Genetics of behavioural adaptation of livestock to farming conditions

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Behavioural adaptation of farm animals to environmental changes contributes to high levels of production under a wide range of farming conditions, from highly controlled indoor systems to harsh outdoor systems. The genetic variation in livestock behaviour is considerable. Animals and genotypes with a larger behavioural capacity for adaptation may cope more readily with varying farming conditions than those with a lower capacity for adaptation. This capacity should be exploited when the aim is to use a limited number of species extensively across the world. The genetics of behavioural traits is understood to some extent, but it is seldom accounted for in breeding programmes. This review summarizes the estimates of genetic parameters for behavioural traits in cattle, pigs, poultry and fish. On the basis of the major studies performed in the last two decades, we focus the review on traits of common interest in the four species. These concern the behavioural responses to both acute and chronic stressors in the physical environment (feed, temperature, etc.) and those in the social environment (other group members, progeny, humans). The genetic strategies used to improve the behavioural capacity for adaptation of animals differ between species. There is a greater emphasis on responses to acute environmental stress in fish and birds, and on responses to chronic social stress in mammals.

Keywords: behavioural genetics, fish, cattle, pig, poultry

Implications

At a time of rapid change in animal genetics, with the development of genome-wide analyses with potential applications in the improvement of traits related to livestock welfare, the authors were interested in reviewing the knowledge obtained so far on the quantitative genetics of behavioural traits in four main livestock productions: cattle, pigs, poultry and fish. The mixing of complementary information from these different livestock productions gives arguments for the integration of behaviour into selective breeding programmes.

Introduction

Today, the breeding of livestock species is moving towards the complementary use of local breeds and high-production genotypes to ensure stable production in a wide range of climates and production systems (Food and Agricultural Organization (FAO), 2006), in an attempt to overcome the worldwide nutritional and ecological challenges of the 21st century (Knap, 2005; Ten Napel et al., 2006). The adaptation of animals to the stress elicited by their physical and social environments is one of the first functions under consideration when the objective is to increase production in diversified breeding systems. At all times, animals respond behaviourally to challenges in order to maintain homoeostasis (Koolhaas et al., 1997). Density, food allowance, housing conditions, that is, more or less extensive husbandry and more or less close relationships with other group members, progeny and humans, are among the many factors mediating the behavioural strategies of an animal. High-production livestock genotypes are exported more and more frequently to South America and other tropical countries. Their capacity for adaptation to hot conditions will have a large role to play in their survival, especially when they are sent to countries with both a warmer climate and a lower feed allowance than their country of origin.

Adaptability is defined as the degree to which animals adapt to different environments (Barker, 2009) and is related to functional traits (reproduction and health) that preserve or enhance fitness, that is, survival. In general, functional traits show low heritability and depend more on genotype–environment interactions than production traits (Frankham, 2009). As a consequence, their improvement through artificial
selection is inherently more difficult than that of production traits. The behaviour of an animal (e.g. feeding behaviour, maternal behaviour) contributes to its fitness and can be used as a welfare indicator because its modification may reveal both the existence of stressors and a lack of adaptation to these stressors. Through behavioural adaptation, the animal adjusts its behaviour to favour its fitness in the local environment. Resource allocation theory states that when too much energy is allocated to production, an animal will be unable to cope successfully with environmental changes and/or novel pressures of selection (Beilharz et al., 1993; Schütz et al., 2004). More robust animals are those that maintain performance despite environmental changes (Knapp, 2005).

In recent decades, a combination of genetic selection for production traits and changes in production systems has induced a rise in the prevalence of Behavioural disorders (Rauw et al., 1998; Rauw, 2007). Animals may even develop redirected behaviours, including stereotypes, when stressed, under stress or when pathogens. It appears that the domestication of fish reduces the sensitivity of an animal to its physical environment, to limit excessive fear of humans and to eliminate social disorders that environmental modifications cannot resolve. Genetic research designs are developed to allow the investigation of behavioural genetic strategies that can be used to reduce the sensitivity of an animal to its physical environment, to limit excessive fear of humans and to eliminate social disorders that environmental modifications cannot resolve. Genetic research designs are also developed to allow the investigation of behavioural genetic strategies that can be used to reduce the sensitivity of an animal to its physical environment, to limit excessive fear of humans and to eliminate social disorders that environmental modifications cannot resolve.

The review was performed to investigate whether trends can be observed, across the four major livestock productions: cattle, pigs, poultry and fish, in the genetic capacity of animals for adaptation. Gregariousness and for social skills that enable reproduction even when the population density is high (Mignon-Grasteau et al., 2005). Domesticated populations have diverged from their wild ancestors with respect to a decreased level of activity, as observed in poultry (Jensen et al., 2005; Branciari et al., 2009) and pigs (Bergeron et al., 1996). Fish species for which domestication is at a relatively early stage will shed new light on the topic of this review in comparison with other species. As a result of polikholothemia and because they are raised in fluctuating environments, fish are highly sensitive to stressors in the physical environment. They allocate much energy to maintaining homoeostatic balance when they face environmental perturbations such as changes in the water quality, which occur frequently. This process of coping starts at the fingerling stage, when the eggs are exported to countries and regions with greatly different production ecology from that of the original home of the fish (with respect to water quality, management and pathogens). It appears that the domestication of fish reduces their sensitivity to stressors. Hatchery-reared fish generally exhibit different distribution in the water column, higher boldness and a higher risk of predation when foraging than wild fish (trout: Johnsson and Abrahams, 1991; Lepage et al., 2000; Alvarez and Nicieza, 2003; Sundstrom et al., 2004; salmon: Eunum and Fleming, 1997; Johnsson et al., 2001).

Intensive genetic selection for production causes significant changes in a limited number of traits (e.g. muscle growth, milk yield and egg production). As side-effects, some harmful morphological changes can be observed, and physiological and behavioural disorders may emerge (Rauw et al., 1998; Rauw, 2007). Intensive selection for a few traits tends to increase sensitivity to stressors in the physical environment. This was shown by Väisänen and Jensen (2003) and Huff et al. (2007) in the males of modern breeds of poultry, which display greater difficulties in adjusting to a novel environment than their wild ancestors. However, the main alterations observed relate to the global activity of animals and their social behaviour. Pigs seem to be the most physically sound, whereas both broiler chickens and dairy cows suffer from leg weakness, with the result that disorders of locomotion are reported in these species (Le Bihan Duval et al., 1996; Lovendahl and Munksgaard, 2005) and morphological changes can also develop in Atlantic salmon (Gjerde et al., 2005). Livestock species show increased appetite and feeding activity, which is required to sustain their increased genetic potential for production (e.g. dairy cattle: Dado and Allen, 1994; brown trout: Mambirini et al., 2004). Pure line broilers illustrate an...
extreme case in which selection has increased appetite and growth so greatly that the feed supplied to the breeding animals has to be restricted severely in order to maintain their reproductive potential (Beaumont et al., 2010).

In poultry, there is evidence that chronic stressors have made modern laying hens more fearful of humans than their ancestors (Jones et al., 1988). Selection for early sexual maturity and egg production in hens has increased aggression and social dominance, which leads to higher levels of feather pecking and cannibalism in a large variety of environments (Craig et al., 1975; Kjaer and Mench, 2003). Beak trimming, which was introduced to reduce the prevalence of these behavioural disorders, now causes welfare concern because it inflicts pain in both the short and the long term (Gentle et al., 1997). In fish, an increase in aggression is often feared because the recent selection for growth, which was applied to high-density stocks, has been successful. In pigs and cattle, there is no clear evidence that selection for growth has had a negative influence on the aggression of animals towards other group members, progeny or humans.

