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Welfare, Stress, and the Evolution of Feelings

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I. Feelings, Their Role and Their Evolution

A. Feelings, Emotions, and Consciousness

Three of the ways in which feelings can arise in an individual are as follows. First, inputs to sensory systems may result in changes in the brain, which we refer to as sensations or perceptions. Some of these have wide-ranging effects within the brain in addition to information processing, storage as memory, or initiation of activity modification. They lead to feelings in the individual, for example, pain or sexual gratification (Ottoson, 1983; Swenson and Reece, 1993). Second, various neural and hormonal changes result in physiologically describable conditions in individuals, which we refer to as emotions. The emotional state may involve electrical and neurochemical activity in well-defined parts of the brain, hormone release, and peripheral consequences. These various changes may also result in feelings, such as lust or anxiety, although emotional states may exist without any accompanying feeling, for example, as active regions of the amygdala with no cortical activity or during sleep (Guyton, 1982). Third, even in the absence of sensory input, or hormonal change, or activity in emotional centers in the brain, complex or simple brain processing can lead to the existence of feelings, for example, pleasure of achievement, guilt, or boredom. Each feeling is an internal brain construct, which the individual concerned may be able to describe but which will not necessarily have any external manifestations. As Dawkins (1993, p. 142) has pointed out, feelings may have observable signs, for example, happiness can lead to laughter, but happiness is not laughter and cannot be defined in terms of laughter. It is part of the state of the individual at that time. Some of the characteristics of feelings and examples of feelings are detailed in Table I.

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TABLE I
CHARACTERISTICS AND EXAMPLES OF FEELINGS

1. A feeling is a brain construct within an individual, sometimes with peripheral links.
2. The brain construct includes something additional to that required for other functioning.
3. A feeling is recognizable by the individual when it recurs.
4. Feelings may change behavior immediately or eventually but need not do so.
5. Feelings often act as reinforcers when learning.
6. Feelings can be positive or negative in that they promote approach or avoidance.
7. Examples of feelings are: pain, malaise, tiredness, hunger, thirst, thermal discomfort, fear, anxiety, grief, frustration, guilt, depression, boredom, loneliness, general suffering, lust, jealousy, anger, sexual pleasure, eating pleasure, exhilaration, other sensory pleasure, achievement pleasure, general happiness.

Each kind of feeling can vary greatly in strength according to the magnitude and duration of the eliciting input. The mechanism for initiating the feeling in the individual in response to an input can also vary. Indeed, individuals will vary in sensory functioning, other physiological processing, and analytical ability according to their genotype and environment during life. Hence feelings will vary from one individual to another. As indicated above, some feelings are largely elicited by low-level neural processing, while others depend on very complex processing. Pain depends on inputs from nociceptive pathways, usually originating in nociceptive receptor cells, and does not require high-level processing in the brain. Similarly, thirst is principally dependent on inputs from body fluid monitors and mouth receptors, thermal discomfort results from local or general peripheral input, and pleasure associated with food or sexual intercourse is principally due to sensory input. Fear, in contrast to pain, requires high-level processing, usually involving the comparison of sensory inputs with established models in the brain of what constitutes a familiar or a dangerous stimulus. Likewise, frustration is complex because it necessitates precise expectations to compare with actual inputs. The most complex processes may be involved in deriving pleasure from the solving of a difficult problem, or in some situations that lead to anxiety. Simpler, perhaps more primitive, processes leading to feelings are likely to be more widespread in the animal kingdom than the most complex process. However, the existence of a range of levels of complexity in the origins of different feelings does not mean that the feelings themselves, or any behavioral consequences that they may have, also differ in complexity. All may be equally simple. It is also likely that most feelings, whatever the complexity of their initiation, can be amplified by complex brain processes when much attention is devoted to the source of the feeling, or diminished by active reduction in the brain resources employed in that area.

The variation in the extent of high-level processing, which is likely to be involved in the initiation of feelings, is clearly relevant to the relationship between having feelings and being conscious or aware. Emotion, in the sense of neural activity in the emotion centers of the brain or specific hormonal changes, can occur without any feelings being reported, but how aware does an individual have to be in order to feel something such as pain or the pleasure associated with eating a favorite food? Pain is universally referred to as a feeling, indeed the definition of pain given in a veterinary dictionary by Blood and Studdert (1988) starts with the words "a *feeling*." The feeling is what distinguishes pain from nociception. Most medical and veterinary usage of the words "conscious" or "aware" would imply that an individual cannot have a feeling without being conscious and aware. Blood and Studdert (1988) define conscious as "capable of responding to sensory stimuli; awake: aware," a definition that refers to the lower threshold of what people might call conscious. The Oxford English Dictionary defines a feeling as "pleasurable or painful consciousness, emotional appreciation or sense." Others wish to elevate the terms conscious and aware to mean something more complex, in some cases defining them so that they are exclusively human qualities. Griffin (1981) says that "awareness involves the experiencing of interrelated mental images" and (1984) defines conscious as "aware of what one is doing or intending to do, having a purpose and intention in one's actions." It would seem likely that many feelings involve mental images, and hence are associated with being aware and conscious as defined by Griffin but we cannot know this for certain. Statements by others, on the other hand, as Rodd (1990, pp. 51–54) has pointed out, seem designed to specifically exclude feelings from consciousness. Gallup (1983) refers to consciousness as the demonstrable capacity to reflect about the self, specifically the ability to recognize oneself in mirrors, and Humphrey (1986, pp. 93–94) states that there is no consciousness in the development of a human baby until it recognizes itself in a mirror or makes guesses about other people's feelings. Dennett (1991) uses the term consciousness in a much wider and vaguer way but tends (pp. 171–226) ot equate the complexity of the individual's world with the existence of and necessity for consciousness. The definition of awareness that will be used here is: "awareness is a state in which complex brain analysis is used to process sensory stimuli or constructs based on memory." It is clear that there is a range of degrees of awareness (Sommerville and Broom, 1998), the highest of which might require a greater extent of intellectual processing than is needed for most feelings; but it is also clear that, according to the commoner meanings of the concept, feelings involve awareness. The term consciousness, however, is so widely used in the Blood and Studdert

sense (discussed earlier) that it would be simplest to limit its meaning to this and use awareness when referring to different degrees.

When the word "feelings" is used, some authors qualify it with "subjective." This usage seems redundant, as every feeling is necessarily limited to one individual or subject. The word subjective can also be confusing because it is sometimes used to refer to a conclusion that is based not on the observations, but on self-examination by the observer.

The various feelings are discussed later with reference to their possible evolutionary origins, but it is useful at this stage to consider the widely used categorization of feelings into pleasant and unpleasant. Unpleasant feelings are those that the individual concerned would avoid if possible, whereas efforts are generally made to experience pleasant feelings. Single unpleasant feelings or combinations of unpleasant feelings may sometimes be referred to as suffering. Dawkins (1990) stated that "suffering occurs when unpleasant subjective feelings are acute or continue for a long time because the animal is unable to carry out the actions that would normally reduce risks to life and reproduction in those circumstances." However, as Broom and Johnson (1993, p. 81) have pointed out, most people would include all but the milder, briefer kinds of pain and malaise within the term suffering and such problems do not necessarily involve inability to reduce risks to life and reproduction. Hence, a better definition might be "suffering is an unpleasant feeling, which is prolonged or severe." An individual in distress may well have unpleasant feelings, but could also be showing physiological consequences of adverse conditions without having such feelings. Hence "distress" is not listed as a feeling.

