STRESS AND ANIMAL WELFARE

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When individual vertebrates loose grip on their life conditions stress symptoms appear and their welfare becomes problematic. Present day research supports the view that stress can originate when an organism experiences a substantial reduction of predictability and/or controllability (P/C) of relevant events. Behavioural (conflict and disturbed behaviour) and physiological (neuro-endocrine and autonomic processes) aspects of a reduction of P/C are reviewed. The highly dynamic patterns of the homeostatic mechanisms activated during stress make it difficult to deduce any simple relationship between stress and welfare. Nevertheless the following conclusions are drawn and defended:

- *moderate stress may be necessary to optimize vigilance*
- *both the occurrence of one dramatic life event and a long lasting low P/C of relevant life conditions may lead to chronic stress symptoms with a pathological character*
- *the coherence of pre- and post-pathological symptoms is decisive for an evaluation of individual welfare.*

A list of relevant stress symptoms has been presented, all of which indicate some stage of serious welfare problems. Their occurrence should never be typical of animals living in a farm, laboratory or zoo housing system. However, if after all this is the case, such systems have to be corrected and replaced by more appropriate ones as soon as possible.

Keywords: *animal welfare, captive environments, controllability, predictability, stress*

Introduction

Recently we (Wiepkema & Koolhaas 1992) argued that individual vertebrates give great priority to those activities that promote and maintain a reliable grip on their actual life conditions. These activities imply learning to predict or to control future events and construction of a cognitive map of their living area (Wiepkema & Koolhaas 1992). We emphasized these learning and exploratory processes since it is precisely here that failures may lead to welfare problems.

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In nature, many relevant temporal (causal) and spatial relationships have a certain degree of variability as they depend on a wide range of circumstantial factors or determinants. Although these variations imply some novelty or uncertainty and although they may evoke stress responses (see below), their quality and quantity is normally within the range of the coping capabilities of the individuals involved. In fact organisms have been adapted to such natural variations or fluctuations and readily survive in life conditions that are not entirely stable. It is even quite likely that some environmental instability or uncertainty is necessary in order to avoid boredom and to optimize individual vigilance. This peculiarity often makes it difficult to indicate exactly the limits of acceptable individual welfare or of unacceptable stress.

However, the reliability of individual knowledge about existing causal and spatial relationships may be reduced so drastically and for such a long period when kept in captivity, that organisms really have lost grip on their life conditions. Under such circumstances stress symptoms may arise, that precede or reflect a pathological state. When this happens welfare is at stake.

This brief introduction not only indicates that stress and welfare are opposite to each other, but also that both concepts refer to states of an organism that vary from slight and temporary to severe and long lasting.

In the following paper we will describe and briefly discuss behavioural and physiological characteristics of stress as they emerge from modern stress research. We consider this information necessary to make sensible statements about individual animal welfare.

Stress

The concept of stress has been connected strongly with the name of Hans Selye (1935) and was considered as the non-specific response of the body to any demand made upon it and was called the 'General Adaption Syndrome'. In this syndrome the pituitary-adrenocortical axis was the central one. Due to the work of Mason (1976) and others (Mason *et al* 1976, Levine *et al* 1989) it became clear that 1) different stressors evoke their own and often specific stress responses (behaviourally and physiologically) as well as possibly causing the non-specific and 2) most if not all stressors are characterized by some aspect of novelty that has great psychological impact. In the following we consider stress as a state of the organism that can be recognized by the occurrence of stress responses and evoked by one or more stressors.

Stress responses like the performance of conflict behaviour or an increased corticosteroid plasma level (see below) can easily be evoked by events or signals that announce oncoming danger or a risk situation, but do not hurt the organism directly or immediately. The inherent psychological or cognitive element associated with such stress responses is illustrated well in a classical experiment performed by Weiss (1972) as follows.

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The basic design of this experiment comprised rats kept in three different situations (A, B and C in Figure 1) in separate identical cages. The tail of each rat protruded out of the cage as indicated in the diagram. Rats in situations A and B could receive a shock from a weak electric current. Since the tails of these rats were connected in series the shocks the rats experienced were exactly the same in frequency, duration, intensity and timing. All shocks were given at random. Rats in situation C were controls and never received shocks. In front of each rat a small lamp could give a light signal. The crucial point was that for rats in situation A this light signalled the imminent arrival of a shock, while this was not the case for rats in situation B; for these latter rats 'light on' had no relationship with the occurrence of a shock. Therefore the difference between situations A and B was not in undergoing electric shocks, but in either having (A) or not having (B) information about the arrival of these shocks. In further experiments rats in situation A could even prevent or interrupt a shock by turning a wheel as it observed the light. When doing so this rat also prevented or interrupted the shock for rat B. Although B could activate its own wheel, this had no influence on the occurrence of a shock. Therefore rat A could predict, or in other experiments, could influence the occurrence of a shock: rat B could never predict or control this negative event.

