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Daniel Nettle

Centre for Behaviour and Evolution

Institute of Neuroscience

Newcastle University

Henry Wellcome Building

Framlington Place

Newcastle

NE2 24HH

daniel.nettle@ncl.ac.uk

Abstract

It has been suggested that low mood in humans is an adaptive response to unpropitious circumstances, and that the anhedonia, pessimism and fatigue that often accompany it function to minimise risk until circumstances improve. While this is plausible, it would be possible to make the opposite prediction equally plausibly: individuals in bad circumstances should take greater risks in order to improve their situations. Here, I present a simple analytical model adapted from the risk-sensitive foraging literature. It shows that in dire states, individuals should be risk-prone, in poor states, risk-averse, and in good states, risk-prone again. I discuss how the various kinds of mood state observed in humans might be understood as mechanisms for adaptively adjusting behavioural risk-taking to the current situation.

Key words: depression, mania, mood, risk-sensitivity

Introduction

Low mood describes a temporary emotional and physiological state in humans, typically characterised by fatigue, loss of motivation and interest, anhedonia (loss of pleasure in previously pleasurable activities), pessimism about future actions, locomotor retardation, and other symptoms such as crying (Allen and Badcock, 2003; Keller and Nesse, 2006). When low mood is extreme or prolonged, it is designated clinical depression (Nesse, 2000). Since the generic trigger of low mood is loss of or lack of access to some important resource, low mood may usefully be seen as an evolved suite of responses to unpropitious or adverse situations (Allen and Badcock, 2003; Nesse, 2000; Nesse, 2006; Watson and Andrews, 2002). Note that this does not mean that clinical depression itself represents adaptive behaviour; clinical cases may represent instances where the evolved mechanisms are chronically overactive or have become dysregulated (Nesse, 2000; Nettle, 2004). However, evolutionary reasoning may still be useful for understanding why low mood has the fundamental features that it does.

Low mood probably has multiple adaptive functions in unpropitious circumstances, subserved by its various different symptoms. For example, crying signals to others the need for support, and rumination may aid in devising alternative behaviours that will be more effective in the current environment (Keller and Nesse, 2006; Watson and Andrews, 2002). This paper focuses on a central triad of symptoms which are common across many types of low mood, namely anhedonia, fatigue and pessimism. Theorists have argued that, whereas their opposites facilitate novel and risky behavioural projects (Fredrickson, 2001), these symptoms function to reduce risk-taking (Allen and Badcock, 2003; Badcock and Allen, 2007; Engel and Schmale, 1972; Keller and Nesse, 2006). They do this, proximately, by making the potential payoffs seem insufficiently rewarding (anhedonia), the energy required seem too great (fatigue), or the probability of success seem insufficiently high (pessimism). An evolutionary

hypothesis for why low mood has these features, then, is that is adaptive to avoid risky behaviours when one is in a relatively poor current state, since one would not be able to bear the costs of unsuccessful risky endeavours at such times (Allen and Badcock, 2003).

Whilst this seems plausible, there is always a danger in relying on purely verbal arguments about what might be adaptive under what circumstances. Sometimes the hypothesised strategy could only in fact be adaptive given restrictive assumptions or unrealistic parameters, and formal models can aid in clarifying whether the claims really do follow from the premises. In this particular case, if low mood had been associated with exactly the opposite symptoms (increased energy and optimism, greater risk-taking), that would have been equally easy to formulate an adaptive logic for. It would suffice to claim that the individual in a poor current state needs to obtain a large payoff to improve her position to an acceptable level, whereas the individual in a good position does not need to take the risk of doing so.

In fact, the opposite prediction – that an unpropitious situation would be associated with risk-proneness, not risk aversion – has greater precedent in the evolutionary and comparative literature. Food restriction in animals, for example, leads to an increase, not a decrease, in energy expenditure (Boakes, 2007; Routtenberg and Kusnezov, 1967), and increased rather than decreased risk-taking in terms of coming out of cover in the presence of predators (Krause et al., 1998). Food-restricted animals of many different species also switch from preferring less variable to more variable food sources (Caraco et al., 1980; Kacelnik and Bateson, 1996), in line with the predictions of risk-sensitive foraging theory (Stephens, 1981). Food-restricted humans become hyperactive, risk-prone, and impulsive, not anhedonic or fatigued (Fessler, 2002; Holtkamp et al., 2006; Holtkamp et al., 2003). Thus, a key theoretical question is when, in

general, we should expect a worsening organismic state to lead to risk-aversion and passivity, and when we should expect it to lead to risk-proneness and hyperactivity.