B. Evidence for Feelings

The existence of a feeling in an individual may result in a change in its physiology or behavior that can be recognized by other individuals, including a human scientist. If the change were unique to individuals with such a feeling, the possibility would arise for the existence of the feeling to be recognized whenever the change occurred. For example, persons who feel grief exhibit particular facial expressions and may produce tears. Individual actions are often not unique to particular feelings, but combinations of actions can be good indicators. However, we know that such expressions and tears can be faked, and although the observer might be quite efficient in ability to identify the signs of grief and to discriminate between fake and real signs, the achievable precision in the identification of grief will be no more than a high probability. A person can also use words to express aspects of his or her grief, but words are more easily faked than the behavior changes, and so are generally less reliable as indicators of feelings. Despite

the possibilities of deliberate deceit or other simulation, words and behavior observation can often provide evidence for reasonably confident recognition of feelings in other people. For most observers, the recognition of grief is initiated after personal experience of such a feeling and facilitated by previous experience of what was assumed, from observing context and consequences, to be grief in others.

Examples of other feelings that can substantially affect behavior are pain and guilt and those feelings easily related to particular needs. Some needs are associated with feelings and these feelings are likely to change when the need is satisfied (Broom, 1996). Examples of such feelings include hunger, eating pleasure, lust, and sexual pleasure. As needs are part of motivational state and motivational state alters the likelihood of occurrence of behaviors, the existence of needs can be deduced from the frequency and pattern of behavior (Fraser and Broom, 1990, pp. 31–38, 263–264). Hence, reasonable predictions about various feelings can be obtained from observations of behavior.

The major problem with the recognition of feelings from observations of behavior is that feelings may often exist without any behavioral or physiological change to indicate them. Abdominal pain can lead to particular postures and movements and leg pain can lead to limping (for other examples, see Fraser and Broom, pp. 296–304), but severe pain can exist without any detectable sign. In some cases an observer or experimenter can contrive situations so as to maximize the likelihood that a measurable behavioral or physiological change will indicate the existence and extent of a feeling. For example, suspected localized pain may be identified by palpation of the area and measurement of behavioral, heart rate, and adrenal cortex responses. Experimental studies of animal preferences may also be carried out in order to obtain some information about a feeling such as hunger, frustration, or an aspect of sensory pleasure. The existence of a strong preference for some resource or possibility to carry out a behavior gives some indirect information about what an animal is likely to be feeling, but may not discriminate between working hard because of the existence of a negative feeling and working hard in order to obtain a positive feeling. Some feelings are not easy to investigate experimentally in this way, for example, malaise or boredom, because, for different reasons, the feeling may affect the likelihood of carrying out the preference test.

Some information that can help in the recognition of feelings can be obtained from measurement of physiological changes including brain state. Heart rate and adrenal cortex activity changes, as already mentioned, and measurements of hormonal or neural activity changes may coincide with or precede changes in feelings. Brain scanning techniques can indicate sites and pathways in the brain where activity is occurring. Such activity in the

brain may be related to reports or behavior changes that give other evidence of the existence of feelings and hence may themselves come to be used as evidence for particular feelings.

The general conclusion about evidence for the existence and extent of feelings is that, even with sophisticated techniques, it is not possible to know exactly the feelings of any other individual, whatever the species, but reasonable predictions may be made using evidence, most reliably that from carefully studied behavior. The argument that no feelings can be recognized in others unless the individual can describe the feeling in words is wrong.

C. Are Feelings Functional or Just Epiphenomena?

1. Feelings in General

It is thought by some scientists that all feelings are merely trivial by-products of processes within the body. Skinner (1974, p. 17) said "what is felt or introspectively observed is not some non-physical world of consciousness, mind or mental life but the observer's own body. This does not mean . . . that what are felt or introspectively observed are the causes of behavior." Further, he said (1978, p. 124), "One feels various states and processes within one's body, but these are collateral products of one's genetic and personal history. No creative or initiating function is to be assigned to them." This view of feelings as solely an accident of individual development with no function or relevance to any other individuals is certainly not held by many people. As Dawkins (1993, p. 5) points out, the actions of people are much affected by a belief that these might cause pain, happiness, or sorrow in others.

Once it is accepted, as it is by most people, especially pet owners, that feelings exist in other individuals of our own and other species, the idea that they must have some function often follows. Y.-K. Ng (personal communication) says that consciousness is a major mechanism in individuals and hence it "must contribute to fitness to survive natural selection." Although adaptive characteristics will survive in populations because selection will favor their survival, if feelings were just an accidental, nonadaptive consequence of other adaptive mechanisms, would they persist in a population? Provided that a nonadaptive characteristic has some genetic component (as almost everything has) and some cost, it is likely that it would disappear from the population. Because various feelings have persisted, they are probably adaptive. The nature of any advantage to animals of having feelings is explored here in some detail, but first it is necessary to consider possible origins of feelings and the possibility that they are still accidental and nonfunctional.

An assumption outlined in Section I.A is that feelings involve brain activity additional to the minimum required for information processing, storage as memory, and motor output. During the early stages of development of systems such as those for recognizing and responding to predators or for recognizing and ingesting food, it seems very likely that there would have been some accidental activation of parts of the brain that were not essential for the neural function. Also, as the system became more efficient, it is likely that pathways that were at first necessary, perhaps to ensure effective communications between receptor and effector, became redundant but were not immediately eliminated from the functioning system. Both of these are examples of nonfunctional epiphenomena of the system, which might have the kinds of effects in the brain that became feelings. Some of these epiphenomena might continue to be nonfunctional but inevitable side effects of an essential system. Others might have had effects that eventually became functional, as discussed later in relation to the various feelings. It is also possible that there are feelings that were once functional in the ancestors of present-day animals but that now have little or no function. Finally, it is important to consider the extent to which feelings might sometimes be harmful (Broom and Johnson, 1993, p. 80), perhaps by making it more difficult for individuals to show the most appropriate responses.

The idea that pain has the function of preventing body damage has been espoused on many occasions, but the more general concept of all feelings being functional is relatively recent. Dawkins (1977) stated that "It is reasonable to assume that subjective feelings (like other characteristics) evolved because animals which possessed them were fitter than those which did not" and "feelings must be a product of natural selection. They are part of biology." In a much more extensive exposition, Cabanac (1979) said,

> We experience feelings of hunger because that is part of our mechanism for rectifying a food deficit and getting something to eat. We experience fear and pain because they are part of our body's way of removing us from situations that are life-threatening. Conscious experiences are there as survival aids.

A similar argument was presented by Wiepkema (1985) who asserted that feelings are involved in monitoring the effectiveness of regulatory actions, being positive when the regulation is successful and negative when it is not. A further statement that the evolutionary advantage of having feelings is considerable was made by Dawkins (1990), and Broom and Johnson (1993, p. 334) said,

> A final point about the evolution of adaptation to the vicissitudes of the physical and social environment is that a very important part of that evolution has been the develop-

ment of the complex appreciation of the interactions of an individual with the world in which it lives, which we call feelings. Complex brains, like those of vertebrates, have complex systems for regulating those interactions which are not just the product of automatic responses to stimuli. If an individual has a system of feelings which involves changes in its mental, and perhaps in its hormonal, functioning because a certain kind of body regulation or because an anticipated event has not occurred, such an individual will have increased fitness in comparison with a genetically different individual which has no such system.

Similarly, Y.-K. Ng (personal communication) argues that awareness contributes to fitness but is limited to species in which there is plasticity in brain and behavior, and that "affective feelings must have evolved fairly quickly after the evolution of awareness, if not concomitantly."

In order for feelings to confer an adaptive advantage it is essential that they should have an effect (Dawkins, 1993, p. 169): the exploration of such effects and how they might be recognized is a major part of this paper. The effect of the feelings might be "that the individual is more likely to carry out some adaptive action and hence more likely to survive" (Broom, 1996). The most likely way in which this would occur is that the feeling acts as a reinforcer, which makes it more likely that the individual will learn to carry out the adaptive action. Indeed "if the state of the individual in certain conditions is desirable from an evolutionary viewpoint, there should be a propensity for that individual to have good feelings. On the other hand, if a state is one which should be quickly altered, it should be associated with unpleasant feelings which prompt avoidance or some other action" (Broom, 1996). If a feeling does have an effect such that it can act as a reinforcer to promote adaptive behavior, the effect might be coincident with the occurrence of the feeling, or it could be that the feeling is remembered so that its beneficial effect occurs long after the feeling itself has finished. Such effects would be difficult to distinguish from the effects of other events in the life of the individual and hence to attribute to the feeling.

