

Contribution of genetics to the study of animal personalities: a review of case studies

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Summary

The need for evolutionary studies on quantitative traits that integrate genetics is increasing. Studies on consistent individual differences in behavioural traits provide a good opportunity to do controlled experiments on the genetic mechanisms underlying the variation and covariation in complex behavioural traits. In this review we will highlight the contribution of genetic studies in animal personality research. We will start with reviewing the evidence that shows how much variation in animal personality traits is genetic, and connect this to knowledge from human personality studies. We will continue by considering the nature of that variation, its generation and maintenance. Finally we will point to further possibilities for studying the genetics of animal personalities. We will underline the importance of integrating both proximate and ultimate approaches when studying the evolution of animal personalities.

Keywords: behavioural syndrome, quantitative genetics, genotype environment interaction, reaction norm, phenotypic plasticity, context dependence, *Parus major*.

Introduction

Individual differences in e.g. aggression, neophobia, exploration and boldness in social and non-social conditions have been investigated in behavioural, physiological, psychological, ecological and agricultural studies, and

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have been demonstrated in many domesticated and wild animal species (for reviews see Gosling & John, 1999; Koolhaas et al., 1999; Wilson et al., 1994). Individual differences in a range of correlated behavioural traits have been labelled as temperament (Réale et al., 2000), coping strategies (Bennus et al., 1991; Wechsler, 1995), coping styles (Koolhaas et al., 1999), behavioural syndromes (Sih et al., 2004a, b) or animal personalities (Dall et al., 2004; Gosling & John, 1999), comparable with human personalities (Eysenck & Eysenck, 1985; John, 1990; Zuckerman, 1991). The consistency of trait combinations and the resulting high level of correlation between behavioural traits allow this identification of animal personalities.

The idea that individual behavioural differences were only the raw material natural selection acted on gradually changed to the concept that being different might well be adaptive in itself. In that case, behavioural traits are not only characterised by an adaptive mean flanked by non-adaptive variation, but the variation in itself may also be maintained by natural selection (Barnard & Sibley, 1981; Lott, 1984; Wilson, 1998). A rapidly increasing number of studies demonstrate that this thinking may have consequences for many current ecological models (Dall et al., 2004; Sih et al., 2004a) and some have shown that these behavioural differences shape variation in decisions of individual animals and thereby also in life-history traits (see for a review, Dingemanse & Réale, 2005).

Studies on fitness and natural selection in any trait require models that incorporate explicit genetic mechanisms, since the expected response to natural selection depends on the underlying genetic structure. Although genetic approaches have proven to be important to answer questions about adaptive significance and the evolution of life-history traits, the genetic basis of behavioural traits in studies with an ecological or evolutionary context has been neglected (Boake et al., 2002). Most information available on the structure of inheritance of personality traits comes from either human (Benjamin et al., 1997; Ebstein et al., 2000; Bouchard, 2004) or rodent studies (Sluyter et al., 1996). Although genetic studies on human personalities are immensely valuable, the step from describing variation in personality in humans to a more evolutionary approach is a big hurdle (Bouchard, 1994). Animal models have proven to be a useful tool in getting a better grip on the underlying genetic mechanisms of behavioural traits (e.g. Wehner et al., 2001). Unfortunately, most genetic studies on personality traits were performed on populations bred in captivity over a long time (laboratory animals and husbandry)

and therefore give us little insight into the evolutionary processes that have shaped these traits (Merilä & Sheldon, 2001).

The purpose of this review is to highlight the contribution of animal genetic studies for understanding the evolution of the trait complexes we call personalities, as well as the maintenance of variation in personality in a population. We will start with reviewing the evidence that shows how much variation in personality traits in a bird species is genetic, and connect this to the knowledge from studies on humans and domestic animals. We will continue by considering the nature of that variation. Then we will elaborate the ideas how this variation is generated and how this fits into the theory of the occurrence of variation in personality in natural populations. Finally we will point to future possibilities for studying the genetics of animal personalities in controlled laboratory conditions and in natural populations.