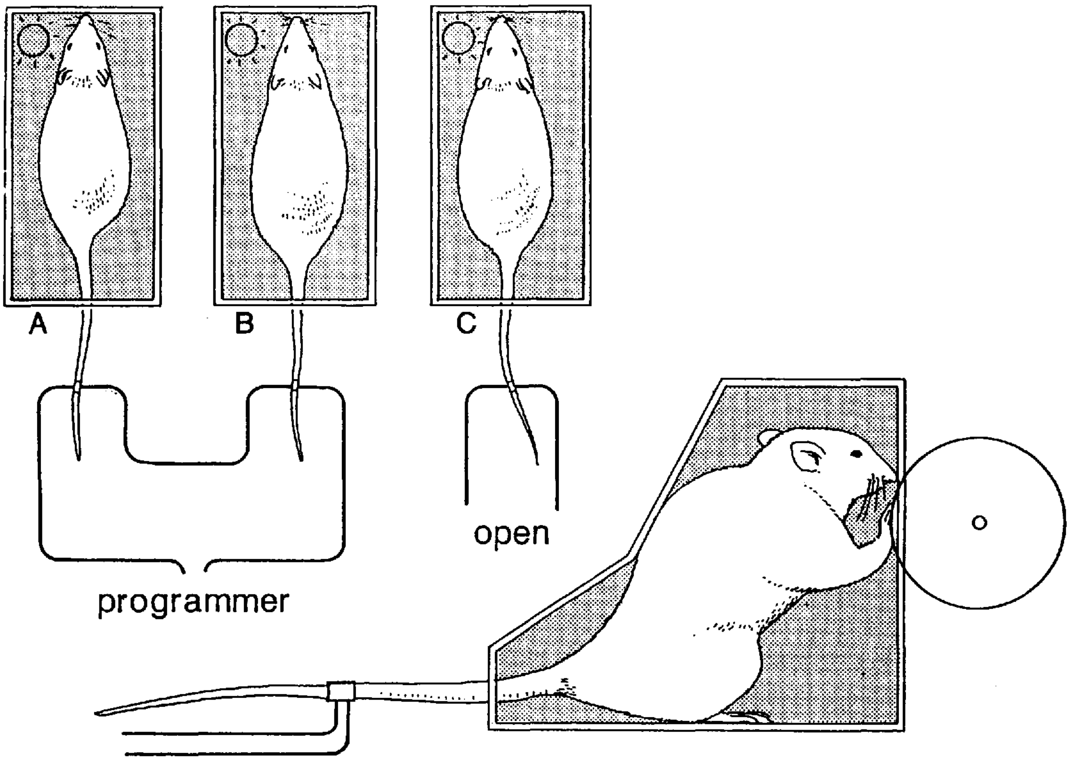

Figure 1 **Design of the yoked rats experiment. For explanation see text.** *(adapted from Weiss 1972)*

If the rats underwent this regime during a 24h period (about 350 shocks were delivered at random), surprising differences in stress responses were registered in the rats in the three situations. The B animals developed high corticosteroid plasma levels, stomach wall lesions (Weiss 1972) and a lowered capability of the immune system (Visintainer *et al* 1982) as compared with similar measures in the A rats. In fact the effects in these latter rats did not differ significantly from those in the C rats, the controls. The B rats that neither could predict nor control the shocks were the actual victims. The relatively positive outcome associated with predictable or controllable punishment seems quite puzzling. This strange relationship is explained by the fact that periods without warning signals appear to represent periods of safety; such safety 'signals' are rapidly learned (cf Weinberg & Levine 1980).

It is relevant to remember that a lowered predictability or controllability of positive events (for instance, obtaining food) leads to comparable responses. In pigs this has been described by Dantzer *et al* (1980), Dantzer and Mormède (1983) and Carlstead (1986). In these cases the effects comprised the performance of agonistic behaviour and increased plasma cortisol levels. In the Carlstead study the interesting point was that well-fed pigs developed stress responses when the signals preceding each food presentation were somewhat unreliable; presumably the non-occurrence of relevant positive events at expected moments of the day frustrated the animals. In experiments on learned helplessness, being a strongly reduced incentive to respond in the face of aversive stimuli (Maier & Seligman 1976), or on poorly predictable/controllable positive or negative reinforcers (cf Overmier *et al* 1980, Weinberg & Levine 1980, Levine *et al* 1989) similar results have been obtained. We will generalize all these relationships by claiming that stress responses are typically evoked when an organism is not able to foresee or control negative or positive events. To make this statement operational we need the concepts of predictability and controllability (P/C) as used in our description of the emotional brain (Wiepkema & Koolhaas 1992).

Both terms P and C form an extremely useful basis for quantitative stress research. For instance, in operant learning, organisms inform themselves about the actual controllability of a given negative or positive reinforcer. By simply changing the probability that a given operant will bring about a well-known reinforcer, the experimenter directly changes the controllability of such an event and can measure its behavioural and physiological consequences. The extreme of such a manipulation is realized during extinction procedures, when the probability of a given reinforcer is reduced to zero. When such P and C changes are only temporary, acute stress responses will be observed; when they are drastic and permanent, chronic stress symptoms become likely (Wiepkema 1990) - see below.

It may be helpful to elucidate briefly the point that predictability and controllability are not identical terms. The natural basis of their distinction is that in nature some relevant events can only be predicted and never controlled actively; for instance the weather tomorrow or the arrival of a predator. When such events are preceded by reliable signals, the organism rapidly learns to predict them (conditioning). Although such events cannot be prevented actively, anticipatory actions (seeking shelter or hiding) may bring about some passive control over future events.

The second type of events is controllable, since their occurrence largely depends on actions of the organism itself (operant learning). Such events are the availability of food, information, presence of a conspecific or a safe place etc. In this latter type of situations animals learn to predict and to control. The relevance of the distinction between P and C can best be illustrated with the feeding regimes in factory farms. Pigs in such farms are able to predict quite reliably the arrival of food in their troughs, however, they cannot control the availability of this food with normal foraging behaviour. Here high predictability is associated with low controllability.

A final but relevant aspect of controllability appears to be that at least the higher vertebrates prefer to do something in order to obtain a reinforcer rather than simply receiving it. When rats or chickens can choose between free food and food for which they have to work, the latter is preferred (Singh 1970, Duncan & Hughes 1972). Recent data strongly suggest that performing species-specific behaviour to obtain food facilitates adequate endocrine changes in the gastro-intestinal tract (de Passillé *et al* 1991). Normal control presumably optimizes ethological and physiological interactions with the environment (cf Breland & Breland 1961).

Evaluation of stress and welfare

Let us assume that the quantity or amount of stress in an organism may vary from low to severe. 'Severe' implies that in a given organism and during a given time interval the P/C of relevant events is extremely low. Such a condition would hold, for example, in an inexperienced but alert rat restrained for an hour on a laboratory table. Over this period, stress would be severe and welfare absent. Although low stress implies high P/C values, such values do not automatically mean good welfare. While a high and long-lasting P/C of most if not all events indeed maximizes certainty, it simultaneously implies the near absence of novelties in the environment. Such a non-changing environment does not provide new and interesting information an animal needs and gathers during its exploratory behaviour. This will introduce boredom associated with a decreased vigilance (cf Inglis 1983). In other words, P/C should not be too high or too low for long periods of time; it should have intermediate or optimal value.

