

Plasticity in the development of animal personality

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Table of contents

Title page	1
Table of contents	2
Abstract	3
Introduction	4
Methods	5
Results and Discussion	
1. Ultimate aspects of personality	5
1a. Selection on personalities	5
1b. Heritability of personalities	6
1c. Function of personality	6
2. Proximate aspects of personality	7
2a. Parental effects	8
2b. Other important factors	9
2c. Stability of personalities	10
Conclusion	10
Acknowledgement	11
References	11

Abstract

Animal personality is a well studied topic in behavioral biology, but most studies have focused only on either the proximate causation or the ultimate function of personality. Within the proximate focus, the development of personality has until recently been mostly neglected. In this thesis I review the evidence concerning the degree of plasticity in the development of personality. I answer the question how animal personalities develop by reviewing both the ultimate and proximate causes of the development of personality. I conclude that personality is shaped by gene-environment interactions during the sensitive periods in the ontogeny. There are still many questions about how the genetics exactly contributes in this interaction. The environmental conditions affect the development of personality most likely through epigenetic changes. The most important environmental factors are the parents. They have great influence on the environment and on the offspring's perception of the environment. This influence depends on the environment during the parents' life and on their personalities. Therefore I conclude that the development of the personality of an individual already indirectly starts during the life of its parents.

Introduction

The term “personality” has its origin in the field of human psychology. There it refers to underlying behavioral tendencies that differ across individuals, that are consistent within individuals over time, and that affect behavior that is expressed in different contexts (Stamps & Groothuis, 2010b). In the past decades this term has been taken into use by animal behavioral biologists as they started investigating individual differences in behavior that are consistent across time and/or space. A host of different terms were used to describe these differences between individuals: animal personality, temperament, coping styles, and behavioral syndromes. Nowadays the terms “temperament” and “coping styles” are out of use as their meaning converged with the definition of personality (Stamps & Groothuis, 2010b).

Until recently, in the field of animal personality research, the majority of studies either describe the existence of individual behavioral consistencies in a particular species, or use a functional and evolutionary approach. Fewer reviews take a more mechanistic proximate approach and even fewer address the issue of development. The latter is understandable since personality deals with individual differences that are stable over time, while development deals with change over time (Groothuis & Trillmich, 2011). In this thesis I will focus on the issue of development of personality, because an understanding of the development of personality is critical for understanding its causation, evolution and function (Stamps & Groothuis, 2010b).

The definition of personality used by animal behavior biologists has its origin in psychology. Although there is not much collaboration between the two research fields currently, there is a strong potential for convergence between these two areas in the coming years (Nettle & Penke, 2010). Animal research has the potential to contribute greatly to the understanding of human personality. This is due to several reasons: With animals one can do studies that have: 1) better experimental control, 2) easier ability to measure physiological parameters, 3) greater opportunities for naturalistic observation, and 4) reduced time investment and cost of longitudinal studies (Mehta & Gosling, 2008). On the other hand behavioral biologist can profit from the literature created by psychologists, who have studied personalities for over a century. However, in order to limit the scope of this thesis, I have chosen to exclude human personality research and to only focus on (non-human) animal personalities.

In this thesis I give an overview of the plasticity in the development of personality and how this plasticity is caused. To be more specific, I will try to explain to what degree the outcome of the development of personality is already determined by genetics, during which periods and/or events during the ontogeny personality is determined, and which mechanisms are involved in the development of personality. I will do this by answering the following question in both the ultimate and proximate way: How do animal personalities develop?

Methods

This literature research project follows from a research project on maternal effects in the development of animal personality in the Behavioral biology research course of 2012. During this project I had already acquired and read several papers on the topic of development of personality. In order to increase the amount of 'data' I used the "Web of Knowledge" database (www.webofknowledge.com) to search for more articles. I used the terms "development" and "personality" as search queries. At first I focused on recent review articles, in particular the articles by Trillmich & Hudson (2011) and Stamps & Groothuis (2010b). I also searched their cited references in order to find more useful articles. I determined the usefulness of articles by first scanning the titles, if papers were not eliminated on the basis of the title I read the abstracts, If the paper was related to the topic I then proceeded to read it fully. As already mentioned in the introduction I decided to exclude humans. The main species I focused on in this thesis were birds and rodents, because these species were the best studied, regarding the number of publications.