Heritability of personality traits

Most behavioural traits are expected to be at least partly heritable and to influence life-history traits, thereby being the target of selection. Therefore, the identification of heritable influence (heritability) is the essential starting point for all evolutionary research on any behavioural trait (Boake et al., 2002). The heritability is defined as the relative amount of genetic variation (V_G) in relation to the phenotypic variation (V_P) (Falconer & Mackay, 1996). Two different types of heritabilities must be distinguished. The broad-sense heritability, is an estimate of the proportion of variance due to additive (V_A) and nonadditive (i.e. dominance variance V_D and interaction variance, V_I), while the narrow sense heritability is an estimate of the proportion of variance due to only additive genetic effects. A special case of a narrow-sense heritability is the realized heritability; a realized heritability corresponds to the change in mean phenotype as a consequence of selection as a fraction of applied selection (Lynch & Walsh, 1998). Therefore, this heritability measure represents an estimate based on the actual genetic change across generations. Narrow-sense heritability is estimated by parent-regression and predicts the selection response; broad-sense heritability is estimated by the variance of groups of full sibs (Table 1).

Many studies have looked at the heritable component of human personalities. In a review, Bouchard & Loehlin (2001) reported broad-sense heritabilities for the Big-Five personality domains in humans (extraversion, agreeableness, conscientiousness, neuroticism and openness; Costa Jr & McCrae,

Table 1. Heritability estimates and the methods how they are derived from studies on personality traits on different animal species. Given are: the method with which the heritability was calculated, the personality trait, the study species. Significant heritabilities are indicated by *.

Method	Personality trait	Study species	h^2	Reference
Bayesian model	Aggression	<i>Gasterosteus aculeatus</i>	0.01/ 0.14	(Bell, 2005)
Bayesian model	Boldness	<i>Gasterosteus aculeatus</i>	0.04/ 0.00	(Bell, 2005)
Parent-offspring	Exploration	<i>Parus major</i>	0.22*	(Dingemanse et al., 2002)
Full-sib	Exploration	<i>Parus major</i>	0.37*	(Dingemanse et al., 2002)
Selection experiment	EEB	<i>Parus major</i>	0.55*	(Drent et al., 2003)
Parent-offspring	Exploration	<i>Parus major</i>	0.25*	(Drent et al., 2003)
Full-sib	Risk-taking	<i>Parus major</i>	0.32*	(van Oers et al., 2004b)
Selection experiment	Risk-taking	<i>Parus major</i>	0.19*	(van Oers et al., 2004b)
Mother-offspring	Boldness	<i>Ovis canadensis</i>	0.21	(Réale et al., 2000)
Animal model	Boldness	<i>Canis domesticus</i>	0.27*	(Strandberg et al., 2005)
Animal model	Dominance	<i>Pan troglodytes</i>	0.63*	(Weiss et al., 2000)
Animal model	Openness	<i>Pan troglodytes</i>	-0.11	(Weiss et al., 2000)
Animal model	Dominance	<i>Pan troglodytes</i>	0.66*	(Weiss et al., 2002)
Animal model	Well-being	<i>Pan troglodytes</i>	0.40*	(Weiss et al., 2002)

1989; John, 1990) that ranged from 40% to 50%. Genetic studies that have calculated heritabilities of animal personality traits include both studies on the basis of the 'Big Five' as in humans, as well as studies that have a more trait oriented approach, e.g., heritabilities for aggression, exploration, boldness and risk-taking behaviour.

Already in the early 1980's rodents have been bred in several major selection experiments for e.g., explorative behaviour, aggression and locomotor activity. They showed a strong response in these artificial selection experiments, which implies strong genetic influences (for a review see Wimer & Wimer, 1985). This is confirmed in more recent laboratory studies on the genetic background of personality traits (Daniewski & Jezierski, 2003; Isles et al., 2004), although most studies on the genetics of personality in rodents and production animals nowadays use different methods (see below) to identify the amount of variation genes have on phenotypic variation (Flint, 2004; Gershenfeld & Paul, 1998; Gordon & Hen, 2004).