Some uncertainty and, derived from this, some arousal are parts of the natural conditions to which organisms (even the domestic ones) are adapted. Therefore a baseline occurrence of behavioural and physiological stress responses is normal or natural and does not necessarily reflect adverse or unacceptable conditions. In order to appreciate this complex relationship between stress and welfare fully, we shall successively deal with behavioural phenomena and physiological processes expressing and underlying stress. To clarify (pre) pathological symptoms of stress we have to discuss briefly physiological mechanisms involved in stress. After this treatise we will list a number of recognizable symptoms that for good reasons indicate serious welfare problems of individual vertebrates.

Behavioural aspects of stress

In daily life, behaviour of a free-living vertebrate may be interrupted and disarranged by a great variety of events. Basically such events evoke uncertainty and as a result some conflict about what to do next. Examples of these events are, the absence of food at an expected location or time, the presence of a rival on a site where it was not expected, the occurrence of an incident that signals a future danger. In all these cases the organism's interpretation of the situation may be expressed in so-called conflict behaviour. This type of behaviour is typical of approach-avoidance conflicts and comprises agonistic behaviour (a mixture of aggressive, threat and flight behaviour), displacement or interruptive behaviour, redirected behaviour and intention movements (cf Baerends & Drent 1970, Huntingford & Turner 1987).

These conflict or uncertainty behaviour patterns are often associated with emotional expressions (activities of the autonomic nervous system as first suggested by Andrew 1956) and as a rule have a relatively short duration. This latter aspect strongly suggests that the underlying conflict is a temporary one. Although during such responses physiological alarm activities can be measured, we assume that as long as the organism is able to solve the conflict (that is finding food, removing or avoiding the rival, or protecting itself actively against a presumed danger) natural stress or welfare problems take place that should not bother us too much, even under domestic conditions. All these events fall within the normal adaptive range of the organism. As stated before, such events may even be necessary to maintain normal vigilance. For that reason we accept the occurrence of conflict behaviour under domestic housing conditions as normal and even as desirable. The situation becomes quite different when housing conditions are such that organisms no longer can solve conflicts. This is the case when retreat or escape from the conflict situation is impossible, or when normal routines (for instance, those underlying foraging) cannot be performed or are 'superfluous'. When this is the case, P/C of relevant events is and remains low. This will result in a variety of symptoms indicating chronic stress. Behaviourally, conflict behaviour gradually changes into disturbed behaviour; for instance, redirected behaviour may change into a stereotypy. Under such conditions organisms can no longer cope adequately and their welfare is seriously at stake.

Chronic stress of the organism is characterized by the fact that some stressors (or set of stressors) have a long lasting after-effect. This may result from the permanent presence of the stressor itself or from a long lasting negative after-effect resulting from one or two experiences with a very radical stressor. For instance, a small cage in which the organism has been confined for a long period may represent the first type of stressors, while a very drastic life event may stand for the second type. In many cases of chronic stress the symptoms involved are often restricted to certain times of the day. For instance, tethered sows, being severely stressed, perform stereotypies (a disturbed behaviour) only during daytime (Figure 2) (Wiepkema & Schouten 1992).

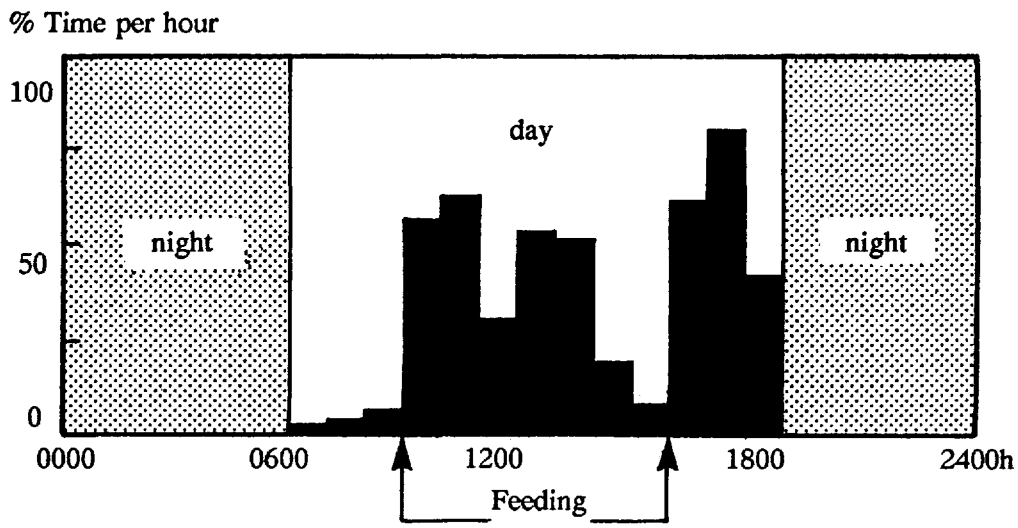

Figure 2 **Percentage of time per hour spent in performing stereotypies (black columns) of one representative sow. Mean of three successive days. Stereotypies are most frequent just after feeding.**

When animals have no control over relevant events in their environment, as is the case in close confinement where no species-specific behaviour is possible, disturbed behaviour may develop (Ödberg 1987, Wiepkema 1987). At least two types of such behaviour can be distinguished (although they may show some overlap): injurious behaviour and stereotypies (Wiepkema *et al* 1983, Fraser & Broom 1990). The first type comprises all behaviour by which an animal damages itself or conspecifics. Stereotypies are characterized by endless repetitions of more or less the same behavioural elements, their idiosyncratic occurrence and the apparent absence of a relevant function (Meyer-Holzapfel 1968, Ödberg 1978). Both types of behaviour will be discussed briefly.

Injurious behaviour

Examples of injurious behaviour are feather-pecking in laying hens, tail-biting in grower pigs, vulva-biting in group-housed sows, finger-biting in isolated monkeys, etc. Although in all these cases the causation is multi-factorial, the impossibility to practise normal foraging behaviour is often crucial. Offering hens a substrate in which they can scratch and peck or pigs one in which they can root, significantly reduces the tendency to feather-peck or to tail-bite respectively (Ruiterkamp 1985, Blokhuis 1989).

