Chronic stress parameters in pigs
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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2000

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

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The aim of this thesis was to identify physiological parameters for monitoring stress in fattening pigs. Because animal welfare is particularly compromised under conditions of chronic stress, we put the emphasis on long-term changes in physiology as indicator of chronic stress. Biotelemetry offers the opportunity for long-term stress-free monitoring of body temperature and heart rate. Therefore, these parameters were studied as possible indicators of chronic stress in fattening pigs. In addition, HPA-axis activity and behaviour were measured as reference indicators of stress. In chapter 2-4, we identified physiological indicators of chronic stress by using the experimental paradigm of barren and enriched housed pigs. In chapter 5 and 6, we determined if body temperature and heart rate were sensitive indicators of social stress. Because deep body temperature depends on metabolic processes, we hypothesised in chapter 7 that the nutritional level may affect the level of body temperature and the circadian rhythm in body temperature.

**Barren versus Enriched Housed Pigs**

Previous experiments indicated that pigs subjected to barren environmental conditions show more signs of chronic stress than pigs housed under relatively enriched environmental conditions. It has been shown that barren housing conditions hamper the development of appropriate social behaviour as compared to more enriched housing conditions (e.g. Beattie et al., 1995a, 1996a; De Jonge et al., 1996; O'Connell and Beattie, 1999; Olsson et al., 1999; Schouten, 1986). However, little attention has been paid to physiological indicators of chronic stress in fattening pigs housed under barren conditions. To obtain further evidence that the barren versus moderate enriched environmental conditions can be used as an experimental paradigm to study indicators of chronic stress, changes in HPA-axis activity and behaviour, as the most commonly used stress indicators, were studied first.

**HPA-axis Activity**

Chronic stress may result in hyper-reactivity of the adrenal cortex and thereby increase the cortisol response to acute stressors or to ACTH (Janssens et al., 1994). For instance, it has been shown that space restriction increased the cortisol response of pigs to ACTH (Meunier-Salaun et al., 1987; Pearce and Paterson, 1993). However, barren housed pigs did not differ from enriched housed
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pigs in cortisol responses to isolation and restraint (chapter 2). Thus, little evidence for increased adrenal sensitivity was found in barren housed pigs as compared to enriched housed pigs. In contrast, in chapter 4 we found that barren housed pigs had a higher cortisol response to mixing at transport and being in lairage than enriched housed pigs. This may be related to differences in behavioural responses to these stressors between barren and enriched housed pigs. Barren housed pigs tended to spend more time active, manipulating other pigs and fighting in the lorry and in lairage than enriched housed pigs (chapter 4).

Surprisingly, we observed that enriched housed pigs had higher baseline salivary cortisol concentrations during the light period than barren housed pigs (chapter 2). Increased baseline salivary cortisol concentrations are often associated with conditions of chronic stress (Rushen, 1991), although behavioural studies indicated that barren housed pigs were more likely to be subjected to conditions of chronic stress than enriched housed pigs (e.g. Beattie et al., 1995a; De Jonge et al., 1996; Schouten, 1986). Interestingly, in chapter 3 we showed that not only daytime cortisol levels were different, but that there were also differences in the shape of the circadian rhythm in cortisol between barren and enriched housed pigs. At 22 weeks of age, enriched housed pigs had a clear circadian rhythm in salivary cortisol, whereas barren housed pigs had a blunted circadian rhythm in cortisol. Determinations of the salivary cortisol concentration at the circadian peak between 9 and 22 weeks of age, indicated that the differences in cortisol concentration between enriched and barren housed pigs were age-dependent, and became visible from 15 weeks of age (chapter 3).