Results & Discussion

1. Ultimate aspects of personalities

Evolution takes place through natural selection on heritable individual differences. Natural selection is based on the principle that the best adapted individuals will outcompete the less adapted individuals. Since personality is defined as a consistent individual behavioral profile, it is likely that natural selection has played a crucial role in the development of personalities. Therefore one might expect that through selection only the best "adapted" personality will remain, but this idea has changed to the concept that being different might be adaptive in itself (van Oers, et al., 2005). If this is the case, natural selection will maintain the variation in personalities rather than diminish it, as explained below.

Below I give some examples of artificial selection to illustrate that it is possible for selection to act on personalities (section 1a). Then I give an overview of the heritability of personality traits found in recent studies (section 1b) and after that discuss some functional aspects of personality (section 1c).

1a. Selection on personalities

Artificial selection on personality has been performed in several species. Probably the best known example is the study by van Oortmerssen & Bakker (1980). They used bidirectional selection on aggressive behavior in male mice (*Mus musculus*). In a setting where territorial mice were confronted with an intruder, they selected across several generations the animals with the fastest and slowest aggressive response. In this way they created the **Long Attack Latency (LAL)** & **Short Attack Latency (SAL)** mice lines. Apparently selection on this trait caused co-selection on several other traits. For instance R. F. Benus found that mice from the SAL line are more bold and cope more active with social and non-social challenges than LAL mice (Benus, et al., 1992). The lines are also found to differ in their physiology, for instance in the homeostatic regulation of monoaminergic neurotransmission (Wallinga, et al., 2009). These physiological differences might be the underlying reason for the behavioral differences.

Mammals are not the only species in which selection experiments on personality have been successful. Bidirectional artificial selection on explorative behavior in great tits (*Parus major*) by Verbeek et al. (1994) resulted in a 'fast' and 'slow' line. The fast line has high exploration speed and also high aggression, where the slow line has low exploration speed and low aggression.

1b. Heritability of personalities

Selection resulting in different personalities, as shown in the previous section, implies that animal personalities have a heritable genetic basis. Therefore over the past decades researchers have focused on assessing the heritability of these personality traits. Heritability is defined as the relative amount of genetic variation in relation to the phenotypic variation (Falconer & Mackay, 1996). A heritability of 0 means that none of the phenotypic variation is due to genetic variation and a heritability of 1.00 that all of the phenotypic variation is due to genetic variation. Table 1 (copied from van Oers, et al., 2005) summarizes the results of recent studies on heritability of personality. It shows that heritable personality traits are found in mammals, birds. The high heritability found in chimpanzees (*Pan troglodytes*) indicates a strong correlation between phenotype and genotype of the behavioral traits in this species. Where, indicated by the low heritability, in stickleback (*Gasterosteus aculeatus*) almost no correlation between phenotype and genotype is found for personality traits and therefore they are most likely not heritable.

These results illustrate that there is a genetic basis for personality. However the exact genes responsible for the personality traits have in most cases not yet been identified. It is also uncertain whether the genetic basis of personality exists due to pleiotropic effects (individual genes have effect on several traits) or linkage disequilibrium (sets of genes have effect on several traits, but a selective force preserves particular combinations of these gene-sets) (Falconer & Mackay, 1996).

Heritability alone does not tell the complete story about the genetic base for personality. For instance parental effects and epigenetics can also cause the phenotype to pass from parent to their offspring and therefore make the phenotype "heritable". Both these topics will be discussed in more detail in the proximate part of the results (section 2).

1c. Function of personality

A good example of the function of personality comes from the LAL & SAL mice lines. Where the success of both strategies depends on the prevailing environmental conditions (van Oortmerssen & Busser, 1989; cited by Benus, 2001). The more aggressive SAL type is more successful under stable conditions, where the less aggressive LAL type has an advantage in changing and unfamiliar circumstances.

Also, as I mentioned before, in the case of personality being different might be beneficial. This is due to frequency dependent selection; phenotypes that occur in a low percentage in the population have a selective advantage. The processes niche-picking and niche-construction may play a role here. These processes describe if and how individuals either select or create the niche they prefer within a population, thereby facing less competition by being different from others in the population that prefer other niches.

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

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 *. (van Oers, et al., 2005)

2. Proximate aspects of personality

During sensitive periods in the ontogeny of animals proximate causes determine the development of their personality. Most of these sensitive periods are during the early life when physiological processes that are linked to personality traits are in development and when the plasticity of the brain and its neuroendocrine systems is high (Stamps & Groothuis, 2010b). Therefore most of the current research focuses on these sensitive periods in order to identify the proximate mechanisms involved and the processes that take place during the development of personality. Table 2 provides an overview of the main results found in recent studies on proximate causes of the development of personality.