Surveys on the genetics of behaviour in livestock science

Literature surveys on the genetics of behaviour have emerged only recently, with most studies starting at the end of the 20th century. Over the last two decades, publications relating to cattle and pigs were more numerous, but genetic studies accounted for a lower proportion (3.5% and 7.5%, respectively) than in studies on poultry and fish (~10% in the two livestock productions over the 2001 to 2011 period; Figure 1). In human society, genetic selection of livestock is a controversial practice. On the grounds of the evident physical modifications and more subtle changes in homeostasis that may lead to pathology, genetic selection is sometimes claimed to lead to deterioration in animal welfare (Grandin and Deesing, 1998; Beaumont et al., 2010; Oltenacu and Broom, 2010). On the other hand, maternal behaviour that is beneficial to animal welfare can be detrimental to the safety of the handler. In addition, modern poultry may no longer be adapted to large spaces because their drive for foraging, and their motivation to use space and general activity have been decreased by genetic selection (Branciari et al., 2009). Welfare is dependent on the animal’s perception of its environment and its reaction to environmental stimuli (Dantzer and Mormède, 1983), which may evolve with selection. Herein, we use behaviour as an indicator of welfare, assuming that this external response is well correlated to the inner state of the animal. Dawkins (2004) presented the many advantages of using behaviour in this context, because its measurement is the result of the animal’s decision-making processes and, ultimately, it is the expression of the animal’s motivationalaffective state.

Studies have targeted hotspot issues that are species specific. A good relationship between livestock and humans is a priority in large mammals. In pigs, there has also been increased interest in sociality because welfare policies recommend raising these animals in groups. In fish and poultry, experimental approaches that include a greater number of traits can be implemented.

In this review, we will refer mainly to estimates of heritability obtained from the statistical analysis of phenotypes collected either from selection nucleus populations or from experimental lines obtained by divergent selection for a behavioural trait of interest. The emergence of genomic tools has shed light on novel methodologies of investigation and selection in livestock, with the possibility of targeting genes of interest directly. The detection of quantitative trait loci (QTL) in experimental populations is a powerful approach to understanding the genetics of behavioural adaptation to farming conditions. However, the proportion of QTL detected for behavioural traits is low (<3% in the four livestock productions studied, http://www.animalgenome.org/cgi-bin/QTLdb/index).

**Figure 1** Scientific publications dedicated to the genetics of behaviour in cattle, pigs, poultry and fish (Source: Web of Science database http://apps.webofknowledge.com/; keywords: (heritability or QTL) and behaviour and (cattle or poultry or pig or fish) – accessed 15/02/2012). QTL = quantitative trait loci.

**Behavioural tests used to assess the genetics of adaptation**

Tests developed in model species such as laboratory mice can be used for quantitative genetic studies in livestock (Table 1) because they are reasonably meaningful for a wide range of species. However, readers should be aware that different motivational systems and cognitive abilities exist in different species (Dantzer, 2001), so that there are some limits to the extrapolation of results across species. The tests are usually intended to elicit a response in the animal either to its physical environment or, as independently as possible, to its social environment. Response to an acute stress can be assessed in isolated animals placed in an unfamiliar environment or in presence of other group members. The open-field test, which investigates the animal’s reaction to a non-social situation, is a basic test that is common to the four livestock productions. Its principle is to induce a conflict between aversion and voluntary exploration of a novel environment. Locomotion and exploration are good indicators of adaptation to change, if they decrease as fast as the animal adjusts to novelty. However, some animals may react with a state of apparent tetany when they enter the test environment. This observation illustrates that a large range of variation in the behavioural response to challenges exists among families, populations and species. This remark is valid
Table 1 Tests used for the genetic assessment of the behavioural response of animals to stressors in the physical and social environments of production in cattle, pig, poultry and fish

<table>
<thead>
<tr>
<th>Test and descriptiona</th>
<th>Cattle</th>
<th>Pig</th>
<th>Poultry</th>
<th>Fish</th>
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</thead>
<tbody>
<tr>
<td>Response to the physical environment</td>
<td>D: Dairy; B: Beef</td>
<td>H: laying Hen; B: Broiler; Q: Quail; T: Turkey</td>
<td>S: Salmon; T: Trout; Z: Zebra</td>
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<tr>
<td>NO RESTRAINT – ISOLATED OPEN-FIELD TEST: reaction when isolated from group members</td>
<td>D: after removal of the group from home pen, one animal is moved back with cattle present in the adjacent pen [1]b</td>
<td>Pig into a van with floor divided by painted lines into several sections, with wood shavings spread over [3]</td>
<td>Q: in a box with observer hidden [6]</td>
<td>T: 1 week after isolation from the stock tank to a glass tank screened from visual disturbance [8]<em>; ARENA TEST in a tank including a shelter place, an open area and a T-MAZE TEST [9]</em></td>
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<td>NO RESTRAINT – GROUP NOVEL OBJECT TEST</td>
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<td>Response to the social environment</td>
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<td>Response of dam to offspring SOCIAL CONTACT MAINTAINED PROGENY-HANDLING TEST</td>
<td>B: during catching, removing and earmarking of the calf [20]</td>
<td>Handler picks up a piglet in the pen and squeeze it or plays the tape record of a screaming piglet [SCREAM TEST 21]</td>
<td>When piglets are weighed [22]</td>
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<td>SOCIAL CONTACT DISRUPTED SEPARATION TEST</td>
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<td>Test and descriptiona</td>
<td>Cattle</td>
<td>Pig</td>
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<td>D: Dairy; B: Beef</td>
<td>H: laying Hen; B: Broiler; Q: Quail; T: Turkey</td>
<td>S: Salmon; T: Trout; Z: Zebra</td>
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<tr>
<td>Response to human or predator</td>
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<td>NO RESTRAINT ACCEPTANCE OF HUMAN: voluntary approach of the animal or human approach</td>
<td>B: GROUP: human approach at the feeder [1]</td>
<td>GROUP: a human, who the pigs are unfamiliar with, enters the pen and stands motionless in the pen [10]</td>
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<td>S: ISOLATED: a simulated predator added in the test tank (trout) equipped with a tunnel with refuge [23]*</td>
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<td>MODERATE RESTRAINT – GROUP HANDLING TEST: separation attempt from the flock</td>
<td>B: handler attempt to separate one animal from the group into a smaller arena [24]</td>
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<td>HIGH RESTRAINT – ISOLATED RESTRAINT TEST: reaction of the animal to a restraint (by device or human constraints)</td>
<td>B: CHUTE TEST: while restrained in the head gate [27]</td>
<td>BACK TEST: pig placed gently onto its back and restrained [10]</td>
<td>Q: BACK TEST: quail placed on its back and restrained with a hand on sternum and the other cupping the head [12]</td>
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</table>

*Test is defined according to the level of restraint applied by the experimenter on the animal, whether the test is performed on animals isolated from the rearing group (ISOLATED) or on animals kept among the rearing group (GROUP) and the name of the test (in capital). When the experimental condition is specific, precisions on the test are given in the cell of the species.


*Tests used for breed comparison only.
for most recorded behaviours: they show phenotypic variation in relation to different coping strategies that distinguish between animals with a flight–flight response and those with a freeze–hide response (Koolhaas et al., 1997). Accordingly, the novel object test can be used to differentiate between shy and bold animals.

The behavioural response depends on conditional factors. It may be relatively less intense when the test is performed in the home environment rather than in a novel environment, when a period of adaptation to change precedes recording, when other group members are present in the neighbourhood or when humans are not visible or remain at a distance. Conversely, a relatively strong response is elicited when the change is made more suddenly (e.g. switching on the light, forceful handling to move the animal to the experimental location).