However, other factors are involved. For instance, the impossibility to perform normal dustbathing has also been claimed as a relevant factor to feather-pecking in hens (Vestergaard 1989), while in group-housed sows the feeding regime (sows have to queue when feeding) may contribute to vulva-biting (van de Burgwal & van Putten 1990). Finger-biting, however, in monkeys seems to be due to being deprived of any social contact with conspecifics (Sackett 1968).

While everybody agrees that the occurrence of such damaging behaviour is unacceptable in (domestic) housing conditions, our understanding of the causation and development of this behaviour is poor. In part, this results from the fact that a given housing condition does not always evoke this negative behaviour. Furthermore, for ethical reasons this type of research is rarely undertaken; we should be very careful in starting experiments that aim to evoke or facilitate injurious behaviour. For the same reasons we are also uncertain what the biological function or benefit of such bizarre behaviour might be. There is, however, a general consensus that housing and husbandry systems associated with injurious behaviour should be abandoned and replaced by better ones. Finding such better systems is often facilitated by good biological knowledge of the species involved.

Stereotypies

These behaviour patterns were first described in zoo animals, and later discovered in mammals and birds kept by humans (Holzapfel 1938). Stereotypies are common in animals that have been confined in small cages and, as a rule, have been separated from conspecifics. In the last decade these stereotypies have been investigated anew, and one of the most interesting findings is that stereotypies are not without biological significance (Lawrence & Rushen, in press).

A typical example of this behaviour is found in pregnant sows, tethered in individual pens (Figure 3). After being tethered these sows develop stereotypies such as chain- or bar-biting and sham-chewing. In the course of a few weeks these stereotypies ritualize into simple patterns (Stolba *et al* 1983) that are characteristic of the individual animal (Cronin 1985). These stereotypies may be performed for many hours a day (daytime) (Figure 2), but sows may differ greatly in the amount (hours) of stereotypies performed per day.

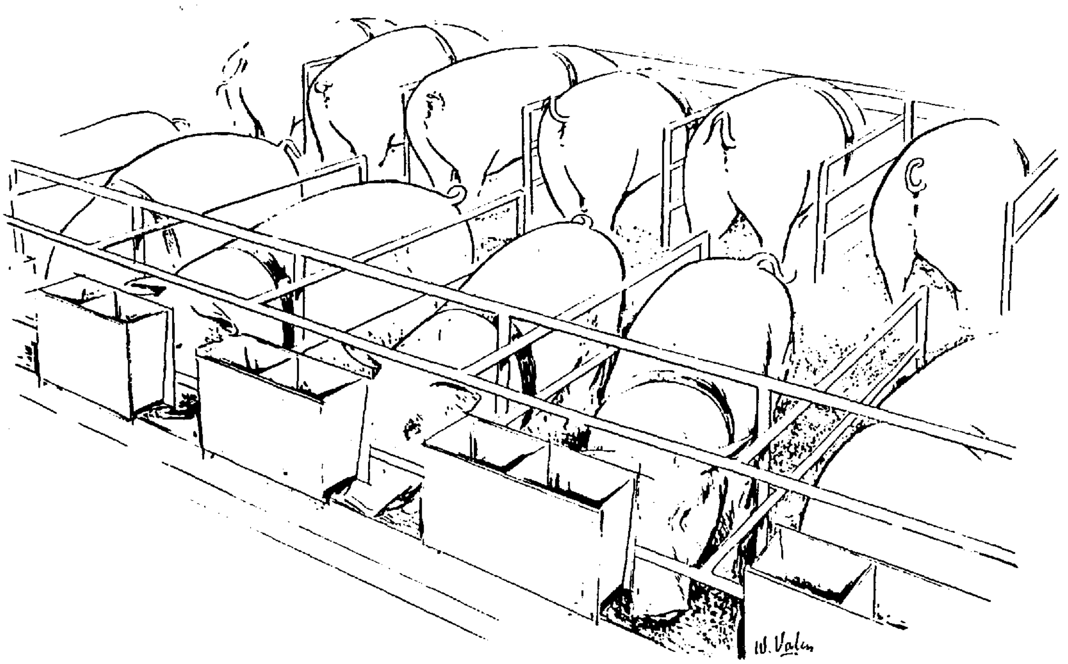

Figure 3 **Two rows of breast-tethered sows. Once or twice a day each sow can eat a restricted amount of food from one of the boxes in front of her.**
(from Wiepkema & Schouten 1992 - reprinted by permission of S Karger AG, Basel)

The causation of these stereotypies is again presumed to be multi-factorial in that the available evidence points to the following possibilities: stereotypies evolve from early escape behaviour and represent a ritualized form of this behaviour (Cronin 1985), they are facilitated by the feeding regime (food shortage) (Appleby & Lawrence 1987), they may have to do with negative contacts with neighbouring tethered sows (Barnett *et al* 1987), they may reflect the absence of exploratory behaviour and of normal social contacts (Cronin 1985), etc.

It has been discovered that these stereotypies are associated with opioid activity (presumably in the brain) that to a certain extent may quiet the performer (Cronin *et al* 1986). The mechanism of the latter process is not as simple as suggested at first (Rushen *et al* 1990, Von Borell & Hurnik 1991, Mason 1991, Schouten *et al* 1991, Schouten & Wiepkema 1991). In this context it is interesting that in conflict situations performing stereotyped behaviour may reduce hormonal stress symptoms (Levine *et al* 1979, Dantzer & Mormède 1981). For this reason a plausible functional explanation for the occurrence of stereotypies may be found in their stress reducing effects. However, this benefit should never lead to accepting stereotypies as a natural way of coping. If we consider stereotypies as behavioural 'scars', that have their origin in former behavioural 'wounds', then we have to conclude that we should never keep animals in such a way that they have to rely on the development of such 'scars', be they behavioural or physical.

Physiological aspects

An environmental challenge (stressor) will not only induce a behavioural response, but also a physiological one. As a rule both are highly integrated. For example, when a rat is put in a cold environment, it can maintain its body temperature not only behaviourally by building a nest or seeking shelter, but also physiologically by reducing peripheral blood flow and increasing metabolism. The physiological parameters of a stress response are frequently used as indicators of reduced welfare. In general, this view is too simple. The physiological response to a stressor is usually a highly adaptive reaction which is essential to cope with the challenge. For that reason we will first describe the main systems involved in the stress response and their functional significance before discussing the relationship of physiological parameters to animal welfare.