In the results consistency was found in the correlation between juvenile body mass and boldness personality traits in rodents. In rats a higher body mass leads to more explorative and less anxious behavior (Rödel & Meyer, 2011), and in rabbits a higher body mass leads to more aggressive behavior (Rödel & von Holst, 2009). However not all results show consistency. R. F. Benus & C. Henkelmann (1998) found that in litters with a male biased sex-ratio the males develop more aggressive behavior than the males from female biased litters. The opposite effect of litter sex-ratio was found by G. Gracceva et al. (2011). These different results are probably due to differences in the experimental design, where G. Gracceva used biological relevant sex-ratios opposed to the unnatural sex-ratios used by R. F. Benus & C. Henkelmann.

Below I give a summary of the results found in studies on development of personality. I will start by discussing the role the parents play in the ontogeny of their offspring (section 2a), follow up with other

important factors during the sensitive periods (section 2b) and also investigate the stability of the personalities formed during the sensitive periods (section 2c).

Species	Result	Author	Year
Rat	Maternal licking and grooming determines the behavioral response to stress.	N. M. Cameron et al.	2005
Rat	Pup with higher body mass become more explorative and show less anxiety.	H. G. Rödel et al.	2011
Rabbit	Males with a higher juvenile body mass show more aggressive behavior.	H. G. Rödel et al.	2009
Birds*	Higher androgen level in the eggs leads to more bold, aggressive and explorative birds.	Reviewed by T. G. G. Groothuis et al.	2005
Mouse	In litters with a male biased sex-ratio the males develop more aggressive behavior.	R. F. Benus & C. Henkelmann	1998
Great tit	Food availability during early rearing has effect on aggressive and explorative behavior	C. Carere et al.	2005

Table 2. Proximate causes for the development of personality found in studies on personality traits. Given are the species and the proximate causes with their effect. *This article showed the effect in multiple different bird species, therefore I don't mention a specific species.

2a. Parental effects

Important factors in the early ontogeny of an animal are its parents. In the first place because the parents give their DNA to their offspring, but there are many other ways in which parents can affect the phenotype of their offspring over and above direct genetic transmission. These are called parental effects (Marshall & Uller, 2007). "Parental effects can be a result of one or both parents influencing offspring phenotypes via nest site selection, nutrient provisioning, hormone transfer, providing particular social experiences or serving as a mentor or model from which to socially learn" (Reddon, 2012). The personality of the parents affects these parental effects, especially when the parents function as mentor or model from which the offspring learn. In these situations the offspring might copy the behavior of their parents. This can lead to a "false" sense of heritability, when it is not taken into account in experimental design.

Parental effects can be split into two general categories: developmentally entrenched effects and context-dependent effects. The first category includes the parental effects that are necessary for the successful development of the offspring. For example in most species the parents take care of delivering food to their young, because without it the young would simply die of starvation.

Through context-dependent parental effects parents are able to shape the personality characteristics of their offspring in a way that makes them better prepared for the environment they will be likely to grow up in. By preparing their offspring the parents increase their own fitness. But these parental effects depend on the knowledge the parents have about the future environment. By this criterion we are able to divide the context-dependent effects into anticipatory and diversifying parental effects. Both effects have their own role in creating variation in personalities (Reddon, 2012).

Anticipatory effects occur when parents have reliable information about the future environment. In

these scenarios they can shape their offspring towards the phenotypes that have the most advantages in the environment they are likely to face. These effects can lead to variation in personality on population level due to local and/or time differences. Animals that live in the same environment could have developed during a different period or in a different place and therefore received different parental programming. A good example of an anticipatory effect is the maternal licking and grooming behavior in rats. Maternal licking and grooming determines the behavioral response to stress of the offspring. Where high amounts of licking and grooming leads to a lower stress response. Chronically stressed mothers show low amounts of licking and grooming and thus produce highly stress-reactive offspring (Cameron, et al., 2005).

Diversifying effects occur when there is a great environmental uncertainty. In these cases the parent cannot predict which phenotype will be most beneficial. Therefore they will increase the variation in the phenotypes of their offspring to ensure that at least some of them will have a phenotype well suited for the environment. In this way parental effects can cause variation in personality to be greater between siblings than between unrelated animals. Androgen deposition in avian eggs can be used as a diversifying effect. Higher androgen levels in the eggs leads to more bold, aggressive and explorative birds (Grootuis, et al., 2005). Avian mothers can vary the androgen levels within a clutch to diversify their chicks to ensure that at least some of them will be successful in the current environment (Eising, et al., 2006).