This paper investigates a simple analytical model of the optimal response to being in a poor state, based on an existing model of risk-sensitive foraging (Stephens, 1981). The objectives are first, to establish whether becoming more risk-averse could be an adaptive response to unpropitious situations, and second, to examine where the boundary lies between adversity which is best responded to by saving energy and taking no risk, and adversity which is best responded to by expending energy and preferring risk.

The Model

Consider a multi-time step situation in which the individual has a current state S (S_t at time t). This state simply represents where the individual is placed along a dimension related to future reproductive success, which could reflect health, safety, resources, social position, or any other parameter of importance for the species under study.

I define a threshold R which represents a dangerously bad state. R plays the same role as starvation in a risk-sensitive foraging model, but I do not interpret here it as death, merely a state so poor as to be dangerous. I stipulate that the goal of the organism at each time step is (1) to make the probability of falling below R at this time step as small as possible; and (2) if this probability is close to zero, to maximise the possible gain in S in this time step. We will take 'close to zero' in this context to be 0.01 or less (i.e. probability of remaining above R equals 0.99 or more), though this assumption is arbitrary and could be varied without affecting the qualitative pattern of results.

At each time step, *S* declines by a quantity *c*. This reflects the energy costs of maintenance, the deterioration of unserviced social relationships, and so on. At each time step, the individual also chooses to take an action, which will improve *S* by a value *b*. Critically for the issue of risk, actions do not have certain payoffs, but instead probabilistic ones. Particular values of *b* are drawn from a normal distribution with mean μ_b and standard deviation σ_b. The larger σ_b, the more risky the action is, though the larger its maximum payoff also. We assume that the individual has a range of different behavioural options available with varying values of σ_b. Thus, to examine how sensitivity to risk should vary with current state, we need to examine the optimal value of σ_b (for a given μ_b) that the individual should seek as S_t changes.

The probability that an individual falls below *R* at time step *t* is given by (1).

$$p(S_t < R) = p(S_{t-1} + b - c < R) \quad (1)$$

Rearranging (1), the probability of remaining above *R* in this time step is the probability that $S_{t-1} + b$ is greater than $R + c$. From the Gaussian distribution with mean μ_b and standard deviation σ_b, this probability is given by (2), where Φ is the cumulative normal distribution function.

$$p(S_t > R) = \Phi\,[(S_{t-1} + \mu_b - R - c) / \sigma_b] \quad (2)$$

The condition for $p(S_t > R)$ to exceed than our arbitrarily set threshold of 0.99 is given by (3) (where the value 2.33 comes from normal distribution tables).

$$[(S_{t-1} + \mu_b - R - c) / \sigma_b] > 2.33 \quad (3)$$

The greater the margin by which S_{t-1} exceeds *R*, the more likely condition (3) is to be met.

Where the organism has several actions available in this time step, all of which satisfy condition (3), but which have different riskiness σ_b, the organism should choose the one with the larger value of σ_b, since a larger σ_b means a larger maximal gain in *S* in this time step. Indeed, under these conditions a larger σ_b should always be preferred over a smaller one up to point where increasing σ_b causes $[(S_{t-1} + \mu_b - R - c) / \sigma_b]$ to fall below 2.33. The optimal action is thus the one which satisfies (4).

$$\sigma_b = \frac{S_{t-1} + \mu_b - R - c}{2.33} \qquad (4)$$

As equation (4), shows, the optimal preferred riskiness increases as the gap between *S* and *R* increases. The closer to *R* the organism falls, the smaller the variance in outcome of its social actions it should seek, since large-variance actions become increasingly likely to make the risk of falling below *R* unacceptable. Conversely, the better the organism's current state, the more risky the actions in can optimally choose, since it is in a position to handle the potential loss if these go badly.