Different tests have been developed to account for different social contexts and various levels of restraint in beef cattle. These tests have been modified more recently for use in pigs. The interference from humans is variable: the animals may be relatively unrestrained, given more room to allow the expression of motivational processes among the rearing group, or tightly restrained, so that both sources of social interaction (humans and other group members) can have confounding effects on reactivity. The docility test, the output of which depends on the animal’s voluntary cooperation, elicits a less intense response than the on-scale test or the chute test.

Single-trait assessment of behaviour is influenced strongly by the environment and past experience of the animal (Forkman et al., 2007). Moreover, interactions between the physical and the social environment may affect the behavioural response in all the tests that are described in the review. Experimental designs often target several behavioural components; this results in a non-specific response but gives a clear advantage in the assessment of the animal’s personality. Even if the use of behavioural tests is generalized to different species, the correlation between genotype and environment with regard to behaviour depends on the animal’s voluntary cooperation, elicits a less intense response than the on-scale test or the chute test.

Genetics of the behavioural response to changes in the physical environment

Estimates of the heritability of the behavioural responses to acute and chronic changes in the physical environment are presented in Table 2. Genetic correlations with production traits are shown in Table 3.

Response to acute stressors

The genetic variation in the response to an open field or novel object has been investigated mainly in poultry. Latency to move and locomotion in the open field show highest heritability in broilers and hens (Table 2). Exploration of a novel object is moderately heritable in broilers, and a few QTL were identified that correlated with a QTL for growth on Golgi-localized, gamma-ear-containing, Arf-binding protein 1 (GGAI) in hens (van der Poel et al. in Buitenhuis et al., 2005). Breed variation in excitability in a novel environment also exists in pigs (Shea-Moore, 1998). The gene associated with the porcine stress syndrome impairs the capacity for adaptation to stressors. Therefore, nn pigs have been eradicated from various populations. Behavioural differences have also been found among other genotypes: pigs with the genotype Nn at the locus for the ryanodine receptor gene RYR(1) are less active than NN pigs in the open-field test (Fabrega et al., 2004). Désautès et al. (2002) found different QTL in pigs to be associated with locomotion on SSC1, or with exploration on SSC8. In beef cattle, locomotion in open field shows moderate heritability and is correlated unfavourably with growth and milk production (Phocas et al., 2006). In dairy cattle, QTL associated with vocalization and locomotion when isolated from the herd are located mainly on BTA16 and BTA19 (Gutierrez-Gil et al., 2008). Using different strains of zebra fish, several QTL for boldness when facing novel objects have been highlighted. In addition, a genomic region that influences anti-predator behaviour shows some co-location with QTL for resistance to heat shock and growth capacity in water of varying salinity (Wright et al., 2006).

Response to chronic stressors

When exposed to chronic stressors, the reactions of animals can be more durable. For example, exposure to high ambient temperature has a direct impact on animal survival and health, and is associated with modification in locomotion and feeding activities. These behavioural responses indicate the level of heat tolerance of an animal. Thermal stress has a significant impact on feed intake and feed efficiency in poultry (Chen et al., 2008).

Global activity. Global activity is assessed by postural changes and locomotion, with low to moderate heritability reported in the three terrestrial species (min $h^2 = 0.05$; max $h^2 = 0.35$). In pigs, lameness is more heritable than locomotion ($h^2 < 0.10$). Conversely, locomotion shows breed variation in genetic estimates for dairy cattle, and high heritability was observed (Boelling et al., 2007). Moreover, locomotion is a good indicator of health because it is genetically correlated with the presence of claw disorders ($r_g > -0.40$; Laursen et al., 2009). On the basis of the results from a study of divergent selection for growth, Nestor et al. (2008) showed alteration in walking ability in turkeys. Walking ability was moderately heritable and correlated favourably with survival ($r_g > 0.60$) and with hip and leg strength ($r_g > 0.85$; Quinton et al., 2011). At the genetic
Table 2  Estimates of heritability ($h^2$) and QTL identification * for the behavioural response of animals to stressors in the physical and social environments of production in cattle, pig, poultry and fish

<table>
<thead>
<tr>
<th>Test situation</th>
<th>Stress applied</th>
<th>Type of behaviour</th>
<th>Cattle</th>
<th>Pig</th>
<th>Poultry</th>
<th>Fish</th>
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<td><strong>Response to the physical environment</strong></td>
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<td>OPEN-FIELD ACTIVITY</td>
<td>ACUTE</td>
<td>LATENCY TO MOVE</td>
<td>D: standing alert QTL 5 [1]</td>
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<td></td>
<td>LOCOMOTION</td>
<td>B: running time $h^2$ 0.23 [5]</td>
<td>locomotion time QTL 1 [6]</td>
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<td>D: locomotion index QTL 6 [1]</td>
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<td>B: N escape attempts $h^2$ 0.09 [5]</td>
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<td>EXPLORATION</td>
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<td>Rooting and sniffing time QTL 1 [6]</td>
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<td></td>
<td>Novel object $h^2$ 0 [9]</td>
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<td>VOCALIZATION</td>
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<td>ON-FARM ACTIVITY</td>
<td>CHRONIC</td>
<td>POSITION</td>
<td>D: lying time $h^2$ 0.01 [12]</td>
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<td></td>
<td></td>
<td>D: standing time $h^2$ 0.14 to 0.23 [13]</td>
<td>Lying time QTL 3 [13]</td>
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<td>Drinking time QTL 6 [15]</td>
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<td>LOCOMOTION</td>
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<td>B: continuous mobility $h^2$ 0.14 [18]</td>
<td>Leg action QTL 7 8 [13]</td>
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<td>D: stepgait $h^2$ 0.05 to 0.10 [19, 20]</td>
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<td>D: lameness $h^2$ 0.01 to 0.22 [20, 24]</td>
<td>Lameness $h^2$ 0.01 to 0.40 [25, 26]</td>
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<td>EXPLORATION</td>
<td>DAILY FEEDING</td>
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<td>B: time $h^2$ 0.28 to 0.36 [27, 28]</td>
<td>Time $h^2$ 0.36 to 0.44 [28, 29]</td>
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<td>QTL 8 [13]</td>
<td>QTL 4/2 [31, 33]</td>
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<td>D: time $h^2$ 0.14 [12]</td>
<td>Frequency $h^2$ 0.43 [28, 29]</td>
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<td>B: frequency $h^2$ 0.38 [27]</td>
<td>QTL 4/2 [31, 33]</td>
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<td>B: rate $h^2$ 0.51 [28]</td>
<td>Rate $h^2$ 0.44/0.50 [29, 34]</td>
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<td><strong>Response to the social environment</strong></td>
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<td>SOCIAL MOTIVATION</td>
<td>ACUTE</td>
<td>SEARCH CONTACT</td>
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<td>DYADIC ENCOUNTER</td>
<td>ACUTE</td>
<td>DOMINANCE</td>
<td>B: score $h^2$ 0.20 to 0.36 [18, 37]</td>
<td>Latency to attack $h^2$ 0 [9]</td>
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* QTL = quantitative trait loci