The general argument that consciousness in general and feelings in particular make a difference in the way in which organisms possessing it function is presented with some force by Dawkins (1993, pp. 9, 143, 167–181). One straightforward but strong argument is that most people report that many of the feelings listed in Table I can have a considerable effect on the way in which they organize their lives. Observation of human behavior supports this. Proposals about the effects and functions of consciousness have suggested that it allows more effective analysis of the environmental and prediction of the future (Crook, 1980, p. 31) or that it improves the efficiency of information processing in general (Weiskrantz, 1987). Dawkins (1993) suggests that "Consciousness might . . . make actions more decisive or give better anticipation of the future" and "have an evolutionary effect

and an effect which we could detect." Dawkins does not claim that every action will be more efficient if the individual carries it out consciously, and refers to the observation by Baars (1988) that certain actions progress more efficiently if the individual is not actively thinking about what is being done. However, this argument about the function of consciousness in the sense used by those authors is more relevant to the control of actions than to areas where feeling plays an important role.

2. *Pain*

Although the word pain is used colloquially to refer to a wide range of unpleasant experiences, its scientific and medical meaning is limited to refer to a sensation, that is, to the immediate consequences of a particular sensory input. The sensation elicits immediate avoidance or subsequent modification of behavior whose effect is to reduce the likelihood of recurrence of the sensation. Hence, a definition of pain is "A sensation which, without involving higher level brain processing, such as that associated with fear, is very aversive" (Broom and Johnson, 1993, p. 27). Pain usually involves specialized nociceptive receptor cells and some degree of injury. Even in the case of phantom limb pain, the specialized nociceptive neural pathways are involved. Pain normally elicits protective reactions, causes emotional responses, and results in learned avoidance behavior.

The pain system includes: specialized receptor cells, nerves in which evoked electrical responses to mechanical or thermal damage can be detected, neural pathways involving characteristic transmitters such as substance P, brain mechanisms, which include endogenous analgesic opioids, and the propensity to initiate avoidance behavior. This system is present in all vertebrates that have been studied, including fish, and most aspects of it are also present in some invertebrates, for example, cephalopod molluscs. As mentioned already, all pain is regarded as being a feeling and if there is activity in the nociceptive system with no feeling, perhaps because of naturally occurring opioid-induced inhibition or the use of an externally applied analgesic, then it is not pain. We cannot know whether pain in another individual is the same as that which we feel ourselves, but observation of behavior in all species with complex nociceptive systems suggests that there is likely to be much similarity among the different kinds of animals in the feeling of pain.

The importance of feeling pain in promoting individual survival is considerable (Melzack, 1973). When pain is felt, the individual can take action to minimize tissue damage being caused, and the greater the feeling of pain, the faster the initial action is likely to be. Once pain has been felt in a recognizable situation, the possibility of learning to avoid any future pain, and hence damage, of the same kind is increased. Again, more intense

pain is likely to have a greater effect. After physical trauma, or during a pathological condition, recovery will often be facilitated by modification of behavior so as to avoid further damage to the affected parts of the body (Wall, 1979). Chronic pain can therefore be functional in that it increases the chances that activity level and type will be modified in an adaptive way. Hence, as explained by Broom and Johnson (1993, p. 29), to suppress pain would in many situations be disastrous.

The existence of a feeling of pain in an individual may not be obvious and it seems very likely that in various species extreme pain can occur without any recognizable modification of behavior (Morton and Griffiths, 1985). Indeed, as pointed out by Fraser and Broom (1990 pp. 269–273), pain is not necessary unless some action has to be taken, and animals of different species will vary in the kind of behavioral response to pain that is most adaptive. For example, vocalization when in pain may be advantageous for a young animal or a social animal that might be helped by its mother or by members of its own social group, but disadvantageous when a dangerous predator is close and no effective help from any other individual is likely. Hence, it is not surprising that young pigs, dogs, and humans, which could be helped, make a lot of noise when in pain, but young sheep, which are less likely to be helped against most predators, do not. Indeed, the sheep response to tissue damage is considerable in terms of physiological change (Shutt *et al.*, 1987) and subsequent avoidance of the situation where the damage occurred (Rushen, 1990), so it is extremely likely that they are feeling pain, but they show little behavioral response at the time of the damage.

Although it is often possible to hypothesize that in many situations pain has a function that would result in natural selection favoring genotypes in which the individuals were able to feel pain, in other situations it is not easy to ascribe any function to the pain. Bateson (1991) refers to the extreme pain associated with a kidney stone stuck in a ureter and other forms of extreme pain that result in the individual writhing in agony. The writhing could conceivably have a function, but this seems unlikely when recovery from surgery seems to be facilitated by analgesia. Perhaps the various gradations of the lower levels of pain are adaptive but some extreme pain is an inevitable but nonfunctional consequence of the system. The possibility that extreme pain interferes with various aspects of normal functioning, and hence potentially impairs the efficacy of adaptive responses, is often quoted as a reason why endogenous opioid analgesic mechanisms evolved. An individual might be in such pain that it could not show an escape response unless the analgesic opioid inhibited or ameliorated the pain.

Another critique of the idea that pain is adaptive is that it should not be necessary for there to be such an elaborate within-individual communication system when all of the cells of the body have the same genotype and hence do not need any more than a very simple message. However, there are other elaborate communications systems within the body and a fast, effective system of messages about actual or potential body damage is important.

The conclusion of these arguments about the function of pain is that many forms of pain are important for survival but some are likely to be accidental and nonfunctional. Functional pain seems to occur in all vertebrates that have been studied and in some invertebrates. Nonfunctional pain probably also occurs in all animals. There is no reason why there should be any differences between humans and other vertebrates in the proportions of functional and nonfunctional pain.

3. *Malaise*

Malaise is a feeling of illness or discomfort associated with some pathology or inadequacy of bodily function. It is more general in its effects than pain, which is localized in a particular part of the body. There could be wide-ranging effects on the body when there is a reduction in the availability of energy providing resources because these are being used to fight pathogens. Similarly, an accumulation of toxins could have consequences in various parts of the body. In both of these examples, the effects on the brain, perhaps mediated via the peripheral nervous system, could lead to the feeling of malaise. The exact details of the feeling are likely to vary according to the kinds of effects of the toxin or pathogen, but a general feeling of lethargy is common to malaise with various causes.

Most people think of malaise, or of feeling ill, as an unfortunate by-product of infection, but it often affects behavior as well as physiology and its major effect may well be adaptive. Although some effects of parasites or pathogens on host behavior are induced by the parasite or pathogen for its own benefit, many of such effects help the host. As Hart (1988, 1990) points out, animals that are sick are often depressed, lethargic, show no interest in eating, and fail to exhibit body care, but such behaviors "appear to comprise an adaptive behavioral mode that facilitates recovery from illness." When the immunological and other defenses of the body are having to work hard and consume a lot of energy, it is advantageous for the individual to rest and to be able to concentrate available energy on fighting the cause of the malaise. Even high fever would be adaptive if the net benefit from killing pathogens and suppressing activity outweighed the net cost of tissue damage (Kluger, 1979; Ewald, 1980, 1983; Hart, 1988). The

general feeling of malaise can be thought of as part of the means by which active defense against pathogens, with its multitude of consequences including increased levels of interleukin 1, can act so that behavior is adaptively modified.

