Applied Animal Behaviour Science 157 (2014) 8–13

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

The role of genes, epigenetics and ontogeny in behavioural development

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ARTICLE INFO

Article history:
Received 2 August 2013
Received in revised form 30 April 2014
Accepted 3 June 2014
Available online 13 June 2014

Keywords:
Behaviour
Genetics
Epigenetics
Ontogeny
Maternal care

ABSTRACT

This review focuses on the role of genes, epigenetics and ontogeny in behavioural development of animals. The behavioural characteristics of an individual are determined by its genes and by its physical and social environment. Not only the individual's early life and current environment are of importance, but also the environment of previous generations. Through epigenetic processes, stress in parents and even grandparents can translate into changes in behavioural and physical characteristics of the offspring. Another influential factor for behavioural development is maternal hormones. Recent studies indicate that hormonal effects may also be closely related to epigenetic changes. Also, the environment during ontogeny has considerable impact on behavioural development: in both mice and laying hens, high quality maternal care resulted in animals that were less fearful. In laying hens maternal care also led to a reduction in cannibalistic pecking. Genetic selection and selection experiments will also play a key role in breeding animals for the housing systems of the future. To optimize behavioural development of farm animals and to minimize risks of damaging behaviour, integral approaches are needed that combine selection of the optimal genotype with provision of a favourable environment for parents and offspring, both during ontogeny and later life.

1. Introduction

The behavioural characteristics of an individual are determined by its genes and by its physical and social environment. Not only the individual's early life and current environment is of importance, but also the environment of previous generations. Through epigenetic processes, stress in parents and even grandparents can translate in changes in behavioural and physical characteristics of the offspring. Epigenetic processes cause changes in gene function without a change in the gene sequence, by changing the folding of the chromosomes and affecting gene expression. Behavioural development of the offspring is also influenced by maternal hormones excreted prior to egg-laying or during pregnancy. Recent studies even indicate that hormonal and epigenetic factors may be closely intertwined, for instance where stressful experiences from the parents are passed to future generations by epigenetic changes in stress-related genes. Further, the environment during ontogeny has considerable impact on behavioural development. Absence or presence of maternal care has been shown to have strong effects. Lastly, an animal's genetic background plays an important role in determining its behavioural characteristics. This review focuses on the role of genes, epigenetics and ontogeny in behavioural development,

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http://dx.doi.org/10.1016/j.applanim.2014.06.002
0168-1591/

aiming to show the relationships among these aspects in shaping the individual characteristics of an animal.

2. Epigenetic processes

Epigenetics was first described by Waddington (1942) as heritable genetic modifications where the DNA-structure itself is unchanged. Epigenetic processes cause changes in gene function, but not in gene sequence. Underlying mechanisms are changes in DNA-methylation, histone modifications and transcription factor binding (McGowan et al., 2008). They lead to changes in the folding of the chromosomes, thereby affecting gene expression (Crews, 2008). Some clear examples of epigenetic effects stem from the Dutch famine studies, reporting transgenerational effects of chronic hunger during the winter of 1944 on children and grandchildren of Dutch women who suffered from this famine. Lummaa and Clutton-Brock (2002) reported that babies conceived during, but born after, the famine were smaller and had a lower body weight than babies born before or during the famine or than babies conceived and born after the famine. Furthermore, the famine affected mortality in the grandchildren: daughters from mothers exposed to prenatal hunger during the third trimester of pregnancy were two times more likely to have a stillborn baby than daughters from mothers exposed to prenatal hunger during the first or second trimester or those unexposed to the famine. Exposure to the famine led to faster ageing, and an increased risk of diabetes, obesity and cardiovascular diseases in the children and grandchildren (de Rooij et al., 2006; van Abeelen et al., 2012). Similar studies have been conducted using animal models. In Zebra finches, Naguib et al. (2004) experimentally created small, medium and large broods, using large broods as a model for a high stress environment. Indeed, birds from large broods were smaller, had higher levels of testosterone and a reduced immune competence. Furthermore, daughters from these large-brood mothers were also smaller, when young (Naguib and Gil, 2005) and as adults (Naguib et al., 2006), as indicated by their tarsus and wing length. This also affected the grand-offspring, as daughters from large-brood mothers had a lower percentage of eggs hatch and a smaller number of hatchlings and fledglings in their first breeding attempt (Naguib et al., 2006). These examples from altricial animals clearly show that stress in the parents can be transferred to the offspring and grand-offspring. In pigs, a precocial species, Rutherford et al. (2009) showed that social stress experienced by the mother translated to increased pain sensitivity in the offspring, when subjected to a tail docking procedure. To date, however, little attention has been given to these effects in farm animal breeding and husbandry.

3. Maternal hormones

Maternal hormones are excreted prior to egg laying or during pregnancy. Birds have been an important model species to investigate effects of hormones, as the hormonal composition of the egg does not change anymore once the egg is laid, unlike the situation in mammals. Further, incubation and hatching conditions after egg laying can be experimentally controlled and the hormone levels can be altered by adding hormones to the egg. Maternal hormones can have strong effects on behavioural development of birds (Groothuis et al., 2005). In wild birds, for instance, it has been suggested that mothers use androgens to regulate competition between nestlings from altricial species, providing eggs that are laid later in the clutch with higher levels of testosterone to boost their competitive abilities and begging behaviour (Gil, 2003). Similar effects have been found in laying hens, a precocial species. Janczak et al. (2007) showed that offspring from mothers that were stressed during egg laying, verified by analyzing faecal corticosterone levels of the mothers, were more fearful and less competitive than chicks from unstressed mothers. Similar effects were found when eggs were treated with corticosterone (Freire et al., 2006), indicating that stress hormones play a key role in this process. Indeed, Almasi et al. (2012) recently showed that high levels of circulating corticosterone in captive barn owls translated to higher corticosterone levels in the yolk of subsequently laid eggs. Interestingly, Goerlich et al. (2012) showed that hormonal effects may also be closely related to epigenetic changes. They used a stress model where they subjected chicken parent stocks to intermittent social isolation during the first three weeks of their lives. The offspring were not stressed, yet when parents and offspring were subjected to restraint stress later in life, male offspring from stressed parents showed a much stronger corticosterone response than offspring from unstressed parents. Furthermore, it was shown that brain gene expression of stress-related genes changed both in the stressed parents and in their unstressed offspring, through transgenerational epigenetic inheritance. The study by Goerlich et al. (2012) indicates that stressful experiences from the parents are indeed passed to future generations by epigenetic changes in stress-related genes. These mechanisms could allow animals to rapidly adapt to stressful environments or circumstances (Goerlich et al., 2012). For poultry, however, this also underlines the importance of the parental environment and condition when laying eggs: high stress levels during this period may have negative consequences for behavioural development of the offspring.

4. Post-natal epigenetic effects

Epigenetic effects not only play a role across generations, but may also be brought about after birth by parental behaviour. Clear examples of this are the studies on maternal licking and grooming in mice, another example of an altricial species. Champagne (2008) showed that maternal licking and grooming mice results in epigenetic changes with strong effects on behavioural characteristics of the offspring. High levels of licking and grooming led to differences in methylation of estragen receptors in the offspring, influencing the estragen–oxytocin interactions. In turn, this had a strong influence on the social and maternal behaviour of the offspring. Curley et al. (2008) demonstrated that offspring from wild-type dams, providing normal maternal care, were much less anxious in a novel object test than offspring from mutant dams, providing poor maternal care. Further, daughters from mutant dams, providing poor care,