The classification of variation in behavioural profiles in terms of their sensitivity to environmental challenges is largely built on the work with lines of captive-bred wild house mice, selected for Long and Short attack latency (LAL and SAL) (van Oortmerssen & Bakker, 1981). Nevertheless, genetic studies on wild species investigating a set of consistent individual differences in behaviour are rare. An exception is a study on Chimpanzees (*Pan troglodytes*). Chimpanzee personality factors consist of the 'Big Five' personality traits as found in humans, and dominance (King & Figueredo, 1997). Weiss et al. (2000) reports a narrow-sense heritability of 63% for the factor causing dominance in Chimpanzees by using the pedigree of known family relationships (Table 1). The heritability estimates for other personality traits were much lower, and not significantly different from zero. In a second study, they expanded this with a genetic analysis on subjective well-being, a subscale of human emotionality (Tellegen et al., 1988) and found a heritability of 40% (Weiss et al., 2002).

Another exception is the study on the great tit (*Parus major*). The great tit is a common monogamous territorial passerine, which breeds in secondary holes and artificial nest-boxes in all types of wooded areas throughout Europe and parts of Asia and North Africa (Perrins, 1965). Individuals have to cope frequently with temporal and spatial variation in their social and non-social environment. Both laboratory studies and studies in natural populations have shown that individuals differ in an array of correlated behavioural and physiological parameters both social and non-social (Groothuis & Carere, 2005). These studies have given evidence for the existence of behavioural profiles or personalities. To investigate the genetic basis of a correlated set of personality traits a four-generation, two-way selection experiment for 'fast' and 'slow' early explorative behaviour was started in 1994 (Drent et al., 2003). Early exploratory behaviour is a combined score for two personality traits: boldness towards a novel object and exploration of a novel environment. In 2000, this was followed by a selection experiment using another behavioural trait: the latency to return to a feeding bowl after a mild startle (van Oers et al., 2004b). Realized heritabilities were $54.0 \pm 5.0\%$ ($V_P = 31.01$, $V_E = 14.27$) and $19 \pm 3\%$ ($V_P = 0.27$, $V_E = 0.22$) for early exploratory behaviour and risk-taking respectively (Table 1). An offspring-parent regression showed that 30% of the variation in explorative behaviour between hand-reared nests of great tits could be attributed to their wild-caught parents (Drent et al., 2003). These findings were confirmed in a field

study, where an analysis on known family relationships revealed comparable heritability estimates (Dingemanse et al., 2002) (Table 1).

In bighorn ewes, boldness was measured by the trappability of an individual. Bold ewes were captured more often in a trap in which they were attracted by salt. A heritability of 21% was calculated through a mother offspring regression (Table 1; Réale et al., 2000). However, probably due to the high standard error and the low sample size this was not significant ($p > 0.05$). An indication that a genetic effect is present was given by the high resemblance of offspring from the same female compared to the resemblance to offspring from other females.

Significance of heritabilities

So, significant heritabilities have been found for several personality traits in different model systems. Yet, differences in the level of heritability of the same trait in the same model system might be considerable. Heritability measures should be interpreted with caution, since they are not simple reflections of the amount of genetic variation in a trait, but a statistic which integrates effects of selection, structure and the interrelationship between variance components (Stirling et al., 2002). A low heritability can indicate a low amount of additive genetic variation, which could be eroded due to natural selection (Houle, 1992; Stirling et al., 2002). However, alternatively, these variation in heritabilities could not be the result from differences in the amounts of additive genetic variance, but also be caused by large differences in residual variation ($V_R = V_P - V_A$) (Houle, 1992; Merilä & Sheldon, 2000; Stirling et al., 2002; McCleery, 2004), where the residual variation consists of variance due to any other genetic or environmental cause (Falconer & Mackay, 1996). Moreover, the heritability depends upon the environment of the population; heritability estimates are sensitive to environmental variation, both including measurement error and small population size, and are only limited to the population in which it is estimated. Furthermore, laboratory estimates of heritability may not be good predictors of heritability in natural populations, owing to the reduction in environmental variability in the laboratory (Riska et al., 1989; but see Dingemanse et al., 2002; Drent et al., 2003). The results of several comparative studies have shown that laboratory estimates are somewhat higher than, but not different from, values in natural populations (Weigensberg & Roff, 1996; Bryant & Meffert, 1998; Blanckenhorn, 2002). Therefore, to get a better understanding of the link between the evolvability of a trait a good knowledge of the structure of its genetic variation is needed.