The integrated behavioural and physiological response is initiated and coordinated by the central nervous system (CNS). With respect to the physiological response, the CNS has two major effector pathways: the autonomic nervous system and the neuroendocrine system.

The autonomic nervous system

The autonomic nervous system has two major subdivisions; the (ortho-) sympathetic and the parasympathetic branch. With some exceptions, all organs are innervated by both systems. It was Cannon (1915) who recognized the importance of the sympathetic nervous system and its innervation of the adrenal medulla in the physiological response to stressors. A stressor may evoke an almost general activation of the whole sympathetic nervous system. Due to the widespread distribution of sympathetic nerve fibres, this will appear in a wide variety of physiological measures such as an increase in plasma (nor) adrenaline levels, an increase in heart rate and blood-pressure, an elevation of body temperature and changes in the immune system. Cannon called this the 'fight-flight' response because the whole is consistent with the physiological preparation for physical activity. Indeed during physical activity such as running or swimming, plasma catecholamine levels, heart rate, blood-pressure and body temperature are elevated. However, when a situation requires physical activity such as flight, but the circumstances do not allow this behavioural response, signs of increased sympathetic activity can be observed. An example of this is given by von Holst (1986). When two male tree-shrews were kept in one cage that did not allow any possibility for the subordinate one to hide or escape from the dominant one, a permanent increase in heart rate and a reduction of the circadian variation in heart rate of the subordinate male was observed, indicating a chronically elevated sympathetic tone.

Recent studies show that sympathetic activity may also be restricted to some parts of the system, depending upon the type of stressor involved. For example, psychological stressors usually result in an increase in plasma adrenaline due to the selective activation of the adrenal medulla, whereas noradrenaline released from the sympathetic nerve endings is mainly associated with physical activity (Scheurink *et al* 1989).

Not only the sympathetic branch, but also the parasympathetic one reacts to a stressor. The fact that the two systems are generally balanced in their activity can be illustrated by the cardiovascular response to a stressor. Handling of an animal usually increases heart rate and plasma catecholamines, demonstrating an increased sympathetic activity. However, when the animal is subsequently placed in a cage in which it previously experienced an aversive event, a sudden drop in heart rate may be observed even though the levels of plasma catecholamines may have risen further. This relative decrease in heart rate or bradycardia is due to an increased parasympathetic activity. Obrist (1981) called this bradycardia response the 'orientation attention response', and indicated that this parasympathetic response might reflect an expected stressor.

Neuroendocrine systems

The system which is classically involved in stress is the hypothalamus-pituitary-adrenocortical (HPA) axis. Selye (1935) was the first to demonstrate that a wide variety of stressors such as heat, cold, or tissue damage is able to activate this system. In later experiments it appeared that also the psychological nature, ie the predictability and controllability of the stressor, may activate the HPA axis. In the experiment using either predictable or controllable electric shocks in rats as described earlier (Weiss 1972), the plasma levels of corticosterone were highest in animals that could not predict or control the stressor.

Studies over the last decade revealed that many neuroendocrine systems respond in reaction to a stressor. These include not only systems involved in the regulation of the adrenals [corticotropic releasing hormone (CRH), vasopressin, adrenocorticotropic hormone (ACTH)], but also in reproduction [follicle stimulating hormone (FSH), luteinizing hormone (LH), testosterone, prolactin], in metabolism [growth hormone, thyrotropic hormone (TSH)] and in the regulation of blood-pressure and body fluids (vasopressin, oxytocin). The effects of stressors on these neuroendocrine systems may be direct, but can also be indirect through the interaction with other neuroendocrine systems.

In summary, a stressor induces a complex pattern of physiological changes dependent upon the type of stressor involved. This complexity is only partially understood in terms of its underlying mechanisms and its functional significance. However, an important consequence is that a wide variety of neuroendocrine and physiological parameters depend upon the degree to which an animal is exposed to stressors, ie on the predictability and controllability of the environment.

Functional significance of the physiological stress responses

Physiological parameters such as enhanced plasma levels of catecholamines or corticosteroids are frequently used as indicators of stress and consequently of a lack of well-being. One should realize however that these measures may reflect the normal activities of the physiological mechanisms of an organism when adapting to existing conditions.

The physiological changes in reaction to a stressor are important at two organizational levels; the peripheral organ systems and the central nervous system. Both the autonomic nervous system and the different neuroendocrine systems affect peripheral organs such as the heart, blood vessels, immune system, gastro-intestinal tract. The general function of these changes is the preparation of peripheral physiological processes for an adequate behavioural and physiological reaction to the stressor. Sympathetic activity and the related hormones adrenaline and noradrenaline, for example, are involved in the mobilization of energy stores, the increase in heart rate and blood-pressure and the redistribution of bloodflow necessary for a sufficient energy supply to active muscles. Corticosterone is also involved in the mobilization of energy stores as it stimulates gluconeogenesis in the liver and by this a rapid glucose mobilization.

Another target organ of the physiological stress responses is the immune system. The relationship between stress and immunity receives much attention in the rapidly developing field of psychoneuroimmunology, because it shows the way in which the appreciation of the environment may affect the incidence of immune system mediated diseases (Dantzer & Kelley 1989, Ader *et al* 1991). It has been found that neuroendocrine parameters affect immune function via receptors situated on lymphoid cells which are sensitive for a variety of hormones. Moreover, lymphoid organs are directly innervated by the sympathetic nervous system. Stress modulates the immune system through both the neuro-endocrine and the sympathetic system (Ader *et al* 1991). Corticosterone, for example, acts as an immunosuppressive hormone, whereas a number of experiments indicate that the sympathetic innervation can stimulate immune function (Croiset *et al* 1987). This opposite action of sympathetic activity and corticosterone led Munck *et al* (1984) to the idea that the function of the increase in corticosteroids during stress is to protect the organism against an over-activation of the normal defense mechanisms, ie corticosteroids seem to play a role in the termination of the stress response. The immune system in turn communicates with the central nervous system. Immune cells produce peptides such as endorphins, ACTH, vasopressin, interleukins, etc which affect brain functioning and consequently behaviour (Dantzer & Kelley 1989). The interleukins in particular are involved in the induction of fever and sickness behaviour, that result from an infection. Due to this two-way communication between the brain and the immune system, stress affects health and disease and therefore welfare as well.