However, we also need to consider cases where *S* is currently close enough to *R* that there is no action available that satisfies condition (3). In this case, the individual should seek to maximise $p(S_t > R)$ (see equation 2). What value of σ_b will achieve this? Since $\Phi [(S_{t-1} + \mu_b - R - c) / \sigma_b]$ increases monotonically with $[(S_{t-1} + \mu_b - R - c) / \sigma_b]$, need only consider the effect of changing σ_b on $[(S_{t-1} + \mu_b - R - c) / \sigma_b]$. The partial derivative of this expression with respect to σ_b is given in (5).

$$\frac{d}{d\sigma_b} = \frac{1}{\sigma_b^2} \bullet \left(R + c - S_{t-1} - \mu_b\right) \qquad (5)$$

Since $1/\sigma_b^2$ must be positive, the sign of (5) is given by the sign of $(R + c - S_{t-1} - \mu_b)$. That is:

$$\frac{d}{d\sigma_b} > 0 \text{ where } S_{t-1} + \mu_b - c < R \quad (6)$$

And

$$\frac{d}{d\sigma_b} < 0 \text{ where } S_{t-1} + \mu_b - c > R \quad (7)$$

The burden of expressions (6) and (7) is that increasing σ_b worsens the chances of avoiding R in this time step as long as the current state net of the expected mean benefits and costs is greater than R, but below this point, that is where the expected benefits and costs are not sufficient to avoid R, then the individual will always do better by choosing a larger value of σ_b over a smaller one, and should seek the riskiest actions possible. (This is equivalent to the conditions for risk-proneness with respect to the threshold of starvation in Stephens [1980]).

Since we assume $\mu_b > c$ (otherwise these behaviours would not have evolved), this means in practice that the point at which the individual should switch to risk proneness is always in the region $S_{t-1} < R$. That is, if the current state is in the dangerously low region, then the individual should take as much risk as possible, whereas being merely down close to that region, it is always better to be risk averse.

Figure 1 illustrates the general pattern of risk-proneness and risk-aversion predicted by the model, with arbitrary values or ranges chosen for R, σ_b, μ_b and c. Where the current state is very low, below $R + c - \mu_b$, the individual should try

anything, however great the risk. Indeed, she should seek the maximum variance in risk possible in an attempt to regain *R*. In a range of current states from just below *R* to somewhat above it, the she should choose actions with the smallest risk available. Beyond this point, as current state improves, so too does the optimal level of risk sought out, so that individuals in a very good current state, like those in a desperately poor one, prefer relatively risky actions.

Discussion

The model predicts that individuals in a good state will be prepared to take relatively large risks, but as their state deteriorates, the maximum riskiness of behaviour that the they will choose declines until they become highly risk-averse. However, when their state becomes dire, there is a predicted abrupt shift towards being totally risk-prone.

The switch to risk-proneness at the dire end of the state continuum is akin to that found near the point of starvation in the original optimal foraging model from which the current one is derived (Stephens, 1981). The graded shift towards greater preferred risk with improving state is novel to this model, and stems from the stipulation that if the probability of falling into the danger zone in the next time step is minimal, then the potential gain in S at the next time step should be maximised. However, a somewhat similar pattern of risk proneness in a very poor state, risk aversion in an intermediate state, and some risk proneness in a better state, is seen in an optimal-foraging model where the organism has not just to avoid the threshold of starvation, but also to try to attain the threshold of reproduction (McNamara et al., 1991). Thus, the qualitative pattern of results may emerge quite generally from models using different assumptions.

In psychological studies, improving mood is associated with greater energy, creativity, optimism, and desire for new projects (Fredrickson, 2001), whereas

low mood, through anhedonia, pessimism and fatigue, leads to reduced risk-taking (Allen and Badcock, 2003). The model shows why these motivational changes might be adaptive. When the individual's state is poor, a risky venture going wrong could push state down further into the danger area, and so behaviours with a small variance in payoff are preferred. When state is better, the individual can absorb potential failures and so is in a position to try out risky options that might just lead to a big payoff. Thus, to a very considerable extent, the model supports existing views for the adaptive functions of low mood symptoms, and of positive emotions in general: when things are going quite badly, it is not the time to take risks, but as things improve, greater experimentation is warranted (Allen and Badcock, 2003; Fredrickson, 2001; Keller and Nesse, 2006; Nesse, 2000).

However, the model also predicts that there comes a dire point beyond which it is maladaptive to avoid risks and conserve energy; the situation is already too dangerous for that. Instead, the individual should be highly motivated to take risks and try new solutions; to do anything, in fact, that has any chance of returning her to the acceptable range of states. Is there any evidence that such moods are found in humans?