Genetic structure of animal personalities

The variation in heritability estimates could be caused by the existence of nonadditive (Falconer & Mackay, 1996) or indirect genetic effects (IGEs; Wolf et al., 1998) in the inheritance of these traits (Table 1: compare the parent-offspring estimates with the full-sib estimates). To study the genetic structure it is necessary to break up the different components of genetic variation: additive genetic, genetic dominance, genetic maternal (additive and dominant) and to look at sex-dependent expression (Mather & Jinks, 1971). Genetic dominance is the consequence of an interaction between alleles at a single locus. Dominance variance was often considered as relatively unimportant since it does not predict the response to selection (Crnokrak & Roff, 1995; Fisher, 1930). It can however influence the heritability of traits when during bottleneck events nonadditive genetic variance can be 'converted' into or affect additive genetic variance (Crnokrak & Roff, 1995). The main candidate for IGEs is a maternal effect. Genetic maternal effects arise when the genotype of a mother has a phenotypic effect on her offspring (Mousseau & Fox, 1998). Maternal effects can influence heritability estimates since they are transmissible from parent to offspring and result in phenotypic correlations between genetic relatives that share the same maternal environment (Mousseau & Fox, 1998). This is especially the case when heritability estimates are derived from mid-parent and maternal full and halve sib families (Falconer & Mackay, 1996).

To date, only one complete quantitative genetic study looked at the genetic structure of a combination of two personality traits (boldness and exploration). In a study on great tits the analyses of crosses (between the selection lines for fast and slow early explorative behaviour, (i.e. using the original lines, F1 crosses and back-crosses) enabled the break up of the components of variation (van Oers et al., 2004c). With the use of least squares methods (Mather & Jinks, 1971), it was shown that besides a considerable additive genetic effect, there is also an important role for genetic dominance in the structure of inheritance (Table 2). The negative sign of the dominance contribution indicates that low exploration is dominant over high exploration and that low boldness is dominant over high boldness (Table 2). Maternal genetic effects were present, but relatively low and the expression of personality traits in the great tit turned out to be independent of the offspring sex.

Table 2. Estimates of composite genetic effects underlying difference in exploration and boldness in great tits. Where: m = group mean, $[a]$ = additive genetic component, $[d]$ = genetic dominance component, $[a]_m$ = additive maternal component, $[d]_m$ = dominant maternal component and $[sde]$ = sex-dependent component. The probabilities of the estimates refer to the t test. ¹Derived from separate model. *Significant at the 0.05 level. **Significant at the 0.01 level. ***Significant at the 0.001 level. Data from (van Oers et al., 2004c).

	Exploration	Boldness
m	0.057 ± 0.044	0.049 ± 0.074
$[a]$	$0.935 \pm 0.044^{***}$	$0.696 \pm 0.092^{***}$
$[d]$	$-0.400 \pm 0.149^{**}$	$-0.839 \pm 0.101^{***}$
$[a]_m$	0.101 ± 0.185	$0.133 \pm 0.049^{**}$
$[d]_m$	-0.317 ± 0.221	-0.155 ± 0.198
$[sde]$	-0.047 ± 0.303^1	0.077 ± 0.090^1
df	3	2
χ^2	0.369	3.704

One possible explanation for a high amount of additive genetic variation is that a mutation-selection balance has been build up, thereby capturing genetic variation (Merilä & Sheldon, 1999). This hypothesis is only valid when the variation in these traits is influenced by many loci and selection pressures are stable. It is commonly assumed, but hardly proven, that many loci with small effects are responsible for the variation in polygenic traits like personality traits. Many alternative models and theories have been developed to determine under what conditions genetic variation may be maintained (Byers, 2005), but we choose not to go into detail about that subject.

The substantial genetic dominance effect in the great tit can have several explanations. First, high dominance leads to high dominance variance. Second, a difference in scaling between traits and fitness leads to non-explained genetic variance surfacing as dominance variance or epistatic variance if variation in the trait is maintained by selection. Relative dominance variance is likely to be higher in traits that are closely related to fitness compared to e.g. morphological characters, since additive genetic variance is expected to be eroded by selection (Stirling et al., 2002). Behavioural traits like physiological traits are expected to be intermediate. A measure for this relative

dominance (D_α) is:

$$D_\alpha = \frac{V_d}{V_d + V_a} \quad (1)$$

In a compilation of studies, Cnokrak & Roff (1995) present the mean D_α for life-history (0.59), behavioural (0.28), physiological (0.53) and morphological (0.10) traits in natural populations. They show that traits closely related to fitness have high relative contributions of V_d compared to V_a . The relative measure of dominance in our study was $D_\alpha = 0.44$, which is, as expected between morphological and life-history traits (Stirling et al., 2002).