Not only peripheral organs are affected; the central nervous system is also an important target organ of the products of neuroendocrine systems. Several hormones, for example the steroids, cross the blood-brain barrier and bind to specific receptors in certain brain areas. Other hormones affect the CNS via pathways still unknown, possibly through specific receptors on afferent autonomic nerve fibres.

This feedback of hormones on the CNS has several functions. At the level of the hypothalamus and the pituitary, it is involved in classical neuroendocrine feedback mechanisms, which play a role in stabilizing hormone levels. At the level of higher limbic structures such as the hippocampus and the amygdala however, hormones may affect behaviour. Many hormones, like adrenaline, ACTH, corticosterone, vasopressin, ß-endorphin, etc that are released in reaction to a stressor are reported to affect learning and memory processes. For example, the plasma concentration of adrenaline immediately after the acquisition of a learning task strongly enhances memory consolidation (McGaugh 1983). This CNS mediated action of hormones on learning and memory processes determines future behavioural and neuroendocrine responsiveness to stressors.

In summary: the central nervous system when aroused by a stressor activates and integrates a highly interwoven pattern of physiological and behavioural stress responses (Figure 4). The neuroendocrine and anatomical activities enable a behavioural response by direct influence on peripheral organ systems like the cardiovascular, the gastro-intestinal and the immune systems. Moreover, the physiological activities facilitate learning and memory processes that allow the animal to react more adequately to a similar stressor in the future. In fact, these physiological mechanisms can be considered as basic for each kind of behaviour.

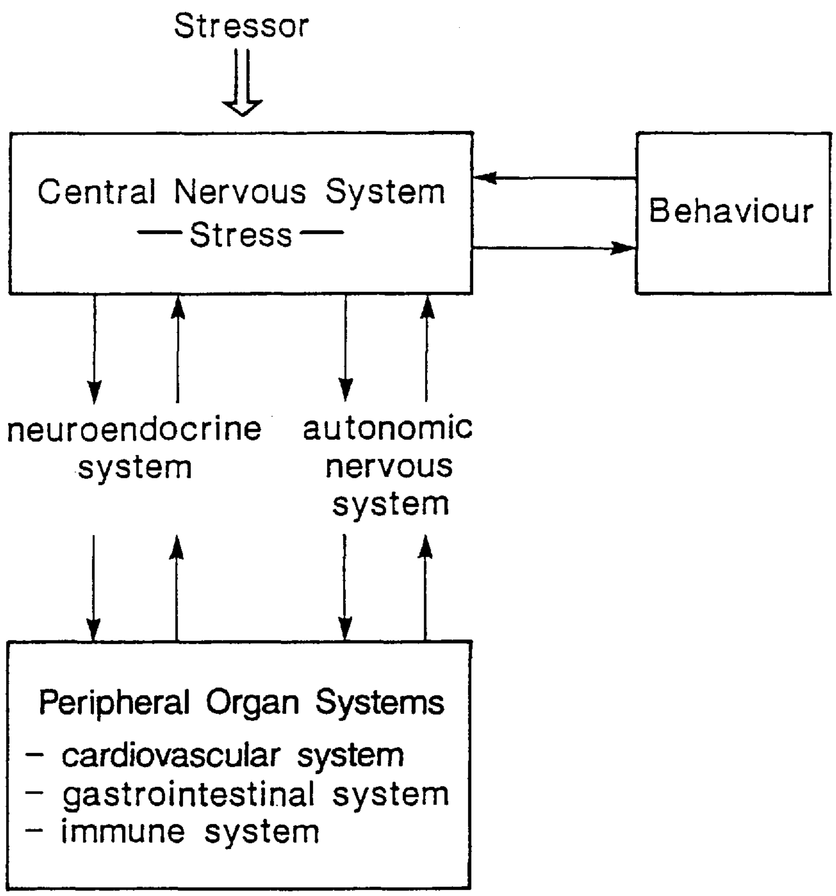

Figure 4 Interconnections between cental nervous system, behaviour and peripheral organ systems during stress.

Physiology, welfare and pathology

Up to this point the physiological and behavioural response to an environmental stressor has been presented as highly functional, coping with any environmental challenge. In other words, these measures reflect the processes the organism uses to control its environment, ie to reach and maintain homeostasis. The question arises to what extent these same processes are involved in the development of stress pathology and how far the physiological measures can be used as indicators of reduced welfare.

The distinctions between physiologically adaptive processes, reduced welfare, and pathophysiology are hard to determine exactly. However, it may be helpful to give a brief outline of the highly dynamic processes involved in the transition from adaptive response to pathophysiology. Although controllability and predictability are the main factors involved in stress, in everyday life these two factors are graded in duration and intensity. One extreme situation concerns the confrontation with a single uncontrollable serious (life threatening) event. Another extreme concerns more chronically existing uncontrollable or only partially controllable aspects of the environment that are not directly life threatening. In the human stress literature the first situation is called a major life event, whereas the second situation is comparable to the hassles in ordinary everyday life. In the case of a major life event, physiological mechanisms are strongly activated, but for a short period of time, whereas the other situation involves a long-term mild activation of the same mechanisms. Both major life events and chronic stress may lead to pathophysiology.

The significance of chronic stress to the condition of animals is illustrated by some experiments on male monogamous tree shrews (von Holst 1986). These males occupy large territories in which they occasionally may meet their neighbours. In the laboratory, two males were allowed daily to have a short social interaction. When these males were housed in a way that they could see each other continuously, the subordinate of the two rapidly lost body-weight and died. Apparently, the continuous presence of the dominant male and the inability to escape from its sight led to serious pathology in the subordinate. Physiologically, these subordinate males were characterized by elevated baseline levels of plasma corticosterone and catecholamines. A surprising result was found in a second experiment, when the two males were housed in one cage that contained places where the animals could hide. Despite the fact that in this situation direct social interactions were much more frequent, the subordinate male survived without serious stress pathology. Apparently the possibility to actively escape from the presence of the dominant (controllability) outweighed the high number of fights to which the subordinate male was subjected.