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<thead>
<tr>
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<tr>
<td>ON-FARM AGGRESSION [GROUP]</td>
<td>ACUTE</td>
<td>AGGRESSION</td>
<td>Female delivery $h^2$ 0.09 to 0.32 [41, 42]</td>
<td>B: reception $h^2$ 0.25 [10]</td>
<td>S: fighting time $h^2$ 0.25 [40]</td>
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<td>Female receipt $h^2$ 0.02 [42]</td>
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<td>Bullying time $h^2$ 0.31 [39]</td>
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<td>Fighting time $h^2$ 0.42 [39]</td>
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<td>Bullying receipt $h^2$ 0.08 [39]</td>
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<tr>
<td>ON-FARM AGGRESSION [GROUP]</td>
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<td>AGGRESSION</td>
<td>Female social rank $h^2$ 0 [47]</td>
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<td></td>
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<td></td>
<td>Male social rank $h^2$ 0.47 [47]</td>
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<td></td>
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<td></td>
<td>Tail-biting $h^2$ 0 to 0.27 [48]</td>
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<tr>
<td>Response of dam to progeny</td>
<td>PROGENY REMOVAL</td>
<td>ACUTE</td>
<td>REACTIVITY</td>
<td>B: reactivity $h^2$ 0.32 to 0.36 [5, 50]</td>
<td>Reactivity $h^2$ 0.08 to 0.16 [44, 52, 53]</td>
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<td></td>
<td></td>
<td>PROGENY</td>
<td>ACUTE</td>
<td>AGGRESSION</td>
<td>Aggression $h^2$ 0.08 [52]</td>
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<td></td>
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<td></td>
<td>Crushing $h^2$ 0.06 [54]</td>
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<td></td>
<td>Cannibalism $h^2$ 0.20 to 0.90 [55, 56]</td>
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<td></td>
<td>Cannibalism QTL 7 [57, 58]</td>
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<tr>
<td>ON-FARM OBSERVATION</td>
<td>CHRONIC</td>
<td>MATERNAL ABILITY</td>
<td>B: protection $h^2$ 0.14 to 0.42 [51]</td>
<td>Maternal score $h^2$ 0.02 to 0.08 [53]</td>
<td>H: egg incubation QTL 3 [59]</td>
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<td></td>
<td>B: protection score $h^2$ 0.09 [49]</td>
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<tr>
<td>Response to human or predator</td>
<td>ON-FARM OBSERVATION</td>
<td>ACUTE</td>
<td>APPROACH</td>
<td>D: flight distance QTL 4 [1]</td>
<td>Voluntary if isolated $h^2$ 0.38 [60]</td>
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<td></td>
<td>Voluntary if in group $h^2$ 0/0.03 [10]</td>
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<td>Aggressive score $h^2$ 0.11 [53]</td>
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<td></td>
<td>Protest to move score $h^2$ 0/0.22 [53]</td>
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<td></td>
<td>Good sow score $h^2$ 0.04 [53]</td>
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<tr>
<td>HANDLING SEPARATION</td>
<td>ACUTE</td>
<td>LOCOMOTION</td>
<td>B: running time $h^2$ 0.21 [5]</td>
<td>B: N attempts $h^2$ 0.26 [5]</td>
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<tr>
<td></td>
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<td>ESCAPE</td>
<td>B: docility score $h^2$ 0.11 to 0.64 [61]</td>
<td>B: docility index $h^2$ 0.18 [5]</td>
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<td></td>
<td>DOCILITY</td>
<td>B: aggression index $h^2$ 0.20 [5]</td>
<td>B: ease handling QTL 9 [62]</td>
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Table 2 Continued

<table>
<thead>
<tr>
<th>Test situation</th>
<th>Stress applied</th>
<th>Type of behaviour</th>
<th>Cattle</th>
<th>Pig</th>
<th>Poultry</th>
<th>Fish</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>D: Dairy; B: Beef</td>
<td></td>
<td></td>
<td>H: Laying Hen; B: Broiler; Q: Turkey</td>
</tr>
<tr>
<td>HIGH-RESTRAINT</td>
<td>ACUTE</td>
<td>LOCOMOTION</td>
<td>B: on-scale mobility $h^2$ 0.14 to 0.36 [64]</td>
<td>On-scale activity score $h^2$ 0.23/0.30 [65]</td>
<td>H: restraint with rope QTL 5 [7]</td>
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<tr>
<td></td>
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<td></td>
<td>B: mobility QTL 6 [64]</td>
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<td></td>
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<td></td>
<td>B: Chute score $h^2$ 0.11 to 0.33 [63]</td>
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<tr>
<td>IMMOBILITY</td>
<td></td>
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<td>Back-test time $h^2$ 0.49 [9]</td>
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<td>H: immobility time $h^2$ 0.28 [66]</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>B: mobility QTL 6 [64]</td>
<td></td>
<td></td>
<td>Q: immobility time $h^2$ 0.12 to 0.23 [62]</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>B: Chute score</td>
<td></td>
<td></td>
<td>Q: immobility time QTL 1 [67]</td>
</tr>
<tr>
<td>ESCAPE</td>
<td>ACUTE</td>
<td>FLYING</td>
<td>B: No. of attempts $h^2$ 0 to 0.05 [61]</td>
<td>No. of attempts $h^2$ 0.53 [9]</td>
<td>Q: No. of attempts QTL 1 [67, 68]</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>B: flying time $h^2$ 0.49 [27]</td>
<td></td>
<td></td>
<td>H: No. of attempts QTL 2 [7]</td>
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<tr>
<td>ON-FARM</td>
<td>ACUTE</td>
<td>MILKING</td>
<td>B: flying time $h^2$ 0.14 to 0.17 [69]</td>
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<tr>
<td>OBSERVATION</td>
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<td></td>
<td>B: speed score $h^2$ 0.11 to 0.44 [73, 63]</td>
<td>D: speed $h^2$ 0.10 to 0.29 [70, 71, 72]</td>
<td>D: speed QTL 5 [72]</td>
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<td></td>
<td></td>
<td></td>
<td>D: docility $h^2$ 0.07 [72]</td>
<td></td>
<td></td>
<td>D: nervosity QTL 5 [72]</td>
</tr>
</tbody>
</table>

QTL = quantitative trait loci.

*The number of different chromosomes where QTL region(s) were detected is specified.

Table 3 Genetic correlations (minimum/maximum) and identified chromosomal co-location between the behavioural response of animals to stressors in the physical and social environments and production traits in cattle, pig and poultry

<table>
<thead>
<tr>
<th>Test</th>
<th>Stress applied</th>
<th>Behaviour trait</th>
<th>Cattle</th>
<th>Pig</th>
<th>Poultry</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>D: Dairy; B: Beef</td>
<td>H: laying Hen; B: Broiler; T: Turkey</td>
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</tr>
</tbody>
</table>

### Response to the physical environment

**OPEN-FIELD ACTIVITY**
- **ACUTE** LOCOMOTION
  - B: GROWTH * running time $0.42/0.37$ [1]
  - B: GROWTH N attempts $0.30/0.24$ [1]
  - B: MILK running time $0.25$ [1]
  - B: MILK N attempts $0.19$ [1]
  - H: GROWTH activity QTL [21]

**OPEN-FIELD ACTIVITY**
- **ACUTE** EXPLORATION
  - GROWTH leg action score $0.12/0.24$ [9]
  - PROBORN $-0.11/-0.07$ [10]
  - PROLOSS $-0.20/-0.05$ [10]

**ON-FARM ACTIVITY**
- **CHRONIC** LOCOMOTION
  - D: MILK lameness $0.24/0.48$ [2]
  - LEANNESS $-0.21/-0.24$ [9]
  - FCR $0.15/0.05$ [9]
  - PROBORN $-0.11/-0.07$ [10]
  - PROLOSS $-0.20/-0.05$ [10]

**ON-FARM ACTIVITY**
- **CHRONIC** ACTIVITY
  - GROWTH walking $0.37/0.31$ [22]
  - T: SURVIVAL walking $0.65/0.69$ [22]

**ON-FARM ACTIVITY**
- **CHRONIC** DAILY FEEDING RATE
  - B: GROWTH $0.53$ [3]
  - B: LEANNESS $-0.22/-0.20$ [3]
  - B: MEAT $-0.39$ [3]
  - B: FCR $-0.83$ [3]
  - FCR $0.21/0.03$ [11, 12]
  - B: FCR $0.15/0.01$ [25]