A blunted circadian cortisol rhythm has also been observed in other situations of chronic stress in rodents and pigs (e.g. in tethered pigs: Janssens et al., 1995; in rats subjected to repeated immobilisation: Makino et al., 1995). Moreover, a blunted circadian cortisol rhythm has been observed during situations of chronic stress in humans, e.g. during certain types of depression (Deuschle et al., 1997; Souèêtre et al., 1989) or during chronic fatigue syndrome (MacHale et al., 1998). We therefore suggested in chapter 3 that the blunted circadian rhythm in cortisol in barren housed pigs as compared to enriched housed pigs similarly is an indicator of a situation of chronic stress.
Behaviour

Effects of barren housing conditions on pig behaviour have been well described by others (e.g. Beattie et al., 1995a, 1996a; De Jonge et al., 1996; O'Connell and Beattie, 1999; Schouten, 1986). We confirmed these results, by showing that barren housed pigs performed more manipulative social behaviour (biting, nosing and massaging of pen mates) than enriched housed pigs, in the home pen (chapter 2) as well as in the lorry during transport to the slaughterhouse (chapter 4).

It has also been shown that barren housed pigs behave more aggressively and display more abnormal agonistic behaviour than enriched housed pigs (De Jonge et al., 1996; O'Connell and Beattie, 1999; Olsson et al., 1999; Schouten, 1986). We could not confirm these results by studying the behaviour of enriched and barren housed pigs in a confrontation test (chapter 2), but we observed that barren housed pigs indeed tended to spend more time fighting in lairage than enriched housed pigs (chapter 4). It has been shown that environmental enrichment plays a role in shaping the social behaviour of pigs. Barren housed pigs have more problems in the establishment of a dominance hierarchy than enriched housed pigs; the establishment of dominance hierarchies in barren housed pigs involves more aggression than in enriched housed pigs. These effects of rearing conditions on social behaviour are shown to be long-lasting, remaining into puberty and adulthood (De Jonge et al., 1996; O'Connell et al., 1999; Olsson et al., 1999).

At the lorry and in lairage, barren housed pigs tended to be more active than enriched housed pigs (chapter 4). This may have been caused by the increased aggression or manipulation of pen mates in barren housed pigs, as compared to enriched housed pigs. However, it has also been shown that barren housed pigs in general respond more actively to a novel environment than enriched housed pigs (Beattie et al., 1995b; Stolba and Wood-Gush, 1980). We showed that barren housed pigs indeed explored more a novel environment than enriched housed pigs at 25 weeks of age (chapter 2), but not at 6 weeks of age (chapter 3). It has been suggested that the increased exploration of a novel environment in barren housed pigs is due to an unsatisfied motivation for exploration (Stolba and Wood-Gush, 1980). As barren housed pigs only showed increased exploration in a novel environment at a later age, our results may than suggest that the motivation to explore increases, or builds up, with time spent in the barren environment (chapter 2, chapter 3). Others suggest that enriched housed pigs showed more avoidance
behaviour in the novel environment than barren housed pigs. It was suggested that avoidance behaviour in a novel environment is a kind of adaptive behaviour, and that barren housed pigs therefore show less adaptive behaviour than enriched housed pigs (Olsson et al., 1999). In conclusion, behavioural observations in the home pen and in a novel environment indeed showed that barren housing conditions may subject growing pigs to a situation of chronic stress as compared to more enriched housing conditions.

The effect of environmental conditions on HPA-axis activity and behaviour may have a common underlying physiological mechanism. In rats, it has been shown that there is a relationship between the behavioural response to novelty and circulating glucocorticoid concentrations, that is mediated by the central mineralocorticoid receptors (MR's). Disturbed, i.e. very low or very high circulating glucocorticoid levels increased the behavioural reactivity to novelty (Oitzl et al., 1994). Our data seem to be in line with these studies in rats (chapter 2, chapter 3), because barren housed pigs had low circulating cortisol concentrations due to a blunted circadian cortisol rhythm, and an increased behavioural response to novelty at a later age, as compared to enriched housed pigs. Circulating glucocorticoid levels also influence learning and memory in rats via central MR's and glucocorticoid receptors (GR's) (Douma et al., 1998). Barren housed pigs had an impaired long-term memory in the maze test as compared to enriched housed pigs. This could therefore have been related to the decreased circulating cortisol levels in barren housed pigs from 15 weeks of age.