Pathophysiological changes due to chronic stress are also observed in (semi) natural conditions. In a study on wild marsupials, a high incidence of lethal infectious disease was observed in aggressive, territorial males during the mating season. These infectious diseases were due to the immunosuppressive action of high plasma levels of corticosteroids. During the short mating season in particular, these levels were enhanced due to the intensive aggressive interactions of the territorial males (Bradley *et al* 1980).

Similarly, high blood-pressure and atherosclerosis were found in dominant or subdominant males in colonies of mice, rats, or monkeys depending on the stability of the social structure (Henry & Stephens 1977, Manuck *et al* 1983).

In these situations pathophysiology develops due to the continuous activation of stress related physiological mechanisms. Indeed, a number of studies show elevated baseline levels of plasma corticosterone and catecholamines under chronic stress conditions (von Holst 1986). An elevated baseline level is generally not pathogenic in itself, but may enhance the risk for certain types of pathology. For example, long-term sympathetic activation will enhance the risks for cardiovascular diseases such as hypertension and atherosclerosis, whereas a more chronically increased adrenocortical activity will increase the risks of infection due to the permanent immunosuppression. A strong parasympathetic activation will enhance the risks of heart rhythm disturbances and sudden cardiac death (Obrist 1981) and of gastro-intestinal damage (Desiderato *et al* 1974). Chronic stress strongly potentiates pathogenic processes when other risk factors are present as well. In stress-induced cardiovascular pathology, these risk factors may be a high level of serum cholesterol or a reduced glucose tolerance, whereas stress-induced immunosuppression will only lead to pathology when infectious agents or malignant cells are present as well. We may conclude therefore that such chronic elevations of physiological stress measures are indicative of reduced welfare.

Major life events may also lead to stress pathology. Experience with an uncontrollable stressor will result in a depression type of disorder called learned helplessness (Weiss & Glazer 1975). Recent evidence suggests that the severity of these behavioural symptoms may increase in the course of weeks after the single experience of an uncontrollable social situation in the form of a defeat by a dominant male (Koolhaas *et al* 1990). In the post-defeat period in which the actual stressor is no longer present, it is hard to detect changes in baseline neuroendocrine and autonomic stress parameters. This may be due to the fact that the stressor is no longer present and hence physiological mechanisms are no longer directly activated. Nevertheless clear signs of stress pathology (decrease of body-weight, loss of temperature, abnormal heart rhythm) are present.

It seems that baseline levels of physiological parameters have very limited significance as indicators of reduced welfare. This may be due to the fact that baseline activities of neuroendocrine systems can be considered as the peripheral end-result of complex centrally and peripherally organized regulatory mechanisms that are highly dynamic and have a considerable degree of compensatory plasticity. With respect to the HPA axis, stress leads to changes in the neuroendocrine regulations at the level of the hippocampus, the hypothalamus, the pituitary and the adrenal cortex itself. For example, a strong elevation of corticosterone may lead to a permanent decrease of corticosterone receptors in the hippocampus. Because these CNS corticosterone receptors are not only involved in behaviour, but also in neuroendocrine feedback, ie activity of these receptors reduces the height and duration of the response, a kind of cascade may develop in which a period of elevated adrenocortical activity will increase the likelihood of subsequent elevations (Sapolsky *et al* 1986, de Kloet 1991). It seems to be a general mechanism for both neuroendocrine and neurotransmitter systems that the receptors adjust to the concentration of the ligand, that is, the substance to be bound (receptor up and down regulation) and by this alter the regulatory range of homeostatic mechanisms; assays for receptor binding capacity represent one way to study these changes in regulatory mechanisms. However, a number of challenge tests have also been developed aimed at testing the reactivity of neuroendocrine systems. These tests may indicate the capacity of physiological systems to deal with environmental challenges, which is an important aspect of regulatory capacities of the organism as a whole (Nemeroff 1992).

Studies on physiological changes in depressed patients and in a number of animal models of depression provide an example of the way in which physiological parameters may be used as indicators of reduced welfare. It is generally accepted that chronic or acute loss of environmental control is an important component in the aetiology of depression (Seligman 1975). The phenomenon of learned helplessness which develops after the experience with uncontrollable foot-shock is a well accepted model of depression in animals. In many, but not all depressed patients a small but consistent increase in baseline cortisol levels is observed, in particular during the lower aspects of the circadian variation in HPA activity (Holsboer 1988). When in depressed patients reactivity of the HPA axis was tested using a standard dose of CRH, the ACTH response was blunted, the cortisol response was normal (Holsboer 1988). A number of experiments suggest that in depressed organisms the amount of central nervous corticosteroid receptors is reduced, whereas some animal experiments indicate that during learned helplessness even neuronal cell death may occur. These data suggest that dynamic compensatory changes have taken place in the regulation of the HPA axis that may not necessarily appear in changes in baseline activity. It seems that a strong or chronic activation of physiological stress mechanisms has its costs in terms of permanent alterations in the regulation of these systems. The net result of these changes, however, can be considered as a reduction in the regulatory range of the homeostatic mechanisms of the organism. This process of stress induced changes in regulatory mechanisms is indicated in Figure 5. It is hard to say at which stage such changes can be considered pathological or affecting welfare. These issues can only be answered when environmental demands are taken into account as well. Clearly high environmental demands in terms of predictability and controllability in combination with serious limitations in the regulatory capacity of the organism will affect welfare. A physiological approach to animal welfare should therefore not only focus on baseline activities of physiological systems, but also on the reactivity of these systems as an indicator of the regulatory range.