**ON-FARM ACTIVITY**
- **CHRONIC** DAILY FEEDING FREQUENCY
  - GROWTH $0.19/0.11$ [11, 12]
  - LEANNESS $0.10/0.15$ [11, 12]
  - MEAT $-0.28/0.12$ [12]
  - B: FCR $0.10/0.25$ [25]

**ON-FARM ACTIVITY**
- **CHRONIC** DAILY FEEDING DURATION
  - GROWTH $0.27/0.48$ [11, 12]
  - LEANNESS $-0.25/-0.11$ [11, 12]
  - MEAT $-0.30/-0.24$ [12]
  - B: FCR $0.19/0.03$ [11, 12]

### Response to the social environment

**SOCIAL MOTIVATION**
- **ACUTE** LOCOMOTION
  - GROWTH $0.13$ [13]
  - LEANNESS $-0.08$ [13]
  - MEAT $-0.21$ [13]
  - PROBORN $0.15$ [14]
  - H: GROWTH 1 QTL [24]

**ON-FARM AGGRESSION [GROUP]**
- **ACUTE** AGGRESSION
  - GROWTH tail-biting $0.27$ [15]
  - GROWTH social rank $-0.66$ [16]
  - LEANNESS tail-biting $0.28$ [15]
  - MEAT social rank $0.40$ [16]

**ON-FARM AGGRESSION [GROUP]**
- **CHRONIC** AGGRESSION
  - H: GROWTH delivery $0/0.66$ [26, 27]
  - H: GROWTH gentle receipt QTL [21]
  - H: GROWTH gentle delivery $-0.11/0.47$ [23]
  - H: EGG severe delivery $-0.38/-0.11$ [23]

**PROGENY REMOVAL**
- **ACUTE** REACTIVITY
  - TNB $-0.23/-0.26$ [14]
  - PROGROWTH $-0.49/-0.13$ [17]
### Table 3 Continued

<table>
<thead>
<tr>
<th>Test</th>
<th>Stress applied</th>
<th>Behaviour trait</th>
<th>Cattle D: Dairy; B: Beef</th>
<th>Pig H: laying Hen; B: Broiler; T: Turkey</th>
</tr>
</thead>
<tbody>
<tr>
<td>Response to human or predator</td>
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<tr>
<td>HANDLING SEPARATION</td>
<td>ACUTE</td>
<td>DOCILITY</td>
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<td>MOTION</td>
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<td>HIGH RESTRAINT</td>
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<td>HIGH RESTRAINT</td>
<td>ACUTE</td>
<td>FLYING</td>
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<tr>
<td>ON-FARM OBSERVATION</td>
<td>ACUTE</td>
<td>MILKING</td>
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**QTL** = quantitative trait loci; **ECG** = electrocardiogram; **FCR** = feed conversion ratio.

*GROWTH: growth rate; MILK: milk yield; LEANNESS: modified from results on backfat depth; MEAT: meat production assessed from muscle areas and carcass lean content; FCR: feed conversion ratio; TNB: total number born; PROGROWTH: progeny growth; PROBORN: progeny number born; PROLOSS: progeny loss. Precisions on the definition of the trait are specified where necessary.

level, ease of locomotion is correlated positively with growth in pigs and milk yield in dairy cattle, whereas a negative correlation with growth was found in broilers (Table 3). In pigs, several QTL related to chronic activity were detected mainly on SSC5 and SSC7 and SSC8 (Reiner et al., 2009). The QTL for chronic locomotion detected on SSC8 may be similar to the one for exploration in open field.

Using a divergent selection for dustbathing activity in quail, Gerken et al. (1988) found a negative relationship with fear-related traits (i.e. latency to emerge from a box and response to a tonic immobility test), which was interpreted as a response to the anxiety associated with not performing this maintenance activity. Later, Olsson and Keeling (2005) suggested that the selection operates directly on the fear response because dustbathing is realized only when the bird is not at risk of predation. The pre-laying behaviour of laying hens (sitting activity) is among the rare stereotypes observed in livestock. Experimental selection for this trait showed that the reestablishment of normal behaviour (increased sitting activity) is possible (Mills et al., 1985). However, Beaumont et al. (2010) did not find sufficient ethical grounds to select for this behaviour, especially now that hens are reared on the floor instead of in cages, which increases their general activity and energy expenditure.

Feeding activity. In recent years, the genetics of feeding activity (duration, rate and frequency of visits to the food source) has been studied increasingly because of its relationship to feed efficiency, and because measurement has been facilitated by the use of automatic devices. Genetic variation in feeding activity exists in the three terrestrial species reviewed and shows large breed variation (e.g. cattle: Nkrumah et al., 2007; pig: Labroue et al., 1997; poultry: Howie et al., 2011). Feeding frequency and feeding rate are more heritable (min = 0.38; max = 0.58) than feeding duration (Table 2). The genetic correlations between feeding behaviour (duration) and daily feed intake are null to positive in mammals and negative in broilers. Animals that show a genetic predisposition to eat more are known to grow faster but they also store more body fat than others. Growth is correlated favourably with feeding rate in cattle and pigs. Feeding rate is correlated unfavourably with meat production, whereas feeding duration and leanness show negative or null genetic associations (Labroue et al., 1997; Robinson and Oddy, 2004). Growth and leanness are not genetically correlated with feeding frequency in pigs, but a G/A substitution at the MC4R gene (SSC1), which encodes a melanocortin receptor, has a positive effect on fatness, growth and daily feed intake, probably mediated through the central control of appetite (Kim et al., 2000). Zhang et al. (2009) identified a QTL for the number of visits of pigs to the feeder on SSC7 that did not co-locate with QTL for feed intake and conversion neither to the QTL for feeding frequency (Houston et al., 2005), and a suggestive QTL on SSC9 that may co-locate with a growth QTL. In broilers, feeding activity is not genetically correlated with growth (Howie et al., 2011), which suggests that no substantial change in this activity has been induced by selective breeding in that species.

Residual feed intake (RFI) is a measure of feed efficiency that accounts for the animal’s energy requirements for production and maintenance. The RFI indirectly measures the quantity of buffer resource available for global activity, and a genetic association between the two traits has been found in the three terrestrial species (hens: Braastad and Katle, 1989; Luiting and Urrf, 1991; cattle: Richardson et al., 1999; Herd et al., 2004; pigs: Sadler et al., 2011): animals with lower RFI are less active. Chronic frustration associated with the reduced feeding activity of the animals may also appear. Negative phenotypic correlations have been estimated between RFI and the response to acute stress in poultry and cattle (Luiting and Urrf, 1991; Richardson and Herd, 2004; Rauw, 2007). The reduction of RFI by selection should increase feed efficiency, with a low impact on growth, but at the expense of reduced feeding activity, owing to its positive correlation with feeding duration (pig: $r_g = 0.44$, von Felde et al., 1996; beef cattle: $r_g = 0.35$, Robinson and Oddy, 2004). Montanholi et al. (2010) observed that high-RFI steers make more visits to the feeder during the night than more efficient steers. Altan et al. (2004) found that low-RFI quail were less fearful, whereas Minvielle et al. (2002) did not find any significant correlation between RFI and the results of the tonic immobility test. In laying hens selected for lower RFI, reduced sensitivity to stress is observed under natural conditions (Schütz et al., 2002), but these genotypes are selected in cages.