Genetic maternal effects should not be confused with phenotypic maternal effects. The method of selection experiment minimized phenotypic maternal effects. Since the intention was to draw conclusions on the genetic structure of personality traits, the social (parental and group) influence was minimised by standardising the treatment of the captive breeding pairs (i.e., the collection of eggs before incubation, and the use of foster parents, cross-fostering and hand rearing after an age of 10 days after hatching to raise the chicks). However, in natural situations phenotypic maternal effects (e.g., through maternal hormones in the egg) may possibly be important sources of phenotypic variation (Eising et al., 2001; Groothuis & Carere, 2005).

Genetic correlations

Since the existence of (genetic) correlations between traits is the main prerequisite for the existence of animal personalities, it is surprising that only few studies have analysed genetic correlations. In Table 3 we report phenotypic and genetic correlations between personality traits in several study systems.

Estimates of genetic correlations are fundamental to understanding the evolution of behavioural constructs like personalities or behavioural syndromes. Genetic correlations between traits might constrain evolutionary change of either of these traits, since during selection on one trait genetic correlations influence the selection response of the other. In a natural population, genetic correlations might provide information on past selection for combinations of particular traits (Lande & Arnold, 1983; Maynard Smith et al., 1985).

Table 3. Some genetic and phenotypic correlation estimates between animal personality traits on different species. Given are: the personality traits, the study species and the correlation coefficient. Significant correlations are indicated by *.

Trait1	Trait2	Study species	<i>R</i>	Reference
Phenotypic				
Aggression	Boldness	<i>Gasterosteus aculeatus</i>	0.48*	(Huntingford, 1976)
Boldness	Reactivity	<i>Euprymna tasmanica</i>	0.13	(Sinn & Moltschanowskyj, 2005)
Exploration	Flexibility	<i>Parus major</i>	-0.53*	(Verbeek et al., 1994)
Risk-taking	EEB	<i>Parus major</i>	0.45*	(van Oers et al., 2004b)
Boldness	Docility	<i>Ovis canadensis</i>	-0.31*	(Réale et al., 2000)
Assertiveness	Sociability	<i>Crocuta crocuta</i>	0.03	(Gosling, 1998)
Sociability	Agreeableness	<i>Crocuta crocuta</i>	0.42*	(Gosling, 1998)
Genetic				
Risk-taking	EEB	<i>Parus major</i>	0.84*	(van Oers et al., 2004a)
Dominance	Well-being	<i>Pan troglodytes</i>	1.00*	(Weiss et al., 2002)
Aggression	Boldness	<i>Gasterosteus aculeatus</i>	0.84*/ 0.26	(Bell, 2005)
Aggression	Boldness	<i>Canus domesticus</i>	0.37*	(Strandberg et al., 2005)

Since consistent individual differences are generally accepted to be adaptive (Buss & Greiling, 1999; Wilson, 1998), the coherence between different personality traits could therefore also be a product of natural selection. This functional architecture of personality traits has already been debated in various approaches to human personality research. All approaches have in common that they report an underlying genetic structure that causes the coherence of these traits (Bouchard & Loehlin, 2001). Genetic correlation between traits is due to pleiotropic effects and/or linkage disequilibrium (Falconer & Mackay, 1996). In the case of pleiotropy, individual genes have effects on several traits. The effects of a gene on two traits might themselves be independent, or structurally linked (De Jong, 1990). Independence of the effect of a gene on different traits is usually assumed in quantitative genetics, rather than structural pleiotropy. A genetic correlation does not act as a constraint on the outcome of selection if the effects of a gene on two traits are themselves independent. Linkage disequilibrium exists when traits are affected by different sets of genes, but a selective force generates and preserves particular combinations of alleles at a particular locus (Price & Langen, 1992; Falconer

& Mackay, 1996; Lynch & Walsh, 1998). Selection against particular combinations of traits, cause other combinations to be more frequent. However, unless correlational selection is strong and chronic (Sinervo & Svensson, 2002), linkage disequilibria build up by correlational selection are expected to weaken rapidly (Bulmer, 1989; Falconer & Mackay, 1996). Linkage disequilibria contribute to genetic correlations if pleiotropy exist, and are the sole source of genetic correlations if pleiotropy does not exist. In total, pleiotropy, the effects of one gene on different traits, is the major cause of genetic correlations.