Measurements of HPA-axis activity and observations of behaviour indicated that barren environmental conditions indeed subject growing pigs to a situation of chronic stress as compared to relatively enriched environmental conditions. In conclusion, the experimental paradigm of barren and enriched environmental conditions could therefore be used to determine if body temperature and heart rate were sensitive indicators of chronic stress in growing pigs.

**Body Temperature and Heart Rate as Stress Indicators**

*Barren versus Enriched Housed Pigs*

Acute stressors induced a body temperature and heart rate response in barren and enriched housed pigs (chapter 2). But, barren and enriched housed pigs did not differ in the body temperature and heart rate response to these stressors. The results of chapter 2 also suggested that barren housed pigs had a higher baseline body
temperature than enriched housed pigs. This may be the result of stress-induced changes in the circadian rhythm in body temperature (Kant et al., 1991; Meerlo et al., 1996; Tornatzky and Miczek, 1993). However, the difference in baseline body temperature between barren and enriched housed pigs could not be confirmed in further experiments (De Jong et al., unpublished results). Thus, in chapter 2 we showed that body temperature and heart rate can be used as indicators of acute stress. However, from the experimental paradigm of barren and enriched environmental conditions it was unclear if body temperature and heart rate could be used as indicators of chronic stress. Therefore, body temperature and heart rate responses were studied in other chronic situations that were expected to be stressful.

Social Stress

It has been shown that mixing of unfamiliar pigs is a severe stressor that has acute as well as long-term effects on behaviour, productivity and health (Ekkel, 1996; Friend et al., 1983; Graves et al., 1978). We studied if mixing of unfamiliar pigs has long-term effects on behaviour and physiology, and if heart rate and body temperature were sensitive indicators of the stress-situation (chapter 5 and 6).

Heart rates increased significantly in response to acute social stress. Social status seemed to affect the acute heart rate responses of pigs to social stress, because dominant pigs initially had lower heart rates during the resident-intruder test than subordinate pigs. The parasympathetic and sympathetic nervous system remained in balance during acute social stress in growing pigs, as the heart rate variability and the occurrence of cardiac arrhythmias did not increase as compared to baseline conditions (chapter 5). When pigs were mixed with unfamiliar congeners, no long-term effect of mixing on heart rate frequency was observed (chapter 6). Thus, although heart rate was an indicator of acute social stress, we showed that heart rate was not an indicator of the long-term effects of social stress.

When pigs were mixed with unfamiliar congeners, body temperature was significantly increased until 8 hours after the moment of mixing. The duration of the body temperature response differed between individual pigs from 3 hours until 24 hours after the moment of mixing. Although the increased muscular activity due to fighting may have contributed to the long-term hyperthermic response, general activity was not higher in mixed pigs as compared to unmixed pigs. Moreover, fighting was only increased in mixed pigs as compared to unmixed pigs during 6 h
after mixing. This indicates that the increased body temperature after mixing of pigs is caused by an increased (muscular) activity due to fighting in the first hours after mixing, as well as by psychological stress of longer duration. Therefore, it was concluded that body temperature may be a sensitive indicator of the long-term effects of social stress in pigs (chapter 6).

It has been shown in rats that after a social defeat followed by social isolation the circadian body temperature rhythm may be changed for days (Meerlo et al., 1996; Tornatzky and Miscek, 1993), indicating a more chronic stress situation. However, in growing pigs, we did not observe a circadian rhythm in body temperature at all (chapter 6), while the average body temperature seemed to be at its circadian maximum. This difference between rats and pigs might be due either to a species difference, or to the possibility that fattening pigs are already at the limits of body temperature control. Since deep body temperature depends on metabolic processes, we hypothesized in chapter 7 that the extreme nutritional level of *ad libitum* fed pigs may have an effect on the level of deep body temperature and the circadian rhythm in body temperature.