Perspectives in selective breeding that account for behavioural adaptation to changes in the physical environment

Reducing the sensitivity of animals to stress is a major issue in the successful expansion of production. The strategies used to produce animals that are able to overcome the perturbations in their physical environment and return homeostasis are dependent on the type of stress the animals face. On the one hand, Mormède et al. (2011) suggest that animals that produce a strong physiological response to acute stress adapt better to the stressor. The parallel cannot be made for behavioural responses where a phase of inhibition of all behavioural patterns is followed by a phase of activity. Selection for a greater activity or a greater exploration in the open field could be a strategy used to increase the capacity of livestock to adapt to acute stressors. However, in beef cattle, the genetic correlations of behavioural responses in the open-field test to production traits contradict this assumption. Conversely, a high degree of heritability has been found for latency to move and locomotion in laying hens. Selection for reduced reactivity to stress could be foreseen in that species to decrease the distress caused by changes in the physical environment. This strategy is acceptable provided that an optimum value is targeted, that favourable genetic correlations with production traits are estimated and that farming conditions are improved at the same time to avoid placing animals under conditions of stress.

When faced with long-term stressors or repeated modifications in their environment, animals with a lower perception of stress should be preferred to avoid large
unfavourable effects on production (Forkman et al., 2007). Animals displaying more exploration might also show a higher behavioural adaptation in both the short and the long term; this trait deserves further genetic investigation. Abnormal behaviours (e.g. pre-laying behaviour in hens, circular shoaling in Atlantic salmon) show substantial genetic variation and heritability but have not been selected against because these reactions do not necessarily indicate poor welfare (Dawkins, 2004) and they may help the animal to cope with its physical environment.

Within a line or a rearing group, animals can exhibit different feeding strategies but achieve the same feed intake (Tolkamp et al., 1998 in Howie et al., 2011). This behavioural flexibility could be used for selective breeding in specific environments, especially in broilers, in which feeding behaviour shows low genetic correlation with growth. This strategy based on feeding behaviour traits could be complementary to strategies based on feed consumption if it is confirmed such as in pigs that different chromosomal regions affect the two traits categories. Selection for lower RFI is a sensitive approach that should be addressed with caution because it might reduce the buffer capacity of the animal in its reaction to stress (Rauw, 2007), especially under hot conditions. For instance, laying hens with high RFI cope better with high temperatures (Bordas and Minvielle, 1997) but are more fearful of humans (Schütz et al., 2004; Wright et al., 2006). A large study was designed by Mills and Faure (1991) to test the genetic impact of social skills on growth, survival and other behaviours in Japanese quail. More social birds (high line) had more affiliation with other group members (use of distress calls), benefited from facilitated access to feed among the flock, performed more non-aggressive pecking and were more easily captured than less social birds (low line). Social motivation persisted in adulthood but was correlated with greater aggression. In subsequent generations, birds from the high line became more sensitive to both acute social stressors (mixing with unfamiliar animals) and chronic social stressors (rearing in large groups), and thus developed a lower capacity for adaptation. They showed social attraction towards any other group member, whereas quail from the low line showed bonding with familiar animals (Schweitzer et al., 2009). Formanek et al. (2008) showed that selection to be also efficient when applied on juvenile quails.

Conversely, social aggression used to establish dominance is assessed most often with the resident–intruder test, which was developed for mice and then generalized to livestock species. Heritability shows mainly low values in mammals (min = 0; max = 0.36), and high values in fish (H^2 > 0.40; Table 2). Growth is reduced genetically in pigs that are aggressive towards intruders (Velie et al., 2009). Measurement of aggressiveness within a group is an alternative procedure that elicits a response to crowding. In fish and poultry, social competition is evaluated mainly by measurement of survival rate and growth, but tests of aggression also exist (Table 1). The outcome of aggression refers to complex genetic determinism that depends on morphological aspects of the opponents (body weight and fur or feather pigmentation) and is strongly sex related.

Lahti et al. (2001) found evidence of a genetic basis for aggressive behaviour in brown trout; they observed that sea-run populations were more aggressive than lake-run or non-migratory populations. Conversely, Reinhardt (2001) did not find such a difference in Masu salmon. Divergent selection for plasma cortisol responsiveness to an acute confinement stress in trout showed that fish from the high line were more mobile in the presence of an intruder (Øverlie et al., 2002). Expected to react to environmental changes that involve other group members, progeny or the farmer. The genetic correlations with production traits are given in Table 3.

**Interactions with other group members**

**Behavioural response to acute stress.** The comfort provided by the presence of other group members after a period of isolation is a welfare-related concept that has been used in the estimation of the genetic tendency towards social motivation in quail and fish models. The experimental approach used to assess re-grouping in fish (shoaling) is similar to the social-reinstatement test used in quail, and is interpreted as an anti-predator response. Associated traits show moderate heritability (min = 0.22; max = 0.66). QTL were detected in the two species and an association with a QTL for growth was found in hen (Schütz et al., 2004; Wright et al., 2006). A large study was designed by Mills and Faure (1991) to test the genetic impact of social skills on growth, survival and other behaviours in Japanese quail. More social birds (high line) had more affiliation with other group members (use of distress calls), benefited from facilitated access to feed among the flock, performed more non-aggressive pecking and were more easily captured than less social birds (low line). Social motivation persisted in adulthood but was correlated with greater aggression. In subsequent generations, birds from the high line became more sensitive to both acute social stressors (mixing with unfamiliar animals) and chronic social stressors (rearing in large groups), and thus developed a lower capacity for adaptation. They showed social attraction towards any other group member, whereas quail from the low line showed bonding with familiar animals (Schweitzer et al., 2009). Formanek et al. (2008) showed that selection to be also efficient when applied on juvenile quails.

**Genetics of the behavioural response to changes in the social environment**

Estimates of the heritability of behavioural responses to acute and chronic changes in the social environment are presented in Table 2, with distinction between cases in which the animal is expected to react to environmental changes that involve other group members, progeny or the farmer. The genetic correlations with production traits are given in Table 3.

**Interactions with other group members**

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Lahti et al. (2001) found evidence of a genetic basis for aggressive behaviour in brown trout; they observed that sea-run populations were more aggressive than lake-run or non-migratory populations. Conversely, Reinhardt (2001) did not find such a difference in Masu salmon. Divergent selection for plasma cortisol responsiveness to an acute confinement stress in trout showed that fish from the high line were more mobile in the presence of an intruder (Øverlie et al., 2002)
than fish from the low line; this suggests a link between fear and an aggressive response.

Aggression shows higher heritability in pigs than in poultry and salmon (\(h^2 = 0.25\)), with the duration of fighting after mixing being more heritable (\(h^2 = 0.43\)) than the number of aggressive episodes and the score of skin lesions (Turner et al., 2009). A candidate gene approach emphasized that the AVPR1B gene, which encodes a vasopressin receptor, and the NR3C1 gene, which encodes a glucocorticoid receptor, are involved in the causation of aggression (Muráni et al., 2010). Age was shown to be an important source of variation in hens, and the heritability of feather pecking increases with age. Buitenhuis et al. (2003) found different QTL on several chromosomes that were related to receiving feather pecking at young and adult ages. When attacker and receiver were distinguished, the heritability of being aggressive was moderate (\(h^2 > 0.20\)) and higher than that of receiving aggression in both pigs and poultry. Genetic correlations between aggression and growth vary among studies in poultry and pigs; they are unfavourable to production in salmon (Vollestad and Quinn, 2003). In hatcheries, strong genotype–environment interactions control aggression (Mesa, 1991; Vandeputte and Prunet, 2002). Selection for rapid growth yields a correlated response in aggression only when food is defensible (experiment on medaka: Ruzzante and Doyle, 1991). In Atlantic salmon, as in rainbow trout, the cortisol response to acute confinement (crowding) is highly heritable (\(h^2 = 0.41\); Pottinger and Carrick, 1999; \(h^2 = 0.50\); Fevolden et al., 2002) and predicts the behavioural response of fish in a number of situations (Overal et al., 2006). With divergent selection, the highly responsive fish were more active but showed a slower return to feeding activity when placed in a novel environment than poorly responsive fish (Overal et al., 2005; Schjolden et al., 2005). The social effects observed on growth relied on the mixing of lines with different personalities. Furthermore, Ruiz-Gomez et al. (2008) demonstrated the complexity of the relationship between line and behaviour; inconsistent changes in behaviour were shown after a change of country. Three suggestive QTL for cortisol response to confinement were mapped in sea bass (Massault et al., 2010) and major genes for the same trait are suspected in rainbow trout (Vallejo et al., 2009). Two studies of divergent selection for behavioural response in the resident–intruder test were implemented by Bakker (1985) and Francis (1984) on three-spined sticklebacks and paradise fish, respectively. The two experiments showed unequal responses but highlighted a common genetic basis of aggressiveness and sexual behaviour. The high line consisted almost entirely of males and the low line of females.

