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Coping and coping strategies: a behavioural view

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Abstract

Coping behaviour is a response to aversive situations. Farm and laboratory animals kept in intensive housing systems use a set of strategies (escape, remove, search, wait) to cope with aversive situations. It is suggested that these strategies have been shaped by evolution as adaptations to fitness-threatening situations with which animals are confronted in their natural environment. In intensive housing systems, however, the animals often fail to change aversive situations by using these evolved coping strategies, and it is argued that abnormal behaviour can originate from unsuccessful coping behaviour. With respect to animal welfare, it is important to design housing systems that allow the animals to perform effective coping behaviour.

Keywords: Coping strategies; Behavioural organisation; Evolution; Animal welfare

1. Introduction

During the last 10 years it has become more and more common to use the term 'coping' in publications on the influence of housing conditions on animal behaviour and welfare (e.g. Dantzer, 1989; Ödberg, 1989; Tennessen, 1989; Schouten and Wiepkema, 1991; Hansen and Damgaard, 1993). An early and important contribution regarding the correlation of coping behaviour and physiological reactions was made by Weiss (1968, 1971). The standard experimental design of his laboratory studies was to allow one group of rats to show a coping response, i.e. to avoid electric shocks by performing a specific behaviour, and to prevent another group (yoked controls) from doing so. Coping behaviour was shown to have a reducing effect on stress. Although the absolute levels of shock received were the same in both groups, rats that were able to perform a coping response had significantly lower values of physiological measures of stress.

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Farm and laboratory animals kept in intensive housing systems are also confronted with aversive situations. But contrary to the experimental situation described above, these animals often do not have the possibility to avoid an aversive stimulus by showing a specific reaction. The aversive situation does not cease and the animals use a variety of behavioural strategies in an attempt to cope with such an environment. Many publications, however, tend to neglect the variety in coping behaviour and emphasise a distinction between two major coping styles, labelled as 'active' or 'passive' coping (e.g. Von Holst, 1985; Koolhaas et al., 1986; Bohus et al., 1987; Wiepkema and Schouten, 1990; Benus et al., 1991; Korte et al., 1992).

The objective of my review is to offer a framework to incorporate coping behaviour into the adaptive behavioural organisation of animals that has been shaped by evolution to enable them to be able to cope with a sometimes aversive environment. I will first give a survey of definitions of coping. Second, I will assign coping responses described in the literature to more general coping strategies. Finally, I will address behavioural problems that arise in artificial housing conditions and discuss them with respect to coping and animal welfare.

2. What is coping?

Coping is a behavioural reaction to aversive situations, i.e. to situations that induce physiological stress reactions, including Cannon's (1929) fight/escape response, with an activation of the sympathetic–adrenomedullary system, Selye's (1950) distress response, with an activation of the pituitary–adrenocortical system, and other neuroendocrine systems (reviews by Henry and Stephens, 1977; Von Holst and Scherer, 1988; Ladewig et al., 1993).

From an evolutionary perspective, aversive situations are likely to result in a reduced fitness if the animal fails to cope (Broom, 1991). The fact that the animal perceives the adversity of the situation and reacts physiologically and behaviourally suggests that both the stress systems and coping behaviour are adaptive mechanisms for which there has been positive selection through evolution. The success of the coping behaviour can be measured by its effectiveness in reducing physiological measures of stress or by its effectiveness in removing an aversive situation and thus restoring fitness.

2.1. Definitions of coping

Many authors define coping by its effect on stress physiology. For example, Dantzer (1989, p. 278) states that "if a stressor elicits a physiological reaction A and if, in an individual engaged in a specific behavioural response, the observed physiological reaction is B, such as $B < A$, then by definition the response displayed by the subject is a coping response", or Schouten and Wiepkema (1991, p. 126) consider coping as "the individual response to a stressor by which normally harmful physiological effects of this stressor are reduced". According to these definitions, coping can be assigned both to aversive situations that can be removed by the coping response and to situations in which the harmful physiological effects can at best be attenuated by the coping response as the stressor cannot be removed. Other authors, however, use the term 'coping' only for the second type of situation.

For example, Levine et al. (1978, p. 6) write that "coping differs from habituation in that the stimuli that elicit the coping response continue to be threatening and aversive but the organism no longer responds to them" and Ödberg (1989, p. 229) defines coping as "the suppression or reduction of the deleterious effects of stress although the mismatch is objectively still present".

Fraser and Broom (1990) published a definition of coping that goes beyond a causal description of effects of a coping response on physiological measures of stress. In the glossary of their book they define 'cope' as follows: "Have control of mental and bodily stability. This control may be short-lived or prolonged. Failure to be in control of mental and bodily stability leads to reduced fitness" (p. 386). Their definition emphasises the functional consequences of coping behaviour and relates the concept of coping not only to the concept of stress, but more widely to the concept of behavioural adaptation. The relationship between coping and behavioural adaptation is also stressed by Wiepkema (1982). In his regulatory model of behavioural organisation he describes coping as the animal's ability to restore a difference between an 'Istwert' (actual value) and a 'Sollwert' (set-point), i.e. to exercise control over the Istwert. In an attempt to combine both the physiological and functional aspects of coping, I propose the following definition of coping in animals. Coping is a behavioural response that aims at reducing the effect of aversive stimuli on fitness or physiological measures related to fitness. The definition implies that the animals' perception has been shaped by evolution to recognise aversive, fitness-threatening situations.

In human psychology, Lazarus and Folkman (1984, p. 141) define coping as "constantly changing cognitive and behavioral efforts to manage specific external and/or internal demands that are appraised as taxing or exceeding the resources of the person". In addition to behavioural responses, this definition also includes cognitive efforts that are usually studied by means of questionnaires (e.g. Thoits, 1991). A second difference between coping in humans and in animals concerns the distinction between problem-focused and emotion-focused coping (Lazarus and Folkman, 1984, p. 150). Although animals perceive and most probably feel the adversity of a stimulus, I see no possibility to collect data on the influence of coping behaviour on emotions in animals because it is impossible to access their private experiences (see also McFarland, 1989, pp. 34–58; Bateson, 1991; Maestripieri et al., 1992).

2.2. *Attempts to cope and failure to cope*

Whether an animal succeeds in changing an aversive situation or not, depends on the effectiveness of its coping behaviour in a given situation. In studies with experimentally induced stress or with animals kept in intensive housing systems, the environmental setting may prevent the animals from performing effective coping behaviour. Von Holst (1985), for example, exposed tree shrew (*Tupaia belangeri*) males to a continuous social stressor, the presence of a dominant conspecific. The experimental situation is quite unnatural as subordinate males would normally avoid this aversive situation and leave the territory of the dominant male. When prevented from doing so, some animals react by sitting almost continually in a corner of the cage and hardly responding to external stimuli. These subordinate males obviously fail to cope. They have increased glucocorticoid concentrations in

the blood, they show a progressive decrease in body weight, and they die between 2 and 20 days after the introduction to the dominant male. Nevertheless, their behavioural response has to be viewed as an attempt to cope with the stressful situation. Their failure to cope is due to the fact that the experimental situation overtaxes their behavioural organisation. The example shows that it is not always possible to identify and define coping behaviour by its success in reducing harmful physiological effects of a stressor. If the aversive situation with which animals are confronted in an experiment or in a housing system is different from aversive situations they find in their natural environment, it is possible that their behavioural organisation lacks an adaptive behavioural response and that their coping behaviour turns out to be unsuccessful.

Tsuda et al. (1983) did a series of experiments on coping behaviour and gastric lesions using the experimental design of Weiss (1971) with three groups of rats. The first group (experimental rats) had the possibility of avoiding shock by performing a disc-pulling operant response. As these rats did not always pull the disc, they were exposed to a certain level of shock. The second group (yoked rats) received exactly the same level of shock but had no control over the shock. The third group was a non-shock control group. Not surprisingly, it was found that experimental rats made significantly more disc-pulling responses than did yoked or non-shock rats. Yoked rats, however, also responded significantly more than non-shock rats. Again, the behavioural response of the yoked rats has to be viewed as an attempt to cope with the aversive situation although the experimental design prevented them from being successful. It should also be noted that the definition of coping for humans by Lazarus and Folkman (1984, see above) does not require that coping is successful but includes all efforts to manage an aversive situation.

3. Coping strategies

Both experimental studies and investigations into the behaviour of animals kept in intensive housing systems describe a variety of behavioural responses to aversive situations. In the following, I attempt to classify these coping responses into four general coping strategies. I suggest that these coping strategies have been shaped by evolution as adaptations to different types of aversive situations with which animals are confronted in a natural environment.

3.1. Escape, remove, search, wait

An effective strategy to get rid of an aversive stimulus is to increase distance to that stimulus. This type of coping behaviour is usually described as escape behaviour. In an experiment of Weiss (1968), for example, rats learned to escape electric shocks by jumping onto a platform. When sows are tethered for the first time, they try to escape by throwing themselves violently backwards (Cronin et al., 1984). Of course, the sows' coping behaviour is unsuccessful, as the tether prevents them from escaping.

Instead of escaping the aversive stimulus an animal can also act upon it and try to remove it. Korte et al. (1992) reported that rats push and kick bedding material toward and over an electrified probe after shock experience. The enhancement of aggressive behaviour that can

be observed in situations of frustration (Azrin et al., 1966; Hutchinson et al., 1968; Duncan and Wood-Gush, 1971) is perhaps also a consequence of this coping strategy. It could be that the aggressive animal aims to remove a competitor that it takes to be responsible for the frustrating situation.

If the aversive situation consists of the absence of a stimulus to release a specific behaviour (e.g. feeding), search behaviour is the adaptive coping response. The traditional label for this coping strategy is 'appetitive behaviour' (Craig, 1918; Hughes and Duncan, 1988). Appetitive behaviour is characterised by high levels of locomotory and exploratory behaviour that enhance the probability of finding an absent stimulus. It is regularly provoked in studies with frustrated feeding/drinking behaviour or with restricted food. McFarland (1965) prevented Barbary doves (*Streptopelia risoria*) from drinking and observed the birds pecking at grain, sand grains and faeces. These objects were generally picked up in the bill and then dropped, but not swallowed. With respect to coping their behaviour can be interpreted as appetitive testing of the objects and rejecting them as they did not contain the liquid the birds were looking for. Savory et al. (1992) found that restricted-fed immature broiler breeder hens spend less time resting and perform more spot-pecking at the pen walls than ad libitum-fed control birds. In sows, food restriction also results in increased activity and in particular in high levels of massaging, chewing or biting on a chain (Terlouw et al., 1991a). If young pigs that have learnt to obtain food by an operant response are frustrated by no longer giving the food reward, they become very restless, rub their noses on the cage floor and scratch the floor with their feet (Dantzer et al., 1980).

If an animal can neither escape from nor remove an aversive stimulus, it is not adaptive to repeat these coping strategies over and over again. As an alternative, the animal may conserve energy and wait for a spontaneous change in the aversive situation. In farm and laboratory animals this coping strategy has been described as apathetic behaviour (Fraser, 1975; Wiepkema et al., 1983; Wemelsfelder, 1990). It has also been noted that animals can transfer this strategy from one aversive situation to another. Overmier and Seligman (1967), for example, found that dogs exposed to inescapable and unavoidable shocks in one situation later failed to learn to escape shock in a different situation where escape was possible. The phenomenon is known as 'learned helplessness' (for a review see Maier and Seligman, 1976).

As aversive situations also occur in natural environments, I suggest that the coping strategies found in farm and laboratory animals form part of their normal behavioural repertoire. The strategies 'escape', 'remove' and 'wait' have possibly evolved to manage challenges from conspecifics and confrontations with predators. Moberg (1985) discussed escape behaviour as an adaptive, stress reducing response of an animal faced with a challenge from a dominant peer and Benus et al. (1991) argued that a passive (waiting) strategy is based on the possibility that an animal may remain undetected and that the source of threat will leave the area itself. Natural situations that may have favoured the evolution of the 'search' strategy are characterised by the absence of essential resources like food or water.

3.2. Active and passive coping styles

Contrary to the variety of coping strategies listed above, many publications on coping behaviour in animals emphasise a distinction between two major strategies, active and

passive coping (e.g. Von Holst, 1985; Koolhaas et al., 1986; Bohus et al., 1987; Wiepkema and Schouten, 1990; Benus et al., 1991; Korte et al., 1992). This classification is much influenced by physiological results. In a variety of species, the physiological response of animals with an active coping style is dominated by an activation of the sympathetic–adrenomedullary system whereas in animals with a passive coping style there is mainly an activation of the pituitary–adrenocortical system (Henry and Stephens, 1977; Von Holst, 1985; Bohus et al., 1987).

With respect to behaviour, however, only passively coping animals show a consistent coping response in different studies. Passively coping animals are generally reported to react to an aversive stimulus with immobility. Passively coping defeated tree shrews sit almost continually in a corner of the cage and accept threats and attacks of a dominant animal without attempting to flee or to defend themselves (Von Holst, 1985). Passively coping rats react with immobility to an electric shock in the defensive burying/probe avoidance paradigm (Korte et al., 1992). Passively coping mice show a dramatic decrease in intertrial activity when exposed to inescapable shocks (Benus, 1988; Benus et al., 1991). Passively coping sows resist little during the first 2 h after initial tethering (Schouten and Wiepkema, 1991) and passively coping piglets make few escape attempts when restrained in a supine position (Hessing et al., 1993). Thus, the characteristic of the passive coping style is to stop performing overt behaviour when exposed to an aversive situation and to wait for a change.

Actively coping animals, however, adopt various strategies. According to Benus et al. (1991, p. 1008) the active coping style of male rodents "is aimed at the removal of themselves from the source of stress or at removal of the stress source itself". With respect to the coping strategies listed above, they either try to escape the aversive stimulus or to remove it. Actively coping defeated tree shrews withdraw from situations which could lead to more intense fights by active avoidance behaviour but also fight back if they are cornered by the dominant animal (Von Holst, 1985). Actively coping pigs resist vigorously and try to escape when restrained (Schouten and Wiepkema, 1991; Hessing et al., 1993). Actively coping mice react with flight behaviour when defeated by a trained fighting mouse (Benus, 1988; Benus et al., 1991). Interestingly, actively coping rats, mice and piglets have also been found to be more aggressive, i.e. to aim at removing their competitors (Koolhaas et al., 1986; Bohus et al., 1987; Benus et al., 1991; Hessing et al., 1993).

The relationship between 'active' or 'passive' coping and search behaviour is not clear-cut. Bohus et al. (1987) reported that actively coping rats show more exploratory behaviour and Benus et al. (1991) found that actively coping male mice keep on exploring the shockbox during inescapable shock sessions. In a maze test, however, Benus et al. (1987) observed that passively coping male mice start exploring the maze once they have learnt the task.

To summarise, by labelling coping behaviour merely as 'active' or 'passive', differences in behavioural strategies are likely to be masked. Especially with active coping behaviour there seems to be a set of more subtle strategies. As the use of these subtle strategies may vary from species to species and according to the type of aversive situation with which an animal is confronted, it may be premature to settle on a generalising theory of active and passive coping styles.

4. Coping with housing conditions

The behavioural organisation of the ancestors of our domestic animals has been shaped by natural selection in adaptation to their natural habitat. Studies with domestic animals kept in a semi-natural environment have shown that their behavioural organisation has not been changed to a great extent by domestication (Duncan et al., 1978; Stolba and Wood-Gush, 1989). Intensive housing systems for farm and laboratory animals are therefore likely not to meet the 'expectations' of a behavioural organisation that has evolved in a natural environment (Wechsler, 1992b). This mismatch is evident in the following husbandry aspects. Intensive housing systems offer the animal a barren environment that does not elicit variable and differentiated behaviour. They include few features that can be manipulated and changed by the animal's behaviour. They are poorly structured, or restrain the animal, preventing the performance of different activities at different sites. Finally, intensive housing systems usually do not allow the animals to live in a stable group and build up long-term social relationships. Although the animals may grow and reproduce well in these systems, they are likely to have behavioural problems in coping with aversive situations that they meet in such an environment.

4.1. Development of abnormal behaviour

The development of abnormal behaviour seems to be closely related to coping behaviour. Cronin et al. (1984), for example, described four stages in the development of stereotypies of sows tethered for the first time. At stage 1 the sows resist frantically and throw themselves violently backwards. At stage 2 they remain laying quietly for long periods. At stage 3 they perform short bouts of repetitive investigative behaviour and at stage 4 they have developed individualistic patterns of stereotypic behaviour. With respect to coping, this sequence of behavioural responses could be interpreted as a series of coping strategies. The sows move from escape behaviour, through waiting to searching. Finally, their investigative behaviour becomes more and more stereotypic.

Tail and earbiting, another abnormal behaviour in pigs, is associated with a variety of housing factors such as high levels of noxious gases or humidity, high temperature, not enough feeding space for all the pigs, parasite infestation and high stocking density (Sambraus, 1985). What all these factors have in common is that the aversive situation cannot be altered at all by the pigs' behaviour. Scheepens et al. (1991) experimentally induced such an aversive situation in growing pigs by exposing them to periods of unpredictable and uncontrollable draught. Again, the pigs reacted with a variety of coping behaviours, namely an increase in total activity, in exploratory behaviour directed at pen structures, in agonistic behaviour and in exploratory behaviour directed at penmates, including earbiting.

Many authors have emphasised the connection between coping behaviour and the development of abnormal behaviour. For example, Wiepkema (1985) hypothesised that coping patterns such as escape behaviour, redirected activities and vacuum activities may be repeated over and again and if, in spite of these repetitions, the external situation does not change substantially, become stereotypic. Dantzer (1991, p. 100) supposed that stereotypies "are remnant of displacement activities or defensive reactions that are initially emitted in an attempt to control the eliciting situation". Duncan and Wood-Gush (1972) interpreted

the back and forward pacing of frustrated domestic fowl as escape movements. Ödberg (1986) suggested that the jumping stereotypy of bank voles consists of abortive intention movements to jump out of the cage, but also mentioned the possible involvement of exploratory behaviour. Wechsler (1991, 1992a) concluded that stereotypic walking in captive polar bears originates from appetitive behaviour. Finally, in a recent study with caged mink, Mason (1993a) hypothesised that pacing movements may stem from appetitive food-searching behaviour, whereas stationary stereotypies such as head-twirling may be derived from attempts to escape.

In conclusion, animals are likely to develop abnormal behaviour under housing conditions in which they fail to cope with aversive situations by performing normal behaviour. It also seems reasonable to assume that abnormal behaviour can originate from coping behaviour itself. There is, however, a lack of detailed studies illustrating the transition from unsuccessful coping behaviour to abnormal behaviour.

4.2. Does stereotypic behaviour reduce stress?

The results of some studies indicate that stereotypies are associated with a reduction in physiological measures of stress and can thus be regarded as successful coping behaviour. Wiepkema et al. (1987) found the occurrence of tongue-playing in veal calves to be negatively correlated with abomasal damage. In rats, increases in stereotypic behaviour of individuals sensitised to amphetamine are accompanied by decreases in plasma corticosterone levels (Mittleman et al., 1991).

In two recent reviews, however, Ladewig et al. (1993) and Dantzer and Mittleman (1993) concluded that the relationship between stereotypic behaviour and physiological measures of stress is not unequivocal. For example, Terlouw et al. (1991b), in a study with sows, found no correlation between the level of post-feeding stereotypic behaviour and plasma cortisol levels and no increase in cortisol concentrations when the animals were prevented from performing the stereotypic behaviour.

With regard to stereotypies and coping, special attention has also been paid to the phenomenon that animals treated with an opioid-receptor blocker show a reduction in stereotypic behaviour (e.g. Cronin et al., 1986; Savory et al., 1992). This observation led to a more specific hypothesis on the function of stereotypic behaviour, assuming that animals performing stereotypies 'narcotise' themselves. However, this conclusion is questioned in recent reviews on coping and stereotypic behaviour (Dantzer, 1991; Rushen, 1993; Dantzer and Mittleman, 1993; Ladewig et al., 1993). Schouten and Rushen (1992) found that the behavioural effects of the opioid-receptor blocker naloxone are complex and difficult to interpret and, contrary to the hypothesis of narcotisation, Rushen et al. (1990) observed that sows with marked behavioural stereotypies had shorter tail-flick latencies on a pain-sensitivity test than conspecifics with low levels of stereotypic behaviour.

To summarise, the results of different studies on stereotypic behaviour and stress are not consistent. This could be due to the fact that stereotypies are rather heterogeneous (Mason, 1991, 1993b). It is also possible that developing stereotypies are more successful in reducing stress than established ones. Therefore, a profitable approach would be to follow individuals and measure stress before, during and after the development of stereotypies.

5. Coping and animal welfare

Coping behaviour is performed in aversive, fitness-threatening situations and it is plausible to assume that the animal experiences negative feelings when exposed to such situations (Wiepkema, 1987). Serious welfare problems are likely to arise when the animal fails to change the aversive situation. Broom (1991, p. 121) stated that "welfare is poor when the individual has difficulty in coping with its environment". This difficulty can be assessed by measures of stress physiology, immunology, injury, disease, mortality, growth and reproduction, but also by behavioural measures. An animal with difficulty in coping may increase the duration, frequency or intensity of coping behaviour. It will probably test a variety of coping strategies and the failure to cope with normal behaviour may result in the development of abnormal behaviour.

With respect to animal welfare, a difficult question to answer is when the animal's ability to adapt to specific housing conditions is exceeded. From an evolutionary perspective adaptation has failed when there is a reduction in biological fitness, i.e. in the number of offspring. This type of argumentation is, however, not sufficient to judge animal welfare. Ultimate causes of behaviour have to be differentiated from proximate causes (Dawkins, 1983; Wechsler, 1993). The animal's behavioural organisation is directed at proximate goals which are only correlatively related to the ultimate functions of behaviour. Therefore, what matters for the animal is to reach these proximate goals and coping behaviour represents a set of strategies that, at least in a natural environment, increase the probability of attaining such goals. The animal's ability to adapt to specific housing conditions has therefore to be assessed by its ability to cope with that environment (Moberg, 1985; Novak and Suomi, 1988; Tennessen, 1989; Fraser and Broom, 1990, p. 258). In order to prevent poor welfare, housing systems should be designed to allow the animals to perform effective coping behaviour when confronted with aversive situations.

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