In great tits, boldness towards a novel object and exploration of a novel environment showed to be phenotypically correlated with several other behavioural and physiological traits within the same context (Table 3, Groothuis & Carere, 2005). Another study analyzed two selection experiments on three independent personality traits, boldness and explorative behaviour (early exploratory behaviour) and risk-taking behaviour. Genetic correlations were calculated using the response and the correlated response to artificial selection (van Oers et al., 2004a). The genetic correlations ranged from 0.51 ± 0.15 to 0.66 ± 0.34 , based on individual values, and from 0.84 ± 0.27 to 1.00 ± 0.32 based on nest means (Table 3). In Chimpanzees a genetic correlation was found between two personality traits, subjective well-being and dominance (Weiss et al., 2002).

The different behavioural traits might therefore have a common genetic basis, possibly favouring the evolution of sets of behavioural traits in natural populations. The large genetic correlations of these studies are one indication for this. A second indication for the selection for sets of behavioural traits was found by Dingemanse and co-workers, showing differences in selection pressures on explorative behaviour for males and females and different selection pressures over three different years, in a study on exploration in a natural population (Dingemanse et al., 2004). Considering the differences in selection pressure together with the prerequisites of correlational selection, the genetic correlations found will be built up and maintained by correlated selection only if variation in natural selection on one trait co-varies with variation in selection on another trait. This seems to be unlikely and therefore structural pleiotropy seems to be a potential explanation for the found genetic correlations.

A question that stays unanswered up till now is which behaviours are correlated across which contexts and how stable these genetic correlations

are (Sih et al., 2004b). A study on sticklebacks (*Gasterosteus aculeatus*) found genetic correlations for some populations but not for others (Bell, 2005), which suggests that the mechanisms that causes traits to be correlated are not necessarily difficult to uncouple.

Domain specificity vs domain generality

Animal personalities seem to be relatively inflexible stable characteristics as is also proposed in human personality research (Kagan et al., 1988). This seems in contrast to theories (Sih et al., 2004a) and findings of e.g. Wilson and co-workers (Coleman & Wilson, 1998; Wilson et al., 1994; Wilson, 1998), who state that every important situation that influences survival and reproduction potentially requires a different adaptive response, at least if these traits are adaptive. In the latter case, it might be therefore reasonable to expect a lack of phenotypic correlations between traits of the same individuals in different contexts. This begs the question whether animal personalities are stable over all environments, and consequently, the question whether animal personalities exist.

Domain specificity or context dependence refers to the existence of phenotypic correlations between traits within a specific context, but decoupled across different contexts (Sih et al., 2004a). Several studies on this matter have produced mixed results. Some studies show positive phenotypic correlations of single traits between domains (Benus et al., 1991; Hessing et al., 1994; Koolhaas et al., 2001; Verbeek et al., 1996), whereas other studies demonstrate domain specificity (Coleman & Wilson, 1998; Réale et al., 2000; Dingemanse & de Goede, 2004; van Oers et al., 2005). To experimentally test this, the relation between two genetically correlated personality traits in two different contexts should be studied. The great tit study showed that the phenotypic correlation between exploratory behaviour and risk-taking behaviour is dependent on the presence and behaviour of a companion that was foraging in an adjacent compartment (Table 3, van Oers et al., 2005). Companions had a complex effect on subjects' response to a startle. Slow explorers of both sexes became bolder in the presence of a companion, whereas the response of fast explorers depended on their sex, with females becoming less bold in the presence of a companion. These results show that despite a strong genetic correlation in one environment (van Oers et al., 2004b), and a possibly rigid underlying physiological mechanism