**Effects of the Nutritional Level**

In chapter 7, we showed that *ad libitum* fed pigs had a higher body temperature and a higher heart rate than restricted fed pigs, that could be explained by a higher metabolism and an increased heat production, due to a higher and more frequent food intake. In addition, *ad libitum* fed pigs were less active than restricted fed pigs. Thus, results of chapter 7 indicate that the nutritional level should be taken into account when body temperature and heart rate are measured as indicators of stress. However, we showed that although both *ad libitum* and restricted fed pigs displayed a circadian rhythm in heart rate, no circadian body temperature rhythm was observed in restricted nor in *ad libitum* fed pigs. Also Ingram and Legge (1970) and Ingram and Mount (1973) reported that no circadian body temperature rhythm was present in growing pigs. In contrast, Becker et al. (1997) and Parrott et al. (1998) observed a circadian body temperature rhythm in growing pigs.

It is questioned why we did not observe a circadian rhythm in body temperature in growing pigs. A pronounced circadian rhythm that is synchronised to the light/dark cycle can be interpreted as a physiological expression of an individual that is well-adapted to its environment (Tornatzky and Miscek, 1993).
Research provided evidence for possible deterioration of light-entrained rhythms by social constraints and demands on animal behaviour (Kant et al., 1991; Meerlo et al., 1996; Tornatzky and Miczek, 1993). This may have played a role in the group-housed pigs studied in the experiments described in this thesis. In intensive pig husbandry, and also under moderate enriched conditions, environmental conditions largely differ from the natural living conditions of pigs. This requires behavioural and physiological adaptation of the pig to a restricted environment. Moreover, genetic selection for growth also requires behavioural and physiological adaptation of the pig to a high production level. Future research should be aimed at studying the meaning of the absence of a circadian rhythm in body temperature in pigs, because this may possibly indicate that limits of adaptation are reached in growing pigs under current husbandry conditions.

**Chronic Stress: Reduced Animal Welfare?**

Some symptoms of chronic stress clearly indicate a situation of reduced animal welfare. For example, it is generally accepted that injurious behaviour, that is damaging for the animal itself or for its conspecifics, has negative implications for animal welfare (Wiepkema and Koolhaas, 1993). In chapter 2 and 4, barren housed pigs show more aggression and more manipulative social behaviour than enriched housed pigs. Both the increased aggression and increased manipulation of pen mates in barren housed pigs as compared to enriched housed pigs may lead to injuries and tail-biting, and it was therefore concluded that barren environmental conditions have negative implications for pig welfare, or increase risks for pig welfare (e.g. Beattie et al., 1995a; Schouten, 1986; chapter 2; chapter 4).

However, in many situations the relationship between indicators of chronic stress and reduced animal welfare is less clear. In this thesis we used changes in biological functioning of pigs as indicator of chronic stress and reduced welfare. However, as described in chapter 1, animal welfare refers to subjective feelings and emotions of the animal (e.g. Dawkins, 1990; Duncan, 1996). Thus, when physiological changes indicate a situation of chronic stress, attempts should be made to relate these symptoms to feelings and emotions, to evaluate animal welfare.

One way of approaching this problem was applied in chapter 3. Parallels were drawn between physiological indicators of chronic stress in pigs and physiological changes during human psychopathologies. Following this approach,
it is assumed that physiological parameters in pigs that are similar to those of human psychopathologies reflect a similar emotional perception of the situation by the individual. For instance, a blunted circadian cortisol rhythm may also in pigs indicate negative feelings and thus a state of reduced welfare. This suggestion needs to be further validated in future research, for instance by using pharmaceutical treatments that reduce or abolish the physiological effects of human psychopathologies, and the negative perception of the situation (e.g. antidepressants). This may be a useful tool in animal welfare research that helps to relate physiological stress symptoms to the emotional perception of the situation.

In addition, it is important to determine the exact relationship between circulating cortisol levels and behaviour in pigs. It has been shown in rats that the ability of an animal to respond adaptively to its environment is dependent on the balance between MR and GR function; a disturbed balance may lead to reduced or enhanced responsiveness to the environment, promote susceptibility to stress and alter behavioural adaptation (De Kloet et al., 1993). Thus, a disturbed balance between MR and GR function may indicate a situation of reduced animal welfare or a risk for animal welfare.