There may also be specific aspects of malaise that are adaptive. For example, disorders of the gut may be remedied fastest if no further food is taken in; therefore, a feeling of nausea is advantageous in this circumstance. Too much consumption of a poison, such as alcohol, may overload liver resources and hence also lead to nausea and reduction in further intake of food or poison. Infection or poison-induced nausea is likely to be adaptive, but some nausea, like that induced by certain forms of motion, might be accidental. The nausea, vomiting, and food aversion that occurs in early human pregnancy could be a mechanism for minimizing the risk that toxins from various normally edible foods might adversely affect the developing fetus (Profet, 1992). These feelings are also likely to suppress activity in the mother and could be a consequence of a risk of mechanical damage to the fetus.

4. Tiredness

Muscular fatigue is a sometimes unwanted consequence of muscular activity, but it may have neural effects that are felt as tiredness. Other forms of exertion and prolonged periods of being awake rather than asleep can also lead to a feeling of tiredness. As sleep tends to occur with a fairly regular rhythm, tiredness could sometimes indicate that the normal time for sleeping has arrived rather than that the individual has been involved in much exertion. Tiredness as an indicator of high levels of exertion can be an adaptive feeling in that it tends to prevent levels of exertion that might be damaging. Tiredness as a prompter of sleeping can be adaptive, just as sleep can, in that it ensures that the individual is inactive and inconspicuous at a time of day when accidents are more likely and predators abound. There may also be some recuperative function.

5. Hunger

The feeling of hunger is generally associated with emptiness at some level in the gut, or low levels of nutrients within some organ of the body, or with input from an internal clock that indicates that the time of day when some food intake normally occurs has arrived (Grossman, 1973). As with other feelings, hunger varies from slight to very severe. The stronger the feeling, the more likely it is that the motivational state will be greatly influenced by causal factors relating to hunger. Hunger is generally rather unspecific, but there can be specific hungers that are satisfied only by the consumption of a particular nutrient. Although individuals can overeat and

can select the wrong nutrients, in most circumstances the feeling of hunger would seem to be adaptive.

6. Thirst

The sensory inputs that lead to feeling thirst come from body fluid concentration monitors, including those in the mouth (Toates, 1986). Thirst varies from a minor feeling, which has little effect on behavior, to an all-pervading feeling, which dominates all behavior in that the individual devotes all possible resources to finding water while conserving it. In most circumstances, the feeling of thirst would seem to be adaptive, although it is possible that some very thirsty individuals behave in a rash way in order to obtain water.

7. Thermal Discomfort

The physiological responses to, and consequences of, exposure to very high or very low temperatures have been described in detail (Milner, 1970). The feeling of discomfort when too hot or too cold results in changes in behavior of various kinds (Broom, 1981, pp. 108–113). Most of the consequences of the feelings that have been described have the effect of increasing survival chances.

8. Fear

Fear is a feeling that occurs when there is perceived to be actual danger or a high risk of danger. Although a fast looming visual stimulus, a sudden sound, or an acrid smell might elicit a startle response, the feeling of fear depends on some more complex analysis in which current sensory input is compared with memories of previously experienced events. Blood and Studdert (1988) define fear as "a normal emotional response to consciously recognized external sources of danger." Hence, the recognition precedes the feeling rather than being a part of it.

There are two very different kinds of response to fear (Broom, 1981, pp. 162–175). One is to actively escape or defend, while the other is to rapidly and substantially reduce behavioral and physiological activity so as to render the individual inconspicuous to an attacker. The propensity of predators to notice fleeing prey and ignore immobile objects is utilized in this response. The physiological changes associated with feeling fear are also of two kinds (Broom and Johnson, 1993, pp. 92–107). If active responses are a possibility, first the adrenal medulla response and then the adrenal cortex response prepare the individual for precipitant activity. If suppression of movement is important, then bradycardia, which tends to suppress movement, occurs. In many cases, however, either the active or the passive kind of response could be shown and animals may show first one and then the other. For

example, when a young domestic chick is startled, it usually freezes for a while and then shows escape activity, the proportions of each response depending on the conditions and the previous experience of the bird (Broom, 1969a,b).

The freezing response can be very effective as a means to survive predator attack, but it would be extremely inappropriate as a response to the immediate risk of a large quantity of rocks falling onto the individual. Hence, the efficiency of analysis of the situation and appropriate selection of response is of great importance. If a predator was detected that would not be deceived by a freezing response but that could be outrun, then it would again be important to choose the response correctly.

The response to feeling fear could also be maladaptive if carried to an extreme. For example, an extreme form of the freezing response is catalepsy. This can be an adaptive response to the presence of a predator but if it leads to hypovolemic shock, the individual can be damaged by the response itself. Shock reactions are on the borderline between the life saving and the clearly disadvantageous, being the former when predator attack is a major factor in the life of the individual, but being the latter if predation risk is insignificant.

9. *Anxiety*

Anxiety is "a feeling of uneasiness, apprehension or dread" (Blood and Studdert, 1988). It depends on an ability to predict future risk, usually based on recent stimuli and always on previous experience. The horse that is reluctant to pass a gateway where it once had a frightening experience is showing the characteristic signs of an individual feeling anxiety. Whenever information about disturbing events is stored, there must be a potential that there will be recall of this information and consequences of the recall that activate emotional systems in the individual. The recall can occur at an entirely cerebral level, that is, with no current stimulus involved, but with consequences of the feeling that may be physiological as well as conceptual. The feelings of anxiety probably potentiate the response to the risk. In some cases, showing an appropriately high level of response to a risk can be life saving, while in other cases anxiety can be damaging to the individual (Nesse and Williams, 1995). A genotype that promoted the ability to explore previous experiences in the brain and to feel anxiety when high levels of risk were deduced would be strongly favored in natural selection, given the very considerable advantages of anxiety in some circumstances. The disadvantages of unnecessary anxiety would not be sufficient to counterbalance the advantages of having the feeling. It could be that anxiety was much more important to our ancestors than to present-day humans so that many individuals, and some in particular, feel much anxiety that confers

no benefit to them. Indeed, the propensity to feel much anxiety might be expected to be greater in females because of the difficulties of maternal care when offspring are young and very vulnerable. The anxiety is of such importance at that time that its selective advantage then outweighs any disadvantages associated with its persistence throughout life during times when it is unnecessary or harmful to the individual. Anxiety may indeed be greater at times of parental responsiblity but may be difficult to switch off at other phases in life.

10. Grief

Grief and sorrow are unpleasant feelings associated with unwanted life events, particularly those connected with social relationships. Grief is a stronger version of sorrow. For the most part they are private feelings with no effect on others, although their outward manifestations may have an effect of maintaining social position, preserving good relationships, or informing others, honestly or dishonestly, of the properness of the individual's feelings. When a significant unpleasant event occurs during life, for example, an important failure to succeed in some endeavor, or the loss of a social relationship, increased brain processing might occur. However, that increase in brain processing and activation of emotional centers that result in grief could then increase even more by positive feedback in a way that may help the individual to respond adequately to the event, both immediately and in terms of later learning. Hence, the grief could be functional in that, by amplifying the effects of the event, it ensures that something of importance is not processed too rapidly and then stored without sufficient likelihood of affecting future decision making.

Grief is only one example of a feeling as an amplifier of the significance of important life events. Simple brain processing of perceived events may not allow sufficient allocation of attentional and analytical resources to those events that demand more consideration if the individual is to survive and reproduce effectively. However, mechanisms whose general effect is amplification can operate too strongly in a particular instance or may frequently exaggerate the significance of real situations in certain individuals. Grief, like other feelings, seems to have adaptive advantages on some occasions but not on others. The most obvious situation in which grief is felt by humans is when a relative or close friend departs or dies, a circumstance in which the amplifying effect of grief helps in the evaluation of the importance of relationships. There are many reports of pets, especially dogs, and monkeys (de Waal, 1996, pp. 54–56) showing the same sort of behavior that humans show in such circumstances. This behavior is sometimes described as mourning and has also been described in horses, pigs, and elephants. As the arguments for the selective advantages of grief would

apply to other species, especially those that have a long-lasting and elaborate social structure, it would seem likely that, as de Waal proposes, some degree of grief occurs in other species.