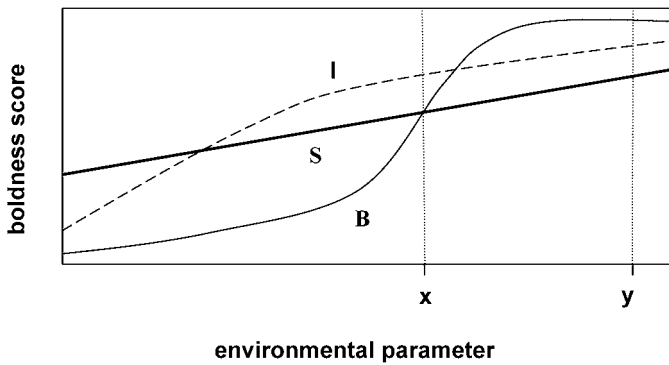


Figure 1. The reaction norms of three boldness genotypes (B = bold, I = intermediate, S = shy) for every value of an environmental parameter (after van Noordwijk & Gebhardt, 1987).

(Koolhaas et al., 1999), phenotypic correlations between personality traits depend on the context in which they are measured. Therefore, domain specificity is derived from the way different genotypes are expressed in different environments, rather than from the ability of an individual to be flexible in its behaviour within one context. The above mentioned phenomenon can be explained by the existence of reaction norms against a dominant environmental factor (De Jong, 1990; Fuller et al., 2005).

We assume the existence of three distinct genotypes, representing the three boldness groups presented by Coleman & Wilson (1998): Bold, Intermediate and Shy. We can plot the phenotypes that are expressed by these genotypes against an environmental parameter (Figure 1). This shows a strong analogy to phenotypic plasticity- and reaction norm theory as used for life history traits (De Jong, 1990; van Noordwijk, 1989; Via et al., 1995). Reaction norms are thereby defined as the function relating a phenotypic response of a genotype to a change in the environment (De Jong, 1990; Lynch & Walsh, 1998). Although this environmental parameter has a continuous scale, this is done in a discrete way at two points: x and y . When we classify the phenotypes of the three boldness genotypes at point x : B individuals get the highest score, I intermediate and S the lowest. When measuring the same genotypes in environment y according to the changes in reproducible reaction norms, the relative order in the phenotypic value of these genotypes has changed. Genotypes B and S produce the same mean phenotype, and I individuals have a higher phenotypic value than B and S. This shows that 'context-dependence' does not necessarily imply that individuals (genotypes) are flexible to behave in any way in every environment, but is merely

caused by a difference in expression at a certain point on an environmental axis.

Hence, consistent individual differences in one context may produce predictable outcomes in other environments, provided that (1) one knows the reaction norms and (2) has a good measure of an individual's phenotype and (3) has determined the changes in the environmental conditions. The interesting cases are those of genotype environment interaction, where the reaction norms of the behavioural traits actually cross over the total environment.

Context dependent behaviour might have huge consequences for our ideas of animal personalities. Two traits that are both context dependent, i.e. that are both described by a reaction norm, need not necessarily have a same-signed genetic correlation over all environments. Context dependent behaviour in more than one trait might impede our ability to define personalities. If in one environment the traits are genetically positively correlated and in another environment the traits are genetically negatively correlated, an animal personality over all environments cannot be defined. Pleiotropy does not prevent such a change in sign of genetic correlations between traits. Structural pleiotropy, where the effects of a gene on two traits are direct functions of each other, does prevent a change in sign of genetic correlations between traits (De Jong, 1990). This implies that structural pleiotropy might be necessary for the existence of animal personalities.

Genotypes are likely to differ in their reaction norms for the different traits, and this has important consequences for the identification of animal personalities over the total environment. Genotype environment interactions might play an important role in the processes that are responsible for generating and maintaining correlations among different traits across individuals (Stamps, 2003). An important challenge for the future is therefore to study the fate of animals with known genetic background in natural populations and thereby measure reaction norms for a number of traits and look at genotype environment interactions and the genetic correlations between behavioural traits as a function of the environment.