In the pig, aggression between sows is moderately heritable (\(h^2 = 0.30\)) and shows a low but favourable correlation with piglet production (Hellbrügge et al., 2008). Assessments on rangeland show that the heritability of aggressiveness in cattle, although rarely estimated, is around 0.36 (Silva et al., 2006).

**Behavioural response to chronic stress.** Social behaviour is associated positively with welfare in mammalian breeds that are less intensively selected for production (Le Neindre, 1984; Breuer et al., 2005). Social rank at the feeder is highly heritable in male pigs with genetic correlations unfavourable to growth but favourable to meat content in pigs (Jonsson, 1985). Behavioural responses to chronic stressors in the physical environment may translate into some stereotypes such as long-lasting deviant relationships with other group members and altered relationships with humans. For instance, in pigs, tail-biting is a redirected foraging behaviour that would correspond to the behaviour shown before feeding. Breuer et al. (2005) identified genetic variation in tail-biting in Landrace pigs (\(h^2 = 0.27\)) but none in Large White pigs. Wilson et al. (2010) performed a genome-wide association study in which different chromosomal regions were suggested to be associated with severe tail-biting. At the genetic level, tail-biting is correlated positively with growth and leanness (Breuer et al., 2005).

It was shown recently that mild and severe feather pecking correspond to different neural mechanisms, which involve responses to acute and chronic stressors in hens (Hugues and Buitenhuis, 2010). Indeed, feather pecking is a normal behaviour, but when its intensity increases, it corresponds to a redirected behaviour (also related to foraging and exploration) that results from multiple causes, including fear (Keeling and Jensen, 1995). There is considerable breed variation in feather damage and cannibalism, and the phenotypic relationship between the two traits varies between populations. The heritability of feather pecking ranges from moderate to high values and severe pecking is correlated unfavourably to egg production (Buitenhuis et al., 2004). The genetic analysis of feather pecking in hens is a topic on which much progress has been made in the last two decades towards a deep understanding of its biological pathways. There is evidence that many genes with minor effects are involved in the causation of feather pecking: QTL have been found, with a majority on GGA1. Keeling et al. (2004) showed that a QTL for feather damage in chickens coincided with the dominant white pigmentation locus. Biscarini et al. (2010) carried out a genome-wide association study and detected different chromosomal regions involved in feather damage in hens. Laying hen populations divergently selected for feather pecking were created successfully in parallel to a control line (Kjaer et al., 2001; Su et al., 2005). More aggressive birds (high line) vocalized and walked for a longer time in an open-field test than birds from the low line (Jones et al., 1995) in association with a neural hyperactive disorder. This was interpreted as indicating differences in social motivation. Flisikowski et al. (2009) demonstrated an association with a dopamine receptor, DRD4, on GGA5, which is known to be associated with exploration behaviour. The same kind of selection was implemented in naked-neck broilers by Boulay et al. (2006), who measured the number of pecks delivered on a bunch of feathers. Birds from the high line exhibited lower pecking activity and higher feather coverage. In fact, the animals reacted to the modification of their physical environment rather than the modification of their social environment. In both experiments, egg production was
lower in the high line. Feed efficiency was lower in hens from the high line as a result of their poor feather condition when compared with that of hens from the low line.

Female feather pecking is associated favourably with earlier egg-laying (Jensen et al., 2005), but the egg production of those who show feather pecking is lower than that of non-peekers (Buitenius et al., 2004).

Maternal behaviour

The survival of progeny depends strongly on maternal care during the first days of life. Bonding is more critical in cattle than in pigs because it is an exclusive link, which makes adoption more difficult in bovine species (Poindron, 2005). The intensity of stress is increased with human handling or with disruption of contact with the progeny. Several indications of maternal care after birth have been scored in cows (Grignard, 2001; Phocas et al., 2006) and sows (Vangen et al., 2005), in order to evaluate the behavioural response to acute and chronic stressors (e.g. birth vs. maternal ability during lactation). Higher heritability was observed for the reaction of the dam to removal of the newborn and handling by humans in beef cattle (−0.30) than in sows (Grandinson et al., 2003; Hoppe et al., 2008). Maternal ability score during lactation in pigs also shows low heritability (Vangen et al., 2005). Heritability is higher in Herefords than in Angus cows and has been shown to vary with age in that breed (Hoppe et al., 2008).

In pigs, abnormal maternal behaviour, including crushing but also savaging the progeny, is an important issue in female European lines. Savaging of progeny is moderately to highly heritable. On-farm assessment has been rarely analysed and provides very low values of heritability. The postural reaction of the female to a screaming piglet produced the highest estimate ($h^2 = −0.10$). This could be a sign of a higher genetic predisposition to react to involuntary crushing in some sows, and these sows also benefit from a higher genetic merit for progeny growth (Grandinson et al., 2002). Several QTL related to maternal cannibalism have been observed, with a promising one on the X chromosome (Quilter et al., 2007; Chen et al., 2009). In hens, Xu et al. (2010) found three QTL involved in egg incubation behaviour, which was put at a disadvantage by selective breeding; among these QTL one was linked to the DRD1 gene, which encodes a dopamine receptor.

Phocas et al. (2006) found, in beef cattle, that the more maternal cows showed a slightly higher milking ability, but Hoppe et al. (2008) found no association of maternal reaction to progeny removal with progeny growth. Higher maternal ability is genetically correlated with lower progeny mortality in pigs (Grandinson et al., 2003; Hellbrügge et al., 2008), whereas Hoppe et al. (2008) found no genetic association in cattle.

Response to human or predator

Genetic influences on fear of humans have been identified by comparison of various genotypes and crosses in the four livestock productions (cattle, Morris et al., 1994; poultry and laying hens, Craig et al., 1983; duck, Arnaud et al., 2010; red jungle fowl, Håkansson et al., 2007; rainbow trout, Woodward and Strange, 1987; pig, Terlouw, 2005). Fear of humans is correlated unfavourably with growth at the genetic level. Although the response to human handling is an important trait in fish, the heritability of associated behavioural traits has not been investigated, according to the literature. In zebrafish, the QTL detected for shoaling tendency could not be linked to QTL for growth or fatness (Wright et al., 2006).