11. Frustration

The existence of elaborate motivational mechanisms in a wide variety of animals has already been mentioned. Whenever a well-organized decision-making process exists, the individuals will sometimes be unable to do what they most want to do. Broom (1985) said that an animal is frustrated "if the levels of most of the causal factors which promote a behavior are high enough for the occurrence of the behavior to be very likely but, because of the absence of a key stimulus or the presence of some physical or social barrier, the behavior cannot occur." The feeling of frustration could originally have arisen as an accident because of some alternative channeling of output from the decision-making system. This feeling could be damaging to the individual in that it might tend to make it carry out behavior such as self-mutilation or to activate physiological systems that either use up energy or promote pathological effects. Alternatively, the feeling of frustration could lead to behavioral and physiological changes that help the individual to cope with the frustrating situation. Some behavior changes resulting from frustration, such as stereotypies, might be adaptive in some situations but harmful in others (Mason, 1991; Broom and Johnson, 1993, pp. 139–141).

Frustration is likely to be an important feeling in most complex animals. Because there will have been strong selection for systems that allocate resources effectively (Broom, 1981, pp. 79–96), as Houston (1997) points out, animals will be strongly motivated to perform certain important activities, and suffering is likely if they are prevented from performing them. The feeling of frustration, which at a high level might be referred to as suffering, is therefore likely to occur in a wide range of animals.

12. Guilt

The feeling of individuals who have behaved in a way that they or their social group members would normally condemn or punish is referred to as guilt. People report that they feel guilt in a variety of situations. It is clear that the brain processing underlying the feeling must often involve sophisticated analysis of actions in relation to experience of the consequences of such actions for the individual carrying them out and for others. This brain activity could easily have been the origin of certain wide-ranging effects that are now grouped together as the feeling of guilt.

The consequences of feeling guilt are often changes in behavior described in some detail for dogs and primates by de Waal (1996). One of the human

responses is blushing, dogs may hang their heads, and monkeys may behave in an unusually submissive way and show "grin" expressions on their faces. The feeling of guilt could be advantageous to the individual in that it forces attention channels and processing capacity to be allocated to consideration of a situation of importance in relation to future decision making. However, behavior generally associated with guilt is shown much more often in social situations than by individuals that are by themselves. The information conveyed to others in the social group could be of value to them and might therefore increase the spread of a gene promoting the feeling and expression of guilt because of close relatedness or the potential for reciprocal altruism. However, the guilt expressor might also derive a direct social advantage in that he or she would be perceived as continuing to be an honest and constructive member of the group. Perhaps without the expressions of guilt he or she would be expelled from the group. Another way of putting this is that the blushing, or other behavioral manifestation of guilt, is an honest signal. Blushing can also be a contrived signal with the intent of making the blushing individual more sexually attractive to the observer.

13. Depression

Depression is a clinical condition associated with certain neurological disorders and with extreme malaise, fear, anxiety, grief, or frustration. It can be described as a feeling separate from all of these, as it is reported by people as being different. Depressed people describe how nothing matters to them and most of their normal activities are reduced or absent. These behavioral signs can exist in individuals of other species, at least in mammals and birds. An experimentally induced parallel is the "learned helplessness" described in laboratory animals by Seligman (1975).

Some of the possible advantages of feeling depressed have already been described as extreme forms of fear, grief, and so on. In social situations in which the individual is performing very badly, behavior and physiology indicative of depression may occur. Extreme examples are the tree shrews and rodents that have been defeated in fights with rival conspecifics but that remain caged with them (Koolhaas *et al.*, 1983; von Holst, 1986). These individuals show very depressed behavior and often die quickly. However, passive responses in such a situation, and perhaps the feeling of depression itself, may be an effective strategy for avoiding future attack (Mendl *et al.*, 1992). Even the tree shrews might benefit from such behavior if they had the opportunity to escape completely from the rival. Similarly, some human depression could be specific to perceived failure in a specific situation, such as inability to compete adequately in a particular segment of society, and could reduce the chances of attack by dominant individuals (Nesse and Williams, 1995). Depression, linked with the possibility to move to a differ-

ent segment of society in which coping is easier, could be an effective response. The depressed period could also allow time to work out a better life strategy. However, it would appear that in some cases, feeling depressed is maladaptive, perhaps because there is no viable alternative lifestyle.

14. Boredom

Boredom is a feeling associated with a lack of novel input, perhaps with a lack of input in total. Its occurrence in various animals has been discussed by Wemelsfelder (1993). She refers to animals in impoverished conditions increasingly directing their behavior toward inadequate stimuli, exaggerating normal behavior, and establishing stereotypies. A threshold in the increasing series, which she defines as boredom, is "that state of behavioral fixation in which the animal's orientation towards a novel stimulus loses its inquisitive and manipulative character."

The feeling of boredom may arise because of severe sensory deprivation or because those potentially interesting stimuli that are detectable are repeated exactly. In the first case, the individual might be in a plain, empty cage; in the second case, there might be a machine present that continually undergoes the same movements with the same periodicity. In either case a sequence of behavior whose function is to carry out useful exploration is continued until lack of useful consequences tend to result in its inhibition. At the same time, or even in the absence of the attempts at exploration, a feeling of boredom arises and increases, sometimes associated with the abnormalities of behavior described here.

It may be that brain function can be impaired when there is too little input, or too little new input, for a prolonged period. Studies of sensory deprivation suggest that this is so. It may be that the existence of the feeling of boredom, with its concomitant behavior abnormalities, provides sufficient neural activity to maintain the brain in a low input situation. Boredom that continues to the point where inadequate input results in greater and greater risk of neural system damage may have stronger and stronger effects on the individual, which, although more and more unpleasant, are more likely to prevent the damage.

15. Loneliness

In social animals, social contact is often important for survival of the individual as well as for reproduction. Hence, it is not surprising that a specific feeling can occur when inadequate social contact occurs. In our human ancestors, predator avoidance, food finding, and control of the physical environment were all very much facilitated by, or perhaps possible only in, a group-living situation. Hence, an individual separated from all

conspecifics might feel lonely and make all efforts to restore adequate social contact.

16. General Suffering

All of the negative feelings mentioned so far could constitute suffering if extreme enough. Combinations of feelings might also be referred to as suffering. Individuals with a range of negative feelings might be able to respond by moving to a new living place, so suffering could lead to adaptive responses. In most cases, however, the most extreme forms of suffering will not have beneficial effects. The various forms of suffering may well be adaptive when moderate but neutral or harmful in relation to fitness when severe. The form of suffering that occurs when there is real or perceived failure to cope with the environment is sometimes called despair, which in its extreme form will probably not help the individual to survive. However, a genotype that promoted the existence of such feelings, and their consequent behavioral manifestations, might spread because close relatives observing the behavior might respond in a way that preserved their lives.

17. Jealousy

Jealousy is a feeling that occurs in social situations when another individual is perceived to have achieved something that the subject would like to have achieved. The term envy may be used when possession of an object or a position, rather than a social relationship, has been obtained. In both of these cases there may be an element of frustration. Some of the most extreme examples of jealousy are those feelings of male humans when they perceive that the female whom they regard as their mate is courted by or attracted to another male. A large proportion of murders of women arise from male jealously and they refer to the relative uncertainty about paternity as compared with the certainty about maternity (Nesse and Williams, 1995). Hence, it would seen that the feeling of jealousy can be adaptive in that it reduces the chances that males will lose their mates or invest resources in offspring that are not their own. The biological situation can exist in various species in addition to humans; therefore, the feeling may also exist in them. On some occasions, jealousy may involve a complex analysis of what might have been achieved as compared with what has been achieved. Such comparison can be useful to the individual and the feeling of jealousy may draw attention to the situation in such a way that future performance is improved. Excessive feelings of jealously or envy can be damaging.