We have already noted the impulsivity, hyperactivity, and risk-proneness of humans who are acutely food-deprived (Fessler, 2002; Holtkamp et al., 2006; Holtkamp et al., 2003). Within mood disorders, there is a clinical state known in the literature as 'agitated' or 'excited' depression. These patients are classified as depressed in that their affective tone is negative, but their symptoms can include locomotor acceleration rather than locomotor retardation, restlessness rather than fatigue, a feeling of thoughts racing, and a desire to follow risky pleasurable impulses (Akiskal and Benazzi, 2004; Akiskal et al., 2005). Agitated depression is more common in patients who also have manic episodes, which leads to the

further question of whether mania could be related to the predictions of the model.

Mania is characterised by feelings of increased energy and locomotor activity, impulsivity and disinhibition; all the features, in short, which would promote the pursuit of high-risk activities. Mania is normally viewed as an extreme of the normal reaction to being in a good state, rather than a poor one (Stevens and Price, 1996), and in particular to the attainment of goals (Johnson et al., 2000). There is strong evidence that the proximate mechanisms involved are those of behavioural approach systems, which facilitate reward pursuit and are associated with pleasure (Urosevic et al., 2008). However, emotional tone is not always positive during manic episodes, and patients can report high levels of negative emotions such as sadness, anxiety, irritability and aggression (Bauer et al., 1991; Cassidy et al., 1998; Goodwin and Jamison, 1990). Indeed, it is possible that 'euphoric mania' and 'dysphoric' or 'mixed' mania (mania accompanied by negative mood) represent distinct states (Cassidy et al., 1998).

The model presented here would provide a natural interpretation of these diverse mood changes. Agitated depression or dysphoric mania might be expected to be follow from situations where the individual appraises their current state as absolutely dire, whereas retarded depression might be expected where the individual appraises their state as merely poor. Appraisal that current state is good would lead to normal high mood, or, in individuals prone to over-react to such appraisals, euphoric mania. Note that the much of the phenomenology of the two types of mania – the expansiveness of thought, the increased activity – would be expected to be the same, and many of the same proximate mechanisms could be involved. What would differ is the individual's appraisal of how well things are going for them, which precisely captures the dysphoric-euphoric distinction.

The clinical literature contains many reports of mania precipitated by strongly negative life situations, such as 'funeral mania', where the symptoms are triggered by the death of an important relative (Hollender and Goldin, 1978; Krishnan et al., 1984; Rickarby, 1977). However, a recent review (Johnson, 2005) concludes that although there are some studies suggesting that manic symptoms increase after negative life events, the best evidence, which comes from comparing life events before and after manic episodes within the same individuals, have not found such a relationship. However, these studies do not separate euphoric from dysphoric mania, a distinction which the current model suggests might be useful to make. It would be the former which would be expected to follow goal-attainment events, and the latter which would be predicted to follow negative life situations.

The foregoing considerations suggest that, from an evolutionary perspective, it is insufficient to classify moods merely by their valence, i.e. as negative or positive, or indeed by the symptoms or proximate mechanisms involved. Instead, we need to understand the class of perceived situation to which the particular suite of behavioural, cognitive and emotional changes observed might be an evolved response. The mood responses to different types of situations will show different suites of design features that represent adaptive strategies in that context, using different combinations of proximate mechanisms to achieve their ends. Thus, a mood representing a response to dire circumstances could involve simultaneous activation of negative emotion systems (because the world is appraised as dangerous), and behavioural approach systems (because the individual needs to be motivated to go out and capture rewards to try to improve her state). Such a mood state would be like depression, in its negativity, but also like positive mood, in its energy and risk-proneness. Thus, the adaptive approach helps explain why there might be states such as dysphoric mania, which seem like depression in some ways and like good mood in others. More generally, evolutionary reasoning

helps explain the situation-specific diversity of human emotional responses (Keller and Nesse, 2005; Keller and Nesse, 2006; Nesse, 1990).

Note that the current adaptive reasoning sheds no light on why some people might be more vulnerable to others to different affective disorders, given particular life situations. That is a question of individual variation, beyond the scope of this paper (Nettle, 2004). Instead, this kind of ultimate reasoning might shed some light on the species-typical design of the mechanisms of mood, which sometimes make us pessimistic and risk-averse, and sometimes impulsive and risk-prone.

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Figure legends

Figure 1. Illustration of the output of the model with representative values chosen for model parameters. The horizontal axis shows the current state of the organism, where R, the point at which state is dangerously low, is set at 6. We assume that the organism has a range of different actions available to it, all of which have a mean payoff $\mu_b = 3$, but which differ in the standard deviation of their payoff σ_b from 1 to 10. The vertical axis shows the value of σ_b which the organism should choose given its state. c is set at 1.

Figure 1: