Motivational systems or motivational states: 
Behavioural and physiological evidence

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Abstract

This paper will critically discuss the available behavioural and neurobiological evidence for the 
existence of motivational systems and motivational states on the basis of our studies on aggressive 
behaviour in male rats and mice. Three types of evidence will be discussed. First, some 
behavioural studies will be evaluated indicating that aggressive behaviour can be considered as 
part of a cluster of behaviours used to cope actively with environmental challenges. Second, it will 
be argued that coping styles are based upon different neurochemical brain states, which may be a 
reflection of motivational states. Third, the neurobiological evidence will be discussed for the 
existence of identifiable neuronal systems for certain behaviour systems, on the basis of studies on 
male sexual and aggressive behaviour. Finally, the relevance of the concept of coping styles to 
stress-pathology will be discussed briefly. © 1997 Published by Elsevier Science B.V.

1. Introduction

Much of our current thinking on the organization of behaviour is based on one of the 
ethological observations that behavioural elements are not performed in a random 
order, but in a more or less structured sequence. Quantitative analysis of such a 
sequential structure revealed that some behavioural elements are more associated in time 
than others. Subsequent cluster analyses led to the idea that behaviour is organized in 
behavioural systems, each of which can be activated by specific motivations. Hence, the 
concept of behavioural systems is often replaced by the concept of motivational systems. 
These systems would be activated by their corresponding motivational states. An elegant 
example of such an analysis is given by the hierarchical organization of social behaviour 
in the bitterling, a small freshwater fish (Wiepkema, 1961)). The clustering of be-
havioural elements is considered to represent independent behavioural systems such as a feeding system, an aggression system, a flight system or a sexual behavioural system. On the basis of a similar cluster analysis in the male rat, Lehman and Adams (1977) suggested behavioural systems for offence, defence and flight. Many experiments in behavioural neuroscience and in applied ethology basically used a rather narrow definition of the term 'behavioural system' to interpret the experimental data. The term 'system' is often thought to reflect a neuronal circuit specifically dedicated to a given type of motivation. However, a number of behavioural and neurobiological studies of aggressive behaviour, stress and adaptation performed in our department are difficult to interpret in such a narrow framework.

2. Aggression and coping

Aggressive behaviour has been the subject of many behavioural and neurobiological studies. Most of these studies were interpreted on the assumption that the aggressive behaviours reflect the action of a motivational system for aggression. However, some of our recent studies use a more instrumental view on aggression in which aggressive behaviour is considered as a way of actively coping with environmental challenges. The basis of this instrumental view goes back to the early studies by Wiepkema (1980) in which he suggested that aggressive behaviour can be considered as behaviour directed at the homeostasis of certain aspects of the social milieu. This placed aggressive behaviour in a similar framework of interpretation as the homeostatic models of bodyweight regulation and food intake. Because stress is considered to occur upon actual or perceived deviations from the homeostatic state, this idea opened new vistas with respect to the interpretation of experimental results in terms of social stress and adaptation. In this view, aggressive behaviour is used instrumentally to reach homeostasis by obtaining control over the social environment.

These ideas led to the hypothesis that the individual level of aggressive behaviour, i.e. the tendency to defend the home territory, is related to the way individual males react to environmental challenges in general. The hypothesis was tested by Benus et al. (1991b) using house mice that were genetically selected for either a short attack latency (SAL) or a long attack latency (LAL). When other indices of aggressive behaviour are taken into account, SAL males are considered to be extremely aggressive, whereas the LAL males have very low levels of inter-male aggressive behaviour (Oortmerssen and Bakker, 1981)). The results of a series of experiments not only in mice, but also in rats, are summarized in Table 1.

Several conclusions can be drawn from these results. First, the individual level of aggressive behaviour is indeed related to the way in which the animals react to a wide variety of environmental challenges. Second, it seems that aggressive males have a more active type of behavioural response, whereas non-aggressive males tend to accept the situation as it is. Third, the data suggest that aggressive males develop routines which means that behaviour, once triggered, is very little affected by environmental stimuli. The behaviour of non-aggressive males, on the other hand, seems to be guided more by environmental stimuli (Benus et al., 1987; Benus et al., 1990; Benus et al., 1991b).
Table 1
Summary of the behavioural differences between aggressive and non-aggressive male rats and mice

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<thead>
<tr>
<th>Behavioural characteristics</th>
<th>Aggressive</th>
<th>Non-aggressive</th>
<th>References</th>
</tr>
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<tr>
<td>Attack latency</td>
<td>Low</td>
<td>High</td>
<td>Oortmerssen and Bakker (1981)</td>
</tr>
<tr>
<td>Active avoidance</td>
<td>High</td>
<td>Low</td>
<td>Benus et al. (1989)</td>
</tr>
<tr>
<td>Defensive burying</td>
<td>High</td>
<td>Low</td>
<td>Unpublished data</td>
</tr>
<tr>
<td>Nest-building</td>
<td>High</td>
<td>Low</td>
<td>Sluyter et al. (1995)</td>
</tr>
<tr>
<td>Routine formation</td>
<td>High</td>
<td>Low</td>
<td>Benus et al. (1987)</td>
</tr>
<tr>
<td>Cue dependency</td>
<td>Low</td>
<td>High</td>
<td>Benus et al. (1987)</td>
</tr>
<tr>
<td>Conditional immobility</td>
<td>Low</td>
<td>High</td>
<td>Bohus et al. (1987b)</td>
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An important fundamental question is whether the two types of behaviour patterns can be considered to represent two styles of coping (Koolhaas and Bohus, 1989). This question can only be answered with an operational definition of coping. Coping can be defined as the behavioural and physiological processes necessary to reach homeostasis. In this view, control can be defined as successful coping. Several experiments indicate that the different behaviour patterns can indeed be considered as coping styles aimed at environmental control (Koolhaas and Bohus, 1989). This is shown, for example, in a recent experiment using domesticated wild rats. This strain of rat shows a large individual variation in aggressive behaviour similar to the variation in wild house mice. After being tested for their tendency to defend the home cage against unfamiliar male conspecifics, the males were tested in a shock prod defensive burying test. In this test, the animal is confronted with a small electrified prod in its home cage. Because this prod is a novel object, the experimental animal will explore it by sniffing at it. Consequently, the animal receives a mild but aversive shock. As soon as it has experienced the shock, the animal has two options to avoid further shocks. It may either hide in a corner of the cage to avoid further contact with the shock prod, or it may actively bury the shock prod with the bedding material of the cage. Under these free-choice conditions, aggressive males spend much more time burying the prod than non-aggressive males. Notice, however, that the two types of response are equally successful in avoiding further shocks. In this particular test, successful coping can be defined operationally as avoidance of further shocks. This leads to the conclusion that both the burying and the immobility response are equally successful. This again supports our conclusion that the individual variation in aggressive behaviour represents a variation in coping style which is expressed in a wide variety of environmental challenges (Bohus et al., 1987a; Koolhaas and Bohus, 1989), a view which is also in line with our data on the functional significance of variation in coping styles in the population dynamics of wild house mice (Oortmerssen and Busser, 1989). However, this conclusion is in contrast to the original idea by Henry and Stephens (1977). They considered the conservation withdrawal response as a form of pathology induced by a loss of control. Although loss of control induces a form of passivity or depressive
symptoms, our studies indicate that the natural variation in aggressive behaviour reflects a biologically functional variation in coping style.

So far we have used the terms active and passive coping to indicate the differences between the two styles. However, the more we learn about the nature of individual variation, the more we realize that these terms are inadequate to fully characterize the two coping styles. As mentioned above, one of the most fundamental differences seems to be the degree in which behaviour is guided by environmental stimuli. Aggressive males develop routines and seem to anticipate a situation, whereas non-aggressive males react to environmental stimuli all the time. This creates a differential degree of flexibility, and may explain why aggressive males are more successful under stable colony conditions, whereas non-aggressive males do better in variable environmental conditions, for example during migration (Oortmerssen and Busser, 1989; Fokkema et al., 1995). We prefer to use the terms ‘proactive’ rather than ‘active’ coping, and ‘reactive’ rather than ‘passive’ coping. Notice that we moved to completely different terms from those used in traditional ethology, and that our studies show that aggression can be associated with flight, something one would not predict on the basis of a classical motivational theory.

3. Implications for the organization of behaviour

Behaviour is the product of a wide variety of central nervous, neuroendocrine and peripheral physiological processes. Hence, the existence of individual differences in coping behaviour implies differences in accompanying physiology as well. In the original model by Henry and Stephens (1977), it had already been suggested that the two coping styles not only differ in behaviour, but also in some of the associated peripheral neuroendocrine and central nervous mechanisms. Table 2 summarizes the state of the art with respect to the differences in neuroendocrinology. It is important to realize that this table is only a qualitative summary of the available data, and does not allow conclusions about which level of organization the differences are located at, i.e. in the brain and/or in the periphery. However, the behavioural and neuroendocrine differentiation strongly suggests the existence of a differentiation at the level of the central nervous system as well.

Studies on the central nervous organization of behaviour indicate that narrow interpretations in terms of specific dedicated neuronal circuits may be misleading. The

<table>
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<tr>
<th>Physiological characteristics</th>
<th>Aggressive</th>
<th>Non-aggressive</th>
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<tr>
<td>Plasma testosterone</td>
<td>High</td>
<td>Low</td>
<td>Schuurman (1980)</td>
</tr>
<tr>
<td>Sympathetic reactivity</td>
<td>High</td>
<td>Low</td>
<td>Fokkema et al. (1988)</td>
</tr>
<tr>
<td>Parasympathetic reactivity</td>
<td>Low</td>
<td>High</td>
<td>Bohus et al. (1987b)</td>
</tr>
<tr>
<td>HPA axis reactivity</td>
<td>Low</td>
<td>High</td>
<td>Koolhaas and Oortmerssen (1989)</td>
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early experiments on the central nervous organization of behaviour were based upon the implicit hypothesis that the brain contains some kind of neuronal representation of these behavioural systems. This approach somewhat neglected the possibility that the temporal organisation of behaviour, as observed in the cluster analysis, is a reflection of the temporal organization of sensory input rather than a reflection of the central nervous organization. This argument was used in a somewhat provocative way by Valenstein et al. (1969), who questioned the behavioural specificity of hypothalamic stimulation inducing feeding behaviour. He presented some experimental evidence that feeding behaviour elicited by electrical stimulation of the lateral hypothalamus could be changed to drinking behaviour when the environment allowed drinking only. This experiment seriously questioned the behavioural specificity of many brain manipulations, and more generally the validity of the concept of behavioural systems to explain the central nervous organization of behaviour. The subsequent debate in the literature emphasized the need to assess animals in more than one test situation, and to analyze at an individual level the consistencies in behaviour across test situations. An early example of such an approach is found in an ethological analysis of the behavioural changes induced by a single intraperitoneal injection of gold thioglucose, a substance known to cause obesity, presumably due to lesions in various brain areas including the hypothalamus (Ruiter and Wiepkema, 1969). He showed that not only feeding behaviour was affected, but also sleep, grooming and exploratory behaviour. Although the change in feeding behaviour was the most striking effect of the drug, in fact a whole behavioural syndrome was created. A similar approach with VMH lesions revealed that not only food intake was affected, but also aggressive behaviour (Olivier, 1977). One may argue that the rather crude brain manipulation techniques at that time do not allow conclusions on behavioural specificity. However, more recent insights into the neurochemical make-up of the brain have strongly enhanced the technical possibilities of more specific manipulations of brain structures. Despite this, and despite the overwhelming number of experiments in the literature applying these specific neurochemical manipulations of brain structures in behavioural studies, a generally accepted view on the central nervous organization of complex behaviours is not yet available. Obviously, the idea of a discrete neuroanatomically localizable neural substrate for behavioural or motivational systems is too simple a view. However, it would also be too simple to suggest clearly distinguishable central nervous substrates for the two coping styles. We favour the view that the individual tendency to cope either proactively or reactively is determined by the detailed neurochemical state of limbic forebrain structures. In the next paragraph we will present some evidence that this view might be correct, based upon our studies on the peptidergic modulation of the central amygdala in coping.

4. Coping and the brain

Several studies show that the reactive coping style is characterized by a high reactivity of the parasympathetic branch of the autonomic nervous system (Bohus et al., 1987b). This can be observed in particular in a conditioned stress situation, i.e. when the animal is confronted with a situation in which it had an aversive experience some time
before. In such a situation, a reactive coping male will show a decrease in heart rate and react with behavioural immobility. This conditioned bradycardia response is mediated by the vagal nerve. Extensive studies by Roozendaal et al. (1990) show that the central nucleus of the amygdala (ACE) plays a major role in this conditioned immobility and bradycardia response. As predicted, specific manipulations of this amygdaloid nucleus by means of micro-infusions with the neuropeptides vasopressin or oxytocin in a conditioned stress situation affected heart rate and behaviour (immobility) in the non-aggressive males only. No behavioural or cardiovascular effects were observed in proactive coping males after this peptidergic manipulation (Roozendaal et al., 1992). This indicates a differential involvement of the central nucleus of the amygdala in the two types of coping styles. Recent studies by A. Wiersma et al. (unpublished results) show that the two types of animals differ more generally in the peptidergic modulation of the central amygdala. The reactive coping animal has a predominant vasopressinergic facilitation of this amygdaloid nucleus, whereas the proactive coping male has a CRH-mediated inhibition.

Several other studies show a more widespread central nervous differentiation between the two coping styles (Table 3), for example at the level of the vasopressinergic neurons in the bed nucleus of the stria terminalis and its innervation of the lateral septum (Compaan et al., 1993), the suprachiasmatic nucleus (Bult et al., 1993), the hippocampal mossy fibre system (Lipp et al., 1989; Cools et al., 1990), and striatal dopaminergic mechanisms (Cools et al., 1990; Benus et al., 1991a). These differences seem to reflect differences in the state of brain mechanisms in terms of number of neurons, degree of arborization of neurons, hormonal and neurotransmitter receptor binding capacity, etc., which in concert may determine the tendency to cope either actively or passively with environmental challenges. Although Cools et al. (1990) suggests a specific role of striatal dopaminergic and mesolimbic noradrenergic mechanisms as a gating mechanism for either of the two coping styles, the overall functional significance of the above-mentioned different brain states in the behavioural and neuroendocrine expression of the two coping styles is far from clear. However, in view of the discussion in the previous paragraph on the central nervous organization of behaviour, we favour the view that it is

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<td>Summary of the central nervous differences between aggressive and non-aggressive male rats and mice</td>
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<tr>
<td>Aggressive</td>
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<tr>
<td>Septum AVP-ir fibres</td>
</tr>
<tr>
<td>SCN AVP-ir fibres</td>
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<tr>
<td>AVP infusion in ACE</td>
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<td>AVP infusion in ACE</td>
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<td>CRH infusion in ACE</td>
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<tr>
<td>CRH infusion in ACE</td>
</tr>
<tr>
<td>Hippocampal mossy fibre</td>
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<td>Striatal dopamine</td>
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<tr>
<td>5-HT turnover</td>
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the detailed tuning of limbic forebrain structures which determines the individual responsiveness to environmental stimuli. When formulated in this way, we are close to the concept of the emotional brain (Wiepkema and Koolhaas, 1992), in which the different behavioural and neuroendocrine responses in a given situation are considered as the expression of emotional phenomena referring to a different emotional or motivational state of the brain, rather than the expression of distinct behavioural or motivational systems.

5. State versus system

In the previous section, evidence was presented that different coping styles may be based upon a differential neurochemical state of brain mechanisms, an interpretation which fits well into the concept of motivational states. However, one may wonder to what extent the concept of motivational systems may hold as well. In other words, to what extent are different behaviours, such as aggression, sex, feeding, and proactive or reactive coping, based upon different dedicated neuronal networks. No studies are available which specifically address this issue. However, an analysis of the neuronal structures involved, for example, in two different motivations like male sexual and male aggressive behaviour suggests that these two types of behaviour share many of the limbic forebrain structures.

Studies of male sexual behaviour in the rat usually include the vomeronasal organ (VNO), the accessory olfactory bulb (AOB), the medial nucleus of the amygdala (MeA), the bed nucleus of the stria terminalis (BNST), the medial preoptic area (MPOA), the ventromedial hypothalamus (VMH), and the ventral premamillary nucleus (PMV). These structures are considered to be part of a neural network involved in male sexual behaviour (Segovia and Guillamon, 1993). The literature on inter-male aggressive behaviour in the rat is not as extensive as that for sexual behaviour, but includes the same neuronal network (Luiten et al., 1985). This raises the question of whether male sexual and aggressive behaviour really share the same limbic forebrain structures, or whether this is only a seeming overlap owing to an insufficient resolution of the methodologies used in these studies. There are several arguments in favour of the idea of overlapping neuronal networks. The two types of male social behaviour share, to a large extent, the same neuroendocrine background, in particular with respect to the pituitary–gonadal axis. A comparison of the network with the distribution of gonadal steroid binding sites reveals a remarkable overlap. Many of these structures contain not only androgen-binding sites (Sar and Stumpf, 1977), but also the androgen-converting enzyme aromatase (Roselli and Resko, 1993) and estrogen receptors (Stumpf et al., 1975).

A wide variety of neuropeptides in this network, including vasopressin (Vries et al., 1983), substance P (Malsbury and McKay, 1989), neurotensin (Herbison and Theodosis, 1992), galanin (Bloch et al., 1992; Miller et al., 1994), and calcitonin gene related peptide are sexually dimorphic and seem to depend upon the presence of gonadal steroids. Several studies show the involvement of these peptides in male sexual and aggressive behaviour (Dorman and Malsbury, 1989; Koolhaas et al., 1991; Bloch et al., 1993).
Most of these brain areas are sexually dimorphic with respect to number of neurons and/or fibre density and neurochemistry (Arnold, 1984; Malsbury and McKay, 1987; Hines et al., 1992). This dimorphism might be causally related to the sexual dimorphism in sexual and aggressive behaviour. Moreover, a recent comparison of the testosterone-dependent (and sexually dimorphic) vasopressinergic neurons in the BNST and fibres in the lateral septal area (LS) between genetically aggressive and non-aggressive strains of mice shows a differentiation in this peptidergic system within the male gender as well that seems to be related to aggression and possibly to coping behaviour (Ferris et al., 1989; Compaan et al., 1993). This gonadal steroid-sensitive network, in particular the MA, BNST, MPOA and PMV, is directly or indirectly involved in the control of the pituitary gonadal axis which plays a dynamic role in both sexual and aggressive behaviour (Beltramino and Taleisnik, 1985; Hines et al., 1992).

Although the present knowledge of this network is based upon advanced neuroanatomical tracing studies and immunohistochemical studies, the functional aspects of the network with respect to sexual and aggressive behaviour are to a large extent based upon anatomically non-specific methods such as electrolytic lesions or electrical stimulation techniques and systemic hormonal treatments. The question about the behavioural specificity of this neuronal network obviously requires a direct comparison of the two types of social behaviour using more selective methods which take into account recent insights into the refined neurochemical make-up of these structures. The methods applied in most of these studies have an insufficient power of resolution to allow conclusions on behavioural specificity at the level of single neurons. Very few studies are available that might give an answer to this question. However, some tools recently became available that may shed some light on this issue. The activation of neurons in the brain during a certain type of behaviour can be visualized using staining methods for one of the immediate early genes c-fos which become active in the early phases of neuron activation. This method allows analysis of the activation of neuronal networks which are active during, for example, aggressive behaviour or sexual behaviour. When this method is combined with a further neurochemical identification of the activated neurons using immunocytochemical double-staining techniques for neurotransmitters or neuropeptides, one may be able to find out whether, and to what extent, different neuronal networks are activated during different behaviours. These methods were used recently in a comparison of the neuronal substrates for male sexual behaviour and male offensive aggression in a resident intruder paradigm in the rat (personal observations) and the hamster. This comparison showed that some brain areas are selectively activated following one of these social behaviours, whereas the activation patterns in other brain areas were the same. Interesting differences were observed in particular in the medial preoptic area, whereas c-fos activation in the bed nucleus of the stria terminalis and the medial amygdala was observed following both sexual and aggressive behaviour (Kollack-Walker and Newman, 1995).

Although the data are preliminary, they indicate that different behaviours are based upon partially overlapping neuronal networks. This idea is consistent with electrophysiological observations on feeding and drinking in sheep (Kendrick and Baldwin, 1989). Measuring the activation of identifiable single neurons in a range of behavioural test situations is necessary to attempt to find a neurobiological basis for the concept of
motivational or behavioural systems. The number of publications analysing the c-fos expression induced by behaviour is rapidly increasing. However, few of these studies combine this approach with a further neurochemical characterization of the activated neurons. Such a characterization is necessary to exclude, for example, the possibility that different behaviours activate different neurons within a given brain nucleus. Unfortunately, no studies are yet available which allow a conclusion as to what extent the neuronal network involved in aggressive behaviour overlaps with the network involved in other forms of proactive coping behaviour. Such a study is necessary for a more refined view of the relationship between behavioural output and the underlying neurobiological systems and neurobiological states.

6. Implications for stress pathology

In the previous sections it was shown that animals which differ in their style of coping with environmental challenges also differ with respect to the state and reactivity of a variety of central nervous and neuroendocrine mechanisms. Although it is beyond the direct scope of this paper, we will briefly discuss the fact that this differentiation may have important implications for the individual’s vulnerability to stress pathology. Several of the physiological mechanisms are causally involved in the development of pathologies. For example, the pituitary adrenocortical system and the sympathetic branch of the autonomic nervous system are important mediators in the communication between the brain and the immune system. For this reason, these mechanisms play an important role in the control of immunocompetence. Similarly, the autonomic nervous system is heavily involved in cardiovascular control, and hence in the development of cardiovascular pathology as well. Also from a behavioural point of view, the term ‘coping style’ already implies a differential capacity to reach homeostasis in different environments. In other words, controllability depends on the individual capacity to cope. It was argued, for example, that an animal with an proactive coping style might have serious problems with a variable or unstable (social) environment. On the basis of these behavioural and physiological arguments, one may predict a differentiation in vulnerability to stress pathology in relation to coping style. Indeed, a number of studies in different species show such a differential vulnerability under conditions of severe environmental challenge (Wiepkema and Adrichem, 1987; Fokkema et al., 1988; Anonymous, 1994; Fokkema et al., 1995).

With respect to these environmental challenges, in most animal experimental studies, the occurrence of pathologies such as stomach ulcers and immune deficiencies are related to conditions that involve lack or loss of control, e.g. inescapable shock or restraint. In the two coping styles, this would mean that both proactive and reactive coping fail to be successful. Although the concept of controllability has strongly contributed to the present knowledge and insights into the development of stress pathology, we would like to make some remarks on the experimental limitations of the concept of controllability. First, in most experiments controllability is operationally defined as a two-stage situation, i.e. full control or loss of control. However, in everyday life situations, controllability seems to be graded from absolute control, via threat to
control, to loss of control. Few studies consider the importance of a different degree of control in the development of stress pathology. Experiments aimed at understanding the development of hypertension indicate that threat to control rather than loss of control is the crucial factor (Koolhaas and Bohus, 1989). In a series of experiments, Fokkema (1985) showed that proactive coping males are sympathetically more reactive, which is considered to be a risk factor in the development of hypertension. Subsequent experiments in colony situations showed that these proactive coping males do develop high blood pressure, but only when they are in a situation of continuous threat to control (Koolhaas and Bohus, 1989). This threat to control may occur when the aggressive male takes a subdominant position in the social structure, or when the dominant male has difficulties in maintaining his dominant position. Loss of control seems to result in a decrease in mean arterial blood pressure rather than an increase (Adams and Blizard, 1986; Koolhaas and Bohus, 1989).

A second problem with the concept of controllability concerns its relationship with the two coping styles. Control cannot be separated from the aims and goals of the individual, i.e. what and how the animal wants to control. By definition, proactive and reactive coping animals have different ways to reach control, but in the proactive coping individual successful coping seems to result in a form of objective control. In other words, the proactive coping individual actively masters the situation. This is far more difficult to assess in the reactive coping animal, which from a behavioural point of view seems to accept the situation more readily, leading to a kind of perceived control. This has direct consequences for what we consider to be a threat to, or loss of, control. Challenges which may be uncontrollable for the proactive copper may be controllable for the reactive copper and vice versa. Further physiological and neuroendocrine measurements are required to assess the cognitive appraisal of a certain environmental challenge by different individuals, and to prove that the differentiation in coping style is causally involved in a differential disease vulnerability.

7. Concluding remarks

The discussion so far may seem to be rather semantic. After all, we have not properly defined what is meant by the term ‘system’. Obviously using the terms behavioural or motivational system as a concept for the central nervous organization of behaviour requires a more specific theory of the representation of systems in the brain. In the literature, three neural architectures have been described for the generation of different behavioural responses: dedicated circuits, reorganizing circuits, and distributed circuits (Morton and Chiel, 1994). In a dedicated circuit, each type of behaviour is generated by a separate, specialized neuronal circuit. In a reorganizing circuit, different behaviours are generated by changes in the properties of the neurons of the circuit. A distributed network is a computational network in which the behavioural response to any input is distributed over a large population of neurons. Small changes in neuronal input and neuronal activity may generate strongly different behavioural outputs.

It seems that the view of motivational systems as dedicated circuits for complex behaviours in vertebrates is too simple. As discussed above, it is more likely that we
have to think in terms of reorganizing and distributed networks. Further theorizing along these lines of thought is important, however, because it determines the way of experimentation, and the types of scientific questions asked in animal experiments. In our opinion, the terms motivational state and motivational system have been used rather loosely in the context of hypotheses on the physiological organization of complex behaviours.

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