18. Lust

There are times when eagerness to behave in a certain way or to obtain a certain objective is so great that a generally pervading feeling of lust

exists in the individual. A clear-cut example of this is the lust of a male mammal to mate with a female. The sequence of events following exposure to an actually or apparently receptive female is an increase in plasma testosterone, which results in approach and display and, by means of a positive feedback loop, more testosterone production, more approach and display, and so on. The feeling of the individual is an increasing lust for mating with that female. Other resources can elicit lust to various degrees.

The biological value of this feeling of lust is to increase the chances that the objective, for example, successful mating, will be achieved. A hazard of lust is that antisocial or directly damaging results may occur.

19. Anger

Anger is a feeling of intense displeasure in situations in which the individual is not able to control events adequately. The lack of control may be because of the actions of other individuals, or changes in the physical world, or inadequacies in the abilities of the individual who becomes angry. The feeling of anger includes emotional components and may involve aggressive and violent behavior. Anger may be preceded by other feelings, especially frustration or pain but also fear, anxiety, grief, or lust.

An individual who is angry can sometimes achieve objectives that would not otherwise be achieved. Some of these objectives are of considerable importance in terms of individual survival or of reproduction. On other occasions, however, anger can have damaging effects on the individual. However, as these damaging effects may be relatively slight, even if anger results in fitness increment only occasionally, those genotypes that facilitate expression of the feeling could spread in the population. The effects of anger are often more extreme where substantial increases in plasma testosterone can occur, that is, in males. The ideal balance, in terms of fitness, between ready anger and retention of individual control over social relationships and other environmental variables will vary according to the effectiveness of the anger in achieving objectives and the kind of environment in which the individuals live. Highly organized societies with much reciprocal altruism leave less room for anger.

20. Sexual Pleasure

The feeling at orgasm is much more wide-ranging in its effects than might be expected from the localized nature of the receptors involved. There can be little doubt that genotypes that led to expression of substantial sexual pleasure survived better in the population than those that led to little sexual pleasure because their bearers would have made more efforts to achieve mating. Indeed, it would be predicted that sexual pleasure would be one of the most substantial forms of pleasure because otherwise individuals would not make effective mating a sufficiently high priority objective. This

argument seems to be widely accepted in relation to males. However, Baker and Bellis (1995) seem reluctant to use the same argument for females, as they present (p. 49) two "hypotheses concerning the functioning of the female copulatory orgasm," which are (1) that it increases the chances that the female will lie down after copulation in order to reduce sperm loss, and (2) that the orgasmic movements tend to suck up sperm during copulation. Hypothesis (1) receives little support from Baker and Bellis, but the more important adaptive advantage of sexual pleasure in general and the orgasm component in particular must surely be to increase the likelihood that copulation will be repeated.

All species would be expected to have some feeling of sexual pleasure, but in those species in which mating would reduce fitness in certain seasons, this feeling might be restricted to the appropriate periods during the year. Some difference in the mechanism that leads to sexual pleasure would also be expected according to whether the ideal was one single mating or multiple matings. A further possible advantage of sexual pleasure that would be more likely to occur in species in which multiple matings and shared parental care occur is that the feeling might serve to encourage bonding between the partners.

21. *Eating Pleasure*

When animals eat, a variety of sensory systems are in operation, and it is not surprising that a generalized feeling of pleasure resulting from the procedure of eating and the taste sensations has arisen. Anticipation of the pleasure of eating would result in one of the causal factors promoting eating. Hence, this feeling would tend to make individuals work harder for food than they would if there was no such pleasure. As some of the pleasure is likely to emanate from sensations obtained during feeding on appropriate foods, the feeling would also have the function of encouraging the individual to eat appropriate rather than inappropriate foods. Some eating pleasure occurs when specific foods that are damaging to the individual are consumed or when overeating occurs, so the effects of this feeling are not always adaptive.

It would seem likely that most species with complex nervous systems have some eating pleasure. The particular actions or substances that elicit this pleasure will vary from species to species. However, Cabanac (1979) described how the relative proportions of different strengths of sugar solutions drunk by rats and humans were very similar. Hence, it would appear that this aspect of eating pleasure is similar in rats and humans.

22. *Exhilaration*

Pleasure is often reported by people as being felt when they walk in the countryside, take various forms of exercise, reach a mountaintop, or stand

by the sea or on a boat. Some of this feeling may be associated with inhaling a high oxygen concentration or a certain small quantity of ozone. Other aspects may reflect a high level of control over muscular activity. Yet another aspect of the feeling may indicate an action of endogenous opioids in the brain. Each of these is likely to be promoting the fitness of the individual; therefore, a feeling that increases the chances of such effects is of value to the animal.

23. Other Sensory Pleasure

A wide variety of events in life can have effects that are detectable by sense organs and that result in pleasant feelings. Particular odors, sounds, sights, or mechanoreceptor inputs can evoke pleasure. In some cases these events are brief, or are subtle and difficult to appreciate. The feeling of pleasure can be an indicator of good sensory and brain function and thus help with the monitoring of body functioning. Other sensations are associated with important life events, so their occurrence should be promoted. Just as with eating pleasure, some of the events may not be beneficial for that individual at that time; not all of such feelings are adaptive.

24. Achievement Pleasure

A variety of intellectual tasks, as well as some that combine physical effort and much brain activity, can result in feelings of pleasure. The feeling could have been a by-product of the processing of information originally but its continuation would have been promoted if the feeling itself conferred an advantage on the individuals. Perhaps the pleasure resulting from effective high-level brain processing helps to make energy available for brain functioning or changes the biochemical or electrical characteristics of a region of the brain so that further efficient brain functioning can occur. In the competitive and difficult social world in which many animals live, those animals that process information in the brain efficiently are at a considerable advantage over those that do not; feelings that promote this should become widespread.

25. General Happiness

Intense pleasure of any kind can lead to people declaring themselves to be happy. If several different kinds of pleasure are combined, this is more likely. However, most people who are asked to say what happiness is will refer to the absence of problems as an important part of happiness. When Cabanac (1979) refers to a widespread control of behavior through pleasure seeking, a major part of this must be the diminution of any bad feelings. It is difficult to identify a general feeling of happiness, but the seeking of this feeling is clearly a major factor in the life of complex animals.

D. Feelings as Part of Coping Systems

Animals have a wide range of systems for trying to cope with their environments. These coping systems include positive and negative aspects: useful actions should be carried out and resources obtained but damaging events should be avoided. Coping is having control of mental and bodily stability (Fraser and Broom, 1990). Coping and control systems are described at length by Broom and Johnson (1993, Chapters 2 and 3). A substantial part of physiology and behavior plays a role in attempts to cope with the environment. This varies from straightforward, low-energy homeostatic mechanisms to high-urgency emergency responses. The general idea that feelings often have a function and help individuals to cope with their environment has been advanced (see Section C.*1*), especially by Dawkins (1990, 1993), Broom and Johnson (1993), and Broom (1996). The central thrust of the arguments is that all feelings can be functional to a greater or lesser extent. Feelings are a part of the biology of the individual that has evolved. They are used in order to maximize its fitness, often by helping it to cope with its environment.

The coping systems used by animals operate on different time scales. Some must operate during a few seconds in order to be effectual, others take hours or months. Optimal decision making depends not only on an evaluation of energetic costs and benefits but on the urgency of action: in other words, the costs associated with injury, death, or failure to find a mate (Broom, 1981, p. 80). In the fastest acting, urgent coping responses, such as avoidance of predator attack or risk of immediate injury, fear and pain play an important role. In longer time scale coping procedures, where various risks to the fitness of the individual are involved, feelings rather than just intellectual calculations are among the causal factors affecting what decisions are taken. In attempts to deal with long-term problems that may harm the individual, aspects of suffering contribute significantly to how the individual tries to cope. In the organisation of behavior so as to achieve important objectives, pleasurable feelings and the expectation that these will occur have a substantial influence. The general hypothesis advanced is that whenever a situation exists in which decisions are made that have a big effect on the survival or potential reproductive output of the individual, it is likely that feelings will be involved. This argument applies to all animals with complex nervous systems, such as vertebrates and cephalopods, and not just to humans. Feelings are not a minor influence on coping systems, they are an important part of them.