Personality genes: top-down and bottom-up approaches

The genes that are considered to be possible contenders for involvement in the genesis of a particular phenotype are so called 'candidate genes'. The

confirmation of a candidate gene requires variation in the gene or polymorphisms (i.e. alleles) of the gene that is statistically associated with the personality phenotype. Several candidate genes for human personality have been identified, but the most promising results are found with the alleles of the dopamine 4 receptor gene (DRD4) and the serotonin transporter gene (SERT) (Savitz & Ramesar, 2004). The DRD4 gene has been found to account for about 10% of the variation in novelty seeking in humans (Benjamin et al., 1996; Cloninger et al., 1996; but see Ebstein et al., 2000; Reif & Lesch, 2003). DRD4 is next to other parts of the cortex expressed in the hippocampus. In several domestic animal species, Lipp and co-workers found a relation between genetic variation in the infrapyramidal mossy fibre projection in the hippocampus and several behaviours (Lipp & Wolfer, 1999). Some other animal studies have looked at the relation between novelty seeking and DRD4 and found contrasting results. Several other studies looking at the serotonin transporter-gene (SERT) have found a relation between a functional polymorphism in a regulatory sequence for this gene and anxiety (Eley & Plomin, 1997; Reif & Lesch, 2003; Gordon & Hen, 2004). Other, not so well studied genes with possible effects on variation in personality include MAOA (Manuck et al., 2000), DRD2 (Noble, 2003), the 5-HT_{2c} receptor (Ebstein et al., 1997), the 5-HT_{2a} (Golimbet et al., 2002) receptor and tyrosine hydroxylase (Persson et al., 2000). Unfortunately results from these genes are ambiguous (Savitz & Ramesar, 2004).

Such candidate genes as the dopamine receptor gene potentially affect many traits, and therefore directly lead to genetic correlations between those traits. Interestingly, on physiological grounds one would expect the effects of a candidate gene on the different traits to be physiologically linked, and therefore lead to 'structural pleiotropy', rather than to the formal pleiotropy usually referred to in quantitative genetics. Structural pleiotropy removes the potential for sign change in the genetic correlations between phenotypically plastic traits over environments (De Jong, 1990).

Genes that are responsible for variation in personality can also be detected through a linkage analysis. With the use of genetic markers, quantitative trait loci (QTLs) can be found that contribute to the variation in a quantitative trait like personality (Lynch & Walsh, 1998). QTL analysis is used in a number of personality studies of both humans (Reif & Lesch, 2003) and domestic animals (Flint & Corley, 1996). The standard method to make genetic maps based upon molecular markers uses a structured F₂ pedigree derived from

inbred lines. Traditionally only one female and one male are used to produce many F1 and F2 crosses. For humans and most non-domestic species however, it is not possible to produce inbred lines and the number of offspring that one pair can produce is fairly low compared to the traditional lab species used for this type of analysis. Therefore, further studies are needed to identify gene polymorphisms in wild animals that show associations with personality traits. Fortunately, genetic maps can now already be developed for virtually any genome (Parsons & Shaw, 2002). Thanks to recent advances in molecular and statistical methods (Erickson et al., 2004) the use of QTL studies on personality in natural populations has come a step closer. Moreover, at the present time studying the interplay between genes and the environment in natural populations is one of the most challenging features in the genetic studies on personality, which could be enhanced tremendously with molecular genetic tools.

Closing remarks

More and more researchers realise that 'in the absence of good genetic data, one simply cannot predict responses to selection or reconstruct the past forces of evolution' (Willis et al., 1991). We have shown that (i) variation in behavioural traits has a clear genetic basis, that (ii) the structure of inheritance is normally not simply additive, that (iii) behavioural traits do not inherit independently of each other, thereby confirming the analogy to human personality, and that (iv) therefore the genetic structure of animal personality has to be taken into account when looking at the expected response to natural selection and past evolutionary forces. Moreover we have introduced reaction norms as a probable solution for the seemingly present contradictory findings that personality traits sometimes seem domain-general and sometimes context specific, and adduced structural pleiotropy as a potential mechanism for the integrity of animal personalities even if the individual traits are phenotypically plastic. Altogether we believe that this should be a good starting point for future personality research including genetics. Thereby, only combining both proximate and ultimate factors will enable us to draw conclusions that will bring us forward in unravelling the complex processes involved in the evolution of animal personalities.

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