Also with respect to body temperature, it should be questioned to what extent stress-induced hyperthermia and the absence of a circadian rhythm in body temperature indicate a situation of reduced animal welfare.

The exact function of the acute stress-induced hyperthermia is not clear yet. It has been shown that stress-induced hyperthermia is not a secondary effect of stress-related physiological changes, but that it is an effect of the stressor itself. Stress-induced hyperthermia shares some common mechanisms with the febrile response induced by infection (Moltz, 1993; Parrott and Lloyd, 1995; Roth, 1998; Singer et al., 1986). The febrile response to infection seems to be adaptive by providing a more suitable internal environment, enhancing specific and non-specific immunity (Kent et al., 1992; Kluger et al., 1998; Moltz, 1993). Possibly stress-induced hyperthermia has the same function as fever. It may stimulate specific and non-specific immunity, and thereby prevent infections caused by the stressor. For example, fighting may lead to injuries that may become infected. Thus, the acute stress-induced hyperthermia may be benificial for the animal.

However, fever may also have detrimental effects. An excessive rise in body temperature may harm cells, in particular nerve cells. This can be observed under conditions of demands on heat defence, e.g. in a hot environment (Moltz, 1993;
It is unknown if (long-term) stress-induced hyperthermia also induces such damaging effects that have negative consequences for animal welfare.

Fever is accompanied by behavioural changes, like depressed activity, loss of interest, disappearance of body care activities and decreased food intake (‘sickness behaviour’) (Kent et al., 1992; Klir et al., 1997). A reduced food intake also seemed to occur during stress-induced hyperthermia in pigs (chapter 6). Long-term stress-induced hyperthermia, as for example occurs after mixing of pigs, may be accompanied by similar feelings as occur during fever, and may therefore represent a state of reduced welfare. It should be further studied to what extent pigs show sickness behaviour during stress-induced hyperthermia.

To elucidate whether the absence of a circadian body temperature rhythm is an indicator of reduced welfare, future research should be aimed at studying the relationship between the absence of a circadian body temperature rhythm in pigs and their ability to cope with environmental demands. Results of chapter 7 indicate that restricted fed pigs are possibly more capable to cope with stressors than ad libitum fed pigs. If physiological observations indicate that the limits of adaptation in fattening pigs are reached, it should also be questioned whether the high selection pressure on growth and food conversion in pigs should be continued.

Physiological Indicators of Chronic Stress in Fattening Pigs

In this thesis we showed that a low circulating cortisol level due to a blunted circadian rhythm in cortisol is a sensitive indicator of chronic stress in growing pigs (chapter 2, chapter 3). Heart rate can be used as indicator of acute stress, but did not seem to be a sensitive indicator of chronic stress in growing pigs (chapter 5, chapter 6). In contrast, body temperature, that is seldom measured in response to stressors in pigs, may be a sensitive indicator chronic stress (chapter 6). Although emphasis was put on physiological indicators of chronic stress, we showed that these indicators were often accompanied by behavioural indicators of chronic stress.

Implications for Further Research

We made a first step in identifying physiological indicators of chronic stress in growing pigs. More research should be aimed at studying the underlying mechanisms of physiological changes due to chronic stress, which is important to relate symptoms of chronic stress to reduced animal welfare. In addition, future
research should determine which physiological indicators of chronic stress and reduced welfare in pigs can be used for monitoring chronic stress and animal welfare at farm level. Monitoring stress at farm level is important for several reasons. It may help the farmer to make decisions to improve welfare, health and productivity, and it is important for certification of products. Moreover, it can be used to evaluate new or existing pig husbandry systems and changes in the legislation with respect to animal welfare.

Body temperature sensors can be included in injectable electronic identification transponders. This system is easily applicable at farm level for monitoring pig welfare and health (Geers et al., 1994). Therefore, in further research special attention should be paid to body temperature as a possible indicator of chronic stress and reduced welfare in fattening pigs.

REFERENCES


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