In circumstances in which individuals are starting to lose control and fail to cope, feelings may exist. These feelings might have a role in damage limitation, which is functional. However, they might also occur when the

individual is not coping at all, and hence the feelings have no survival function. Extreme suffering or despair are probably not adaptive feelings, but an observer of the same species might benefit, and a scientist might use indications of such feelings to deduce that the animal is not coping.

II. Welfare, Stress, and Feelings

A. Defining Welfare, Stress, and Health: The Relevance of Feelings

1. Welfare

Welfare is a term restricted to animals, including humans, and hence not used for other organisms or inanimate objects. It is used in science and in legislation and therefore must have a meaning precise enough for such use. Welfare refers to a characteristic of an individual rather than to something given to it, it must be measurable in a scientific way, and it must vary over a scale from very good to very poor (Curtis, 1986; Duncan, 1987; Broom, 1988, 1991, 1996; Broom and Johnson, 1993, pp. 74–76). The original use of the word welfare, meaning how well an individual fares or goes through life, is followed in the definition proposed by Broom (1986): the welfare of an individual is its state as regards its attempts to cope with its environment. Its state includes how well or how badly it is coping and how much difficulty it is having in coping. As emphasized by Broom (1991, 1996) and Broom and Johnson (1993, pp. 80–82) the feelings of the individual are an important part of that state. The assessment of how good or how poor the welfare is depends on a wide range of measures of behavior, physiology, brain functioning, immune system functioning, pathology, injury, and life expectancy.

This definition of welfare was not found satisfactory by Duncan (1993, 1996), who considered that it understated the importance of feelings. Indeed, this was a valid criticism of the original paper (Broom, 1986), which did not refer to feelings. An aim of the present chapter is to explain, first, that feelings are important biologically, second, that they are very significant contributors to coping systems, and hence third, that they are encompassed properly in this definition of welfare. The key point, which has been made in Section I, is that feelings have extremely important biological functions, especially in coping systems. A further point is that although feelings are part of coping systems, they do not make up all of them, so if the concept of welfare is to be usable it must refer to all aspects of coping systems and not just to feelings (Broom, 1993). The separation of feelings from all other

aspects of coping systems in biologically unsound and impractical when welfare assessment is attempted.

2. *Stress*

Two other important terms in relation to welfare are stress and health. As argued in detail by Broom and Johnson (1993, pp. 57–73), the term stress should be limited to refer to something that is bad for the individual. It should not be used to mean any kind of disturbance of homeostasis, and should not be merely equated with adrenal responses. The use of stress to refer to environmental impacts on the individual, whatever their consequences, and hence the idea that stress can be good for an individual is confusing and renders the term virtually useless. Similarly, the fact that adrenal cortex activity can occur during beneficial activities such as mating and prey catching and may not occur during hemorrhage, dehydration, or harmful increases in body temperature means that such activity cannot be used in defining stress. A measure of what constitutes adverse or harmful effects is needed in the definition of stress, and hence, following earlier versions of the definition by Broom (1983) and Fraser and Broom (1990), Broom and Johnson (1993, p. 72) conclude that: "stress is an environmental effect on an individual which overtaxes its control systems and reduces its fitness or appears likely to do so." The "environment" here is that which is outside the brain. Hence, when an individual attempts to cope with its environment but fails to do so, welfare will be poor and stress will occur.

The failure to cope would usually be associated with one or more of the unpleasant feelings previously described and, although many aspects of stress are psychological, stress is not itself a feeling. It is possible for stress to occur without any associated feelings. An individual knocked unconscious and otherwise injured so that, despite the operation of various coping systems, death occurs without consciousness being regained is stressed but does not suffer. The relationship between stress and welfare is straightforward. Welfare refers to a wide range of states from very good to very poor, but the welfare of any stressed individual is poor. However, there can be poor welfare without stress when the individual is coping but only with considerable difficulty. For example, on some occasions when a person is succeeding in coping with a minor injury, he or she may be in some pain and may show some physiological and behavioral responses; the welfare is poor, but there is no likelihood of any reduction of fitness and therefore no stress.

3. *Health*

The word "health," like "welfare," can be qualified by "good" or "poor" and varies over a range. However, health refers to the state of body systems,

including those in the brain, which combat pathogens, tissue damage, or physiological disorder. Welfare is a broader term covering all aspects of coping with the environment and taking account of a wider range of feelings and other coping mechanisms than those that affect health, especially at the positive end of the scale. Although people regularly refer to poor health, they sometimes use the word to mean absence of illness or injury in the same way that people refer to welfare when they mean good welfare. However, the precise and scientific use of health and welfare must refer to states varying from very good to very poor. "Health" is encompassed within the term "welfare," and indeed is a very important part of welfare.

B. Assessing Welfare, Stress, and Feelings

1. What To Measure?

The assessment of welfare is discussed at length by Dantzer and Mormède (1979), Smidt (1983), and Broom and Johnson (1993), and is not described in detail here. As Mason and Mendl (1993) and Fraser (1995) have pointed out, no single, all-embracing measure of welfare is available, and indeed, all of the authors mentioned above refer to the necessity to use a range of measurements in studies where welfare following different short-term or long-term treatments is assessed. It is occasionally possible to recognize very poor welfare in a set of individuals using a single measurement, for example, when all of the animals show early death or severe abnormalities of behavior, physiology, or immune system function. However, the range of methods used to try and cope, the range of effects of adversity, and the range of feelings that should be considered means that good studies should use an array of measures. Fraser (1995) describes welfare as a "type 3 concept," like "safety," which has multiple attributes so that the results of different kinds of assessment must be weighed one against the other. However, in comparing the welfare of animals in two conditions, each scientific measurement and its interpretation must be objective and unaffected by prejudice about which condition is better. Occasionally the data available may not allow a conclusion to be reached, but eventually the scientific approach will provide data that give information about how good or how poor the welfare is in each case. Once this has been done, a moral judgment about what is acceptable and what is not can be made (Broom, 1996).

Part of the assessment of welfare will involve the various indicators of stress, that is, reduced fitness or potential reduction of fitness as deduced from impaired growth, disease risk, serious injury, and so on. Another part of the assessment will concern effects on health ascertained especially from evaluating any pathological effect. A further part will concern observations that indicate the extent to which the individual has good or bad feelings.

for example, the extents to which strongly preferred behaviors can be shown and the magnitude of physiological and behavioral changes usually associated with pain. Many measures of behavior and physiology reveal the extent of difficulty in coping without necessarily giving direct information about unpleasant feelings, and some measures, such as those of failure in immune system function, may not be related to feelings at all.

2. *The Role of Preference Tests*

Animals normally prefer what is good for them, and studies that provide information about the strengths of individual preferences are of considerable value in designing conditions for animals and deciding what should or should not be done in procedures involving animals (Dawkins, 1980, 1990; Duncan, 1993, 1996; Broom and Johnson, 1993, pp. 145–157). However, preferences are affected by previous experience (Mendl, 1990), and there are various examples of animals choosing something that is not good for them (Duncan, 1978). Dawkins (1990) concludes that several studies with different individuals will often be necessary as a consequence when trying to find out which treatments or conditions are likely to result in good welfare. The preference studies do not provide comprehensive information about the welfare of the individuals, but should be followed up by studies using other welfare indicators to make sure that what is preferred does not lead to poor health or other problems.

Carefully designed preference studies can give good indications about some feelings such as pain, thirst, or thermal discomfort. However, they may not indicate whether the behavior is affected most by a positive or by a negative feeling, they do not always allow discrimination of what kind of feeling is being avoided or sought, and they may not make it possible to recognize some feelings such as guilt and jealousy. Like measures of abnormalities of behavior or physiology, preference tests cannot tell us exactly what the individual studied is feeling.

