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Reply to Dr Hoffer

I sympathise with Dr Hofer's preference for research into proximate rather than ultimate causes, but I would like to comment on his statements that "it is the wrong time to try to draw maps" and that "we know very little about the biological nature of mental illnesses, and have not yet established a basis for their cross-species analysis, two serious obstacles for any attempt to reconstruct their possible evolution." One possible bridge is between psychiatry and behavioural ecology, and I would exhort readers who have not already done so to read Krebs and Davies' Introduction to Behavioural Ecology (1), particularly Chapter 7 on "Fighting and assessment". In this chapter the authors discuss the evolution of ritual agonistic behaviour which they call contest behaviour, or pairwise contests. The variables which are thought to be important in the evolution of pairwise contests are owner/intruder, high/low resource-holding potential (RHP), evaluation of opponent's RHP, resource value (V) and estimate of costs likely to result from fighting. I believe there is a close correspondence between these variables which are thought important in the evolution of vertebrate agonistic behaviour and the cognitive changes which occur in human mood disorders, particularly the switch from normal mood to the depressed state. Let me list the important ecological variables and relate them to the cognitive changes of depression:

1. Resource value (V) (how valuable is the thing which is being fought about?). This may vary between contestants, for instance a female hamadryas baboon which has been impregnated by one of two rival males. The higher the resource value, the more likely is attack rather than yield.

In depression there is a general loss of interest in the environment. Things seem less significant and less important. Psychologists talk about a reduction in incentives and loss of reinforcer effectiveness. Even if the depressed patient thought he could fight and had any chance of winning, he would see things as not worth fighting about.

2. Each contestant evaluates his resource-holding potential (RHP). The higher he thinks his RHP, or fighting capacity, the more likely he is to attack.

In depression there is a marked diminution in self-image. We generally talk of low self-esteem, which is a wider concept that RHP or even self- confidence; but those components of self-esteem which reflect RHP are lowered along with the rest. Paul Gilbert uses the phrase "involuntary subordinate self-perception".

3. Each contestant evaluates his opponent's resource-holding potential (RHP). The higher the estimation, the less likely he is to attack.

In depression other people tend to appear frightening, and their "put- downs" or catathetic signals are more painful. The whole sense of pain is more acute, and there is even spontaneous pain in many cases. Since the power of an adversary is partly judged by the pain (mental and physical) which his insults and blows cause, it follows that the more pain a contestant feels, the sooner he is likely to stop attacking.

4. Likely costs of combat. In the cost benefit analysis of contests, whereas resource value (V) reflects the potential benefit, the possibility of mental and physical damage reflects the potential cost.

This again accounts for the association between depression and pain. Physical pain is an indicator of tissue damage, so that the more pain is experienced, the higher the estimate of likely costs if fighting is continued, and the more likely the contestant is to yield.

5. Ownership. It is a general rule in vertebrate contests, particularly among territorial species, that owners win over intruders. Possession is nine-tenths of the law, it is truly said. Therefore each contestant calculates the degree to which he is the owner of the resource being fought about, or of the territory on which the contest is taking place. The more he feels the owner, the more likely he is to attack.

Depressed patients have a reduced sense of ownership. They sometimes say they have no right to be anywhere at all, or even to exist. A depressed golfer says that he has no "standing" on the course of life. This is in stark contrast to the patient with elevated mood who often feels that he owns the whole world.

If we add to the above a pessimistic view of the future, so that no engagement seems likely to be successful, and a negative view of the world as a hostile place where no allies are to be found, we have identified most of the cognitive changes of depression as likely to result in a decision to yield rather than attack in a pairwise contest. Therefore it does

not seem excessively speculative to suggest that mood changes between mania and depression represent some sort of modulating system which influences the overall tendency to attack or yield in pairwise contests.

I think the advantage of this kind of thinking is twofold. It clarifies our ideas about the core variables of depression; and it identifies contest behaviour in animals as an important subject for research basic to human depressive disorders. Depressed patients are like those Harris sparrows in pale winter plumage who do not attack other birds and are not perceived as a threat by others (1). The Harris sparrows can be induced to attack by injections of testosterone, and it seems to be generally the case that RHP in birds can be raised by testosterone; testosterone does not affect RHP in mammals, but it may well be that some other hormonal system exerts a similar modulating effect, regulating agonistic behaviour by altering those evaluative processes listed above which decide between attack and yielding. The pale Harris sparrows do not get their own way vis-a-vis other Harris sparrows - they survive by picking up the crumbs under other birds' tables - and I think that depressed patients do not get their own way unless they are in the fortunate position of having other people who love and care for them and treat them as sick or old or infirm.

What little experimental work is being done on animal contests is being financed by heart and kidney charities, because the subordinate animals develop hypertension and renal failure. This ignores the fact that by the time it dies of renal failure the animal has probably undergone a long ordeal of conspecific-induced torture and has developed at least a state of learned helplessness, if not more a recognisable dysphoric state. It needs to be accepted that studies of contest and ranking behaviour in animals may well be as important for psychiatry as for cardiology; existing promising work such as that of Michael McGuire (on the relation of blood serotonin to vervet monkey ranking) needs to be replicated and extended, and new searches need to be made for proximate mechanisms underlying the regulation of RHP. The drawing of maps based on ultimate causation may help us to enter the right areas for research into proximate causation, by establishing a biologically valid basis for cross-species analysis. Unless we can produce a promising map, no-one is going to finance the voyage of exploration.

1. Krebs, J.R. & Davies, N.B. (1987) An Introduction to Behavioural Ecology 2nd ed. Oxford: Blackwell.