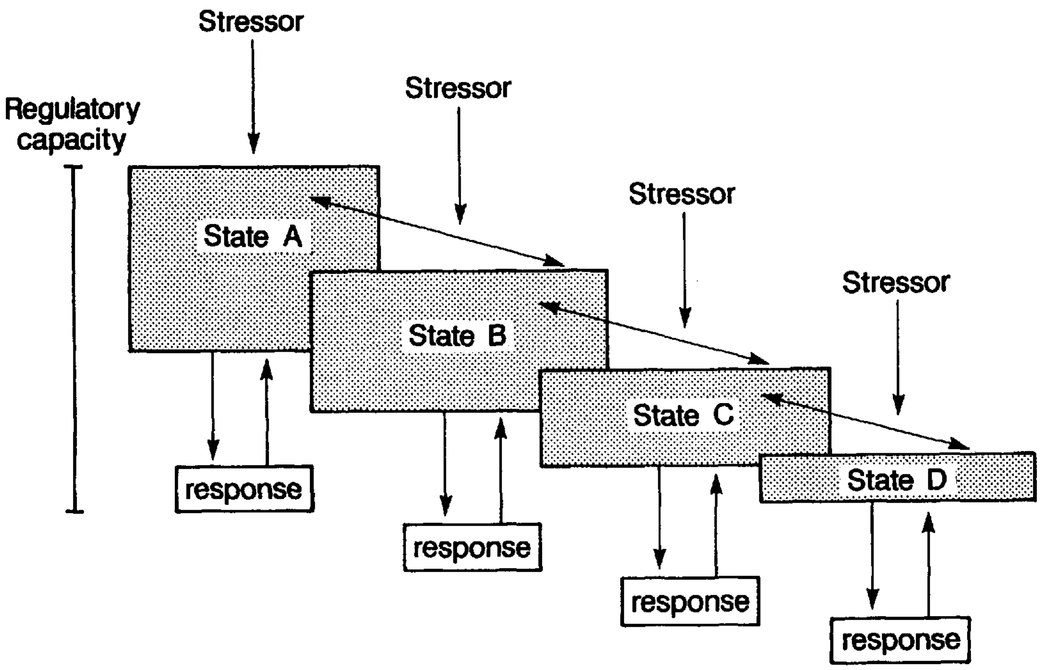

Figure 5 Summary of the dynamic processes involved in the transition from adaption to pathology. The response to a stressor depends on the regulatory capacity of the homeostatic mechanisms (existing state). The feedback of the stress response may increase the regulatory capacity or in case of severe stressors it may decrease that capacity. Such a decrease may enhance the chance of a breakdown in adaptation. This implies a change from State A to State D.

In summary: animals are highly dynamic information-processing organisms that continuously try to adapt to environmental conditions using behavioural and physiological mechanisms. The regulatory range of these adaptive homeostatic mechanisms is limited due to genotypic constraints and the individual's experience with former stressful situations. In nature these restrictions are generally not a problem because animals live in their natural habitat anyway and most stressful situations are predictable and avoidable through learning processes that are facilitated by most stress hormones. However, animals used by humans either in animal experimentation or animal husbandry are subjected to the conditions offered by their caretakers. Under these controlled conditions, the originally highly adaptive physiological and behavioural mechanisms may be no longer functional and even induce a downward spiral of reductions in regulatory capacity leading to a decrease in welfare and finally to pathology.

Conclusions

Welfare of an individual animal has often been characterized as a state of mental and physical health indicating living in harmony with its environment (Lorz 1973, van Putten 1982, Duncan & Dawkins 1983, Wiepkema & Koolhaas 1992). The studies on stress discussed previously in this paper strongly support a biological translation of this characterization: welfare is present when an individual can reliably predict or control relevant events by means of species-specific signals and means. The great advantage of this transformation is that it enables qualitative and quantitative testing of statements about a particular welfare case; predictability and controllability are key concepts in this respect. As put forward elsewhere (Wiepkema & Koolhaas 1992) both concepts also introduce the essence of cognitive and emotional phenomena in the discussions on welfare in vertebrates. The way both terms play a role in present day research also facilitates an integration of behavioural, physiological and psychological data (Moberg 1985, Levine *et al* 1989, Wiepkema 1990) relevant for the welfare debate.

A second somewhat tentative but nevertheless important conclusion is that for optimal welfare some uncertainty, that is some unpredictability and/or some uncontrollability, is of great positive significance. In practice this implies that good welfare is associated with the occurrence of short-lasting stress responses like some conflict behaviour, specific neuroendocrine changes etc. Mild and temporary stress may be necessary in order to optimize vigilance of the animals involved. Complete certainty easily leads to monotony and resulting boredom (cf Wemelsfelder 1990). Therefore, predictability and/or controllability of environmental events should have intermediate (optimal) values.

A third and not entirely new conclusion is that reduced welfare cannot be established by one simple measurement, like an enhanced corticosteroid plasma level, the occurrence of redirected behaviour or even the presence of wounds. Each symptom has to be evaluated in its specific context which also implies to know 1) which symptoms concur and 2) the ontogeny or history of these symptoms. For instance, small wounds on the integument of one week old piglets should not bother us too much, since they belong to the development of a natural dominance order in a group of piglets. All these considerations make it understandable that listing clearcut and significant anti-welfare symptoms is a complicated and nearly impossible matter. Nevertheless in practice such a list or overview of critical symptoms is often needed or, at least, asked for. We will try to give such a list of symptoms that have been categorized into three classes accounting for the fact that adapting individuals (and their responses) change over time. The three categories are symptoms that precede, reflect or follow welfare problems. The boundaries between these three categories are gradual.

1. Symptoms of the first (prepathological) category are:
    - chronically enhanced plasma corticosteroid levels
    - abnormal reactivity of the neuro-endocrine systems: especially heart rate and temperature changes:
    - reduced immune capability
    - reduced reproductive capability.

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2. Symptoms of the second (pathological) category are:
   - continuation of most if not all prepathological features
   - severe disease
   - severe external wounds and/or internal organ damage
   - behaviour associated with being sick, or wounded
   - expressions of fear
   - injurious behaviour, stereotypies.
3. Symptoms of the third (postpathological) category are:
   - conspicuous physical scars
   - disturbed behaviour like stereotypies and injurious behaviour (a list of disturbed behaviours in farm animals can be found in Wiepkema *et al* 1983)
   - apathetic postures.

Since all these symptoms indicate some stage of serious welfare problems, their occurrence should never be typical of animals living in a given farm, laboratory or zoo housing system. However, if after all this is the case, such systems have to be corrected and replaced by more appropriate ones as soon as possible.

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