In cattle, there is large variation among breeds with respect to the fear of human handling. Limousine cows are more fearful than Jersey cows when reared in their natural environment, but the difference disappears if they are placed in a similar environment (Fisher et al., 2001). Under moderate restraint, the heritability of the docility score is generally moderate, but it is higher in Simmental than in Limousine cows and null in Angus (Gauly et al., 2001). Schmutz et al. (2001) found co-locating QTL involved in the determination of a mobility score and habituation to handling with high restraint in beef cattle and suggested an association with genes encoding for dopamine receptors. The reaction of cattle to a crush or a weighing scale is assessed with a test that is used in the United States and Australia as an on-farm selection criterion for personality in calves (Fisher et al., 2001; Beckman et al., 2005), and this trait has the advantage of a null or negative association with growth. A few QTL that influence the unprovoked flight distance of cattle from a feeder, and habituation (represented by the difference in score between two repeats of the same behavioural test), have been detected and co-location or pleiotropic effects between them were found (Gutierrez-Gil et al., 2008). Some QTL have been detected that are common to the test situations described above, on chromosomes BTA1, BTA5 and BTA9. In dairy cattle, behaviour at milking shows moderate heritability and a low but unfavourable genetic correlation with milk yield. A large favourable correlation between behaviour at milking and handling exists ($f_g = 0.74$), and neither trait is genetically correlated with aggression at feeding (Burrow, 1997). It would be of interest to investigate whether the QTL observed on BTA5 that are associated with ease of handling in dairy cattle and beef cattle refer to the same gene.

In pigs, the response to humans often implies a voluntary approach by the animal to the human, and shows higher heritability when assessed on animals isolated from other group members and when close contact with the human is assessed ($h^2 = 0.50$; Table 2). The flight score shows lower heritability in pigs than in cattle. A lower flight speed is correlated favourably with growth in both species, and with leanness in cattle but not in pigs. Vangen et al. (2005) found moderate heritability ($min = 0$; max $= 0.22$) for the response of sows to handling during routine management. The restraint-back test is commonly used in quail and pigs, although the subsequent tonic immobility induced by release of the animal is an innate anti-predator response in birds only (Gallup and Gordon, 1979). This test enables the assessment of emotional reactivity, which influences the facility of handling (Mignon-Grasteau and Faure, 2002) and relates to the coping strategies...
of proactive and reactive animals. Restlessness during the back test shows an unfavourable genetic correlation with leanness in pigs (Velie et al., 2009).

In poultry, the response of tonic immobility shows higher (moderate) heritability in pigs than in laying hens and Japanese quail (Table 2). Relationships to production traits are not obvious (e.g. Schütz et al., 2004). In quail, Minvielle et al. (2002) observed the absence of genetic correlation between tonic immobility and production traits, which contradicts the hypothesis that fear and production are related. Similarly, the QTL found for the duration of tonic immobility did not co-locate with the QTL for growth and feed intake (Beaumont et al., 2005; Minvielle et al., 2005). In hens, different QTL influence fear of humans in birds of different ages and co-locate with QTL for exploration of a novel object. Divergent selection for the duration of tonic immobility was analysed extensively in Japanese quail by Mills and Faure (1991) and Jones et al. (1994) and in hens by Campo and Carnicer (1993). Quail selected for a long period of tonic immobility exhibit stronger fear reactions to various stimuli, human included (e.g. Minvielle et al., 2002; Faure et al., 2006).

Perspectives on selective breeding that account for behavioural adaptation to changes in the social environment

In fish, modifications observed in other livestock species, with respect to negative social interactions, should be considered to anticipate behavioural problems associated with intense selection for growth.

Selection against aggression, applied on young mammals, would be of double benefit if it also made dams more maternal (Lovendahl et al., 2005; Hellbrügge et al., 2008). Aggression and maternal behaviour are genetically correlated negatively in both the pig and some cattle breeds, making it possible to improve both behaviours. A strong limitation on their use in selection, however, is that social traits are poorly repeatable in these species (Janczak et al., 2003; Hoppe et al., 2008). However, selection against aggression and for ease of handling is promoted in beef cattle, and the use of a behavioural index is recommended (Gauly et al., 2001; Benhajali et al., 2010). In dairy cattle, Bowman et al. (1996) incorporated measurement of both docility and milking speed in their breeding programme, which had the objectives of reducing fear and increasing maternal care. There are also several sources of evidence of a positive genetic relationship between fear of humans and aggression in hens (e.g. Rodenburg et al., 2004). In general, the behavioural response to humans can be related to social tendencies or maternal behaviour (in mammals) because fear modulates all reactions. Insights from research using fish models will help to increase the general understanding of the biological mechanisms behind fear and aggression. As in cattle, selection of pigs for docility can make sense, but the best genetic strategy to apply is not straightforward. The example of quail, which shows that selection for social motivation is successful at any age but that too great an increase in sociality is risky because it can increase aggression, ought to be kept in mind (Richard et al., 2008). In any species, optimum behaviour must be targeted in selective breeding in order to avoid deviant responses.

Although it is possible to select against behaviours genetically, the improvement of farm conditions is in many cases chosen as a solution to prevent stereotypes such as tail-biting activity in pigs. However, Craig and Adams (1984) considered that genetic selection is needed to reduce cannibalism in hens, together with feather pecking and injuries caused by escape and behaviour related to avoidance of humans. Feather condition might be useful as a criterion for selection, but discrepancies between studies are highlighted, which stresses the complexity of this social disorder and the attempt to develop realistic tactics. Beaumont et al. (2010) recommend selecting against mortality instead.

Attention should also be paid to the fact that, although the animal is the statistical unit used by geneticists, the group is often the unit studied by ethologists. Variation between and within breeds and populations in the behavioural response to stressors can be large. A major limitation to the success of selection for behaviour is the relationships with other group members, which make individual responses interdependent among the group. An indirect appreciation of sociality can be obtained with the use of social models for production traits. Bijma (2011) and Rutten et al. (2006) reported significant heritable components of social interactions that had effects on growth in beef cattle, laying hens, quail and pigs, but not in cod or Nile tilapia. This approach, which enables integration of both the animal’s performance and its influence on that of other group members in the genetic evaluation, is attractive because it promotes sociality indirectly. Biscarini et al. (2010) showed the advantages of a social genetic model used to select against feather pecking in hens. A better understanding of the molecular mechanisms of action of the genes located on GGA1 (which have a strong effect on growth and a wide array of pleiotropic effects on welfare traits) may precede marker-assisted selection (Wiren and Jensen, 2010).

Conclusions

Accounting for behavioural traits in selective breeding could together improve animal welfare and improve production, reduce labour costs and increase handler safety. The four livestock productions studied do not face the same farming conditions and intensity of selection. The tests and behavioural traits used in experimental design are extrapolated from one species to another, but their validation as predictors of the animal’s capacity to adapt to environmental changes is lacking. The rare genes identified that are associated with behaviour relate to motivational processes that demonstrate clearly that behavioural traits are important welfare indicators. Further genetic characterization, including the discovery of epistatic, pleiotropic and dominance effects among adaptive traits and production traits, and the use of high-output recording techniques are required for the development of strategies of selection. A synthetic variable that encompasses several traits recorded in different tests...
may be more appropriate than a single-trait approach in selective breeding. Both behavioural and physiological measures should be implemented because they are interdependent in allowing the interpretation of the level of welfare (Dawkins, 2004).

Behavioural traits can be as heritable as some production traits that are considered for genetic improvement. The responses to both acute and chronic stressors need to be considered when analysing the capacity of an animal to adapt behaviourally to changes in the environment because they refer to different mechanisms of adaptation. In all species, some behavioural traits and production traits are controlled partially by the same pool of genes, either favourably in terms of improving both animal welfare and production (e.g. lower fear and growth) or unfavourably (e.g. feeding duration and feed efficiency in mammals). The results are influenced by the past history of selection of the species studied. Given the trade-off between fitness and production, it is time to define breeding goals that are more balanced between production and fitness traits (Kanis et al., 2004; Olsson et al., 2006; Barker, 2009). Knowledge of the genetics of behavioural adaptation will expand in the coming decades and should stimulate a greater dynamic in livestock breeding programmes.

References


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Genetics of behavioural adaptation in livestock


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