Preference tests are valuable in some situations but not appropriate in others. Studies of foods and physical and social conditions are readily carried out by measuring how hard animals will work to obtain each resource, and measures of strength of aversion help in determining how painful or frightening some events or stimuli are. However, it would be difficult to assess stunning procedures or disease effects using preference tests, and there are problems in interpreting strong preferences for some harmful foods or drugs (Broom, 1996).

3. *Welfare Assessment and Time*

Sometimes poor welfare is very brief but very severe; at other times, poor welfare is prolonged but slight. Similarly, pleasant experiences may

be intense or mild, and momentary or extended in effect. Time should be considered as a variable in decisions about welfare. In general (Broom and Johnson, 1993, pp. 109–110), it would seem biologically meaningful to make some assessment of intensity. Then, if PW is intensity of poor welfare, and t is time, the multiplicative effect (PW × t) can be calculated (Fig. 1). We cannot be sure that a simple multiplicative relationship is correct, and this requires experimental investigation, but the problem should not be ignored.

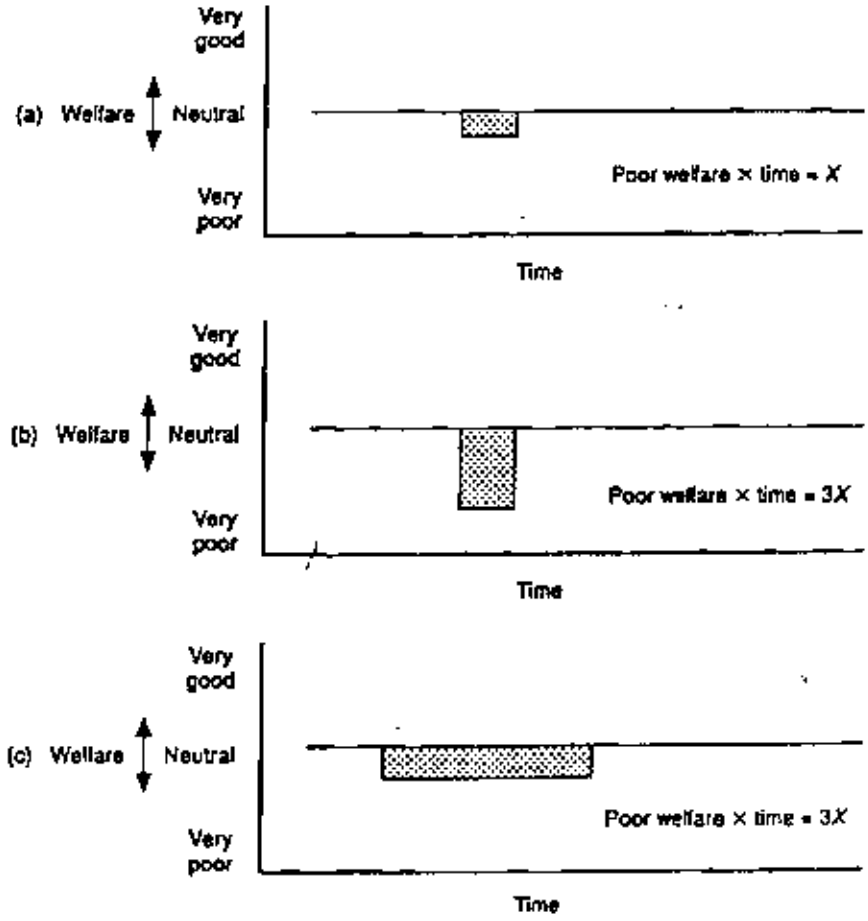

FIG. 1. Relationships between poor welfare and time. The effects of two levels of poor welfare (PW) and two durations of environmental conditions on an individual are shown. From Broom and Johnson (1993).

C. Feelings as Part of Welfare

We are so aware of our own feelings that it is not surprising that they are at the forefront of our minds when we think of our welfare: indeed, some people refer to feelings as being the sum total of welfare. As discussed at length earlier, the propensity to have feelings has evolved because some of the feelings in each of the general categories considered have some function, and feelings are an important part of mechanisms used in coping with the environment. Hence, it is impossible to consider a concept of welfare without feelings being included in that concept (Dawkins, 1990; Broom and Johnson, 1993, pp. 33–34, 80–82; Broom, 1996). However, some feelings may be epiphenomena of neural activity (Broom and Johnson, 1993, p. 80) and hence need not affect coping with the environment.

If the definition of welfare were limited to the feelings of the individual it would not be possible to refer to the welfare of any individual that was asleep, or anesthetized, or drugged, or suffering from a disease that affects awareness. Neither would any disease be considered to affect welfare unless it altered the feelings of the individual. The welfare of an individual who was dying but was briefly euphoric because of drug administration would be described as very good. Most people would say that welfare can be poor in circumstances in which there are no bad feelings.

A further problem results if only feelings are considered in assessing welfare: a great deal of important evidence in assessing welfare in practical studies would not be used. Animals may be studied and found to have neuromas, or extreme physiological responses, or abnormalities of behavior, or immunosuppression, or disease, or inability to grow and reproduce, or reduced life expectancy, but this evidence would not be used to indicate poor welfare unless bad feelings could be demonstrated to be associated with them in such individuals. This argument is already being used by some people to say that systems for housing farm animals are not proved to result in poor welfare, because the abnormalities of behavior and physiology that occur in these conditions have not been linked with certainty to unpleasant feelings. It is often difficult to convince scientists about evidence concerning feelings, and some people are never convinced about feelings in any other individual, even of their own species. Hence, it is dangerous to let decisions about welfare depend entirely on evidence about feelings.

We should carry out research in which we try to find out as much as possible about the feelings of individuals whose welfare we are trying to assess. However, we should incorporate such studies in investigations of the whole range of coping methods by studying coping systems in their entirety. Individuals cope by using their immune systems, adrenal responses,

and behavioral regulatory methods as well as by responding to their feelings. Welfare assessment must take account of all of these. As Broom (1993) and Broom and Johnson (1993, pp. 82–84) point out, welfare is worse when there is an injury than when there is no injury, even if the individual is narcotized or asleep, but the welfare is worse still if the individual is awake and suffering. Similarly, an individual whose immune system functioning is suppressed is coping with its environment less well than an individual with normal immune system functioning, so its welfare is worse even if it is unaware of the immunosuppression. However, the welfare of the immunosuppressed individual would be worse still if it were diseased, especially if the effects of the disease caused suffering. Welfare assessment should involve a combination of studies of feelings and of other factors providing information about coping.

III. Summary

Animals have systems for recognizing harmful or favorable stimuli and for monitoring the effects of environmental conditions on themselves. They also have a range of methods for attempting to cope with perceived or actual adversity. Mechanisms involving learning tend to maximize the chances that things that enhance fitness will happen to them, and tend to minimize the chances that things that reduce fitness will happen. As part of these various methods and mechanisms, positive and negative feelings have evolved. These feelings have a biological role that complements various other anatomical, physiological, and behavioral mechanisms. Each of 24 different kinds of feelings is discussed and the origin and possible function of each is considered. All have some potential for improving fitness and most are likely to have been the subject of considerable selection pressure, but some aspects of feelings are likely to be just epiphenomena of neural mechanisms. With this view that most aspects of feelings have evolved like other biological mechanisms and that they help significantly in coping and responding, a single view of welfare as the state of an individual as regards its attempts to cope with its environment becomes clearer. Feelings are an important part of the welfare of an individual and should be assessed as well as possible. Other coping procedures and effects of the environment on the individual should also be assessed. An effect on an individual that is adverse in the long term is categorized as stress. Programs for trying to evaluate and improve welfare should combine the use of experiments to assess what is important to the individual by measuring the strengths of preferences, with monitoring studies in which feelings and other aspects of welfare are assessed more directly.

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