risk of death (for example [27]), what might be the consequence of widespread pharmacological treatment for moderate anxiety? It is remarkable how little research has been conducted on such questions, and a virtue of the adaptive perspective is that it naturally raises them.

The evolutionary perspective may not solve issues of demarcation between normality and illness, but it does help broaden the debate on how to deal with the burden of mood disorder. Much current therapeutic focus is on either techniques to change the cognitive styles entailed by anxious and depressed mood, or on pharmaceutical technologies to stabilize the proximate neurobiological mechanisms. We do not dispute the importance of both of these. However, thinking in behavioural ecological terms naturally leads us to attend also to how environments might be changed to reduce the burden of suffering. That is, if human environments could be made less punishing and more rewarding for the people who are most at risk (the poor, the unemployed, the vulnerable, the socially isolated), and people's physical condition could be better protected through their lives (through better nutrition and medical care), then we would see a reduction in depressed and anxious mood. This reduction would span those whose mood systems are hypersensitive *and* those whose mood systems have a normal sensitivity, those we currently consider as having a mood disorder *and* also the larger bulk of people who do not meet current diagnostic criteria but are still unhappy. Thus, the behavioural ecological perspective helps us see depression and anxiety not just as problems of the individual brain, but as consequences of how individuals' brains interact with the way we structure societies and environments.

Conclusions

The study of the functions of mood phenomena in different types of animals is much less advanced than the study of the proximate mechanisms underlying mood changes. Although we have sketched an approach here, it is extremely preliminary, and there are many open questions (Box 2). However, understanding what mood is for makes sense of the ways in which environmental conditions, life events, and developmental history interact to affect individuals' moods. Developing integrative theoretical frameworks for the study of mood across taxa provides a bridge between psychology and behavioural ecology, and will be of benefit in applications as diverse as psychiatric epidemiology and the science of animal welfare.

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