2b. Other important factors

Besides the effect that parents have during the early ontogeny there are also other factors that influence the development of personality during the early life. A well studied example (in rodents) is the nest composition. Both the litter size and the sex ratio of the litter have long lasting effects on the behavior of the animals ((Benus & Henkelmann, 1998; Mendl & Paul, 1990; Dimitantos, et al., 2007; Spencer & Tilbrook, 2009) cited by Gracceva, et al., 2011). Competition between siblings for maternal and nest resources and the early social environment are proximate causes to explain the differences in different nest compositions. "Individual differences in early growth, physiology and behavior (potentially important for the development of personality) are shaped to an appreciable extent by early sibling relations." (Hudson, et al., 2011)

Interspecific interactions and ecological influences during the early ontogeny affect the development of personality as well, towards behavior that serves to cope with the environmental challenges (Trillmich & Hudson, 2011). For instance predation was found to induce a correlation between boldness and aggressiveness (Bell & Sih, 2007). Pre-adult sticklebacks were exposed to predation by trout, which predated half the sticklebacks. Boldness and aggressiveness were measured before and after being exposed to predation. Only after the exposure to predation there was a correlation between bold and aggressive behavior.

Also the early life physiological conditions of an individual have an important effect on the development its personality. For instance there are significant differences found in personality traits between individuals that differed in bodyweight at very early age. "Starting from birth, an animal's perception of its environment strongly depends on its physical state, which in turn can strongly influence individual behavioral performance and motor abilities." (Rödel & Meyer, 2011)

There is evidence that epigenetics is the key mechanism during the sensitive periods through which the outcome of the development of personality can be determined (Crews, 2010). Epigenetic effects are the changes in cellular phenotype without changes in the DNA sequence. For example gene expression can be regulated by epigenetics through DNA methylation or histone modification. In a study carried out on rats it was found that maternal care can change the epigenome. The DNA methylation differed in offspring of mothers that showed high levels of licking and grooming and arched-back nursing compared to offspring of mothers with low levels of licking and grooming and arched-back nursing (Weaver, et al., 2004). These differences had lifelong consequences for the offspring in their physiological and behavioral response to stress (Cameron, et al., 2005).

Another example where epigenetics affected the development of personality is found in the study by C. Carere et al. (2005). They used the by Verbeek (1994) created 'fast' and 'slow' lines of great tits (*Parus major*) and found that limited food availability during rearing gave young of the slow line the fast phenotype. The behavior, both lines were selected on, was found to be heritable ($h^2 = 54 \pm 5\%$; Drent, et al., 2003). Therefore the evidence of an environmental factor overruling the differences between both lines indicates epigenetic changes.

2c. Stability of personalities

Even though personality is mainly formed during the early life of an animal, personality traits are not necessarily stable after the sensitive periods. It is possible that a personality trait is only expressed at a certain age later in life, long after it was affected during the sensitive period ((Bateson, 1979; Immelman, et al., 1991; Hogan & Bolhuis, 2005; Leitner & Catchpole, 2007)cited by Stamps & Groothuis, 2010b). Because juveniles may have personality traits, different from those expressed as adults, in response to their own set of selective pressures (B. G. Galef, 1981; cited by Stamps & Groothuis, 2010a). It is also possible that experiences later in life (during a non-sensitive period) change a behavior set by earlier experiences (during a sensitive period). In order to overrule an already present personality trait the new experience needs to have a strong impact on the animal (attacks from predators; starvation; changes in social structure) (Stamps & Groothuis, 2010b). This is also the reason why there is not much documentation about this yet: in a laboratory the conditions and therefore experiences the animals face are usually benign.

Conclusion

The development of animal personalities is determined by gene-environment interactions. The exact contribution of the genetic component in this interaction is uncertain. In most cases the gene(s) responsible for the personality traits are unknown. It is also uncertain whether the genetic basis of personality exists due to pleiotropic effects or linkage disequilibrium (Falconer & Mackay, 1996). The environmental conditions, which affect the development of personality in these gene-environment interactions, influence personalities most likely through epigenetic changes during the sensitive periods in the ontogeny. These sensitive periods are the moments in the ontogeny when the physiological processes that are linked to the personality traits are in development.

The parents have a crucial role in the effect of the environment on the development, since they have

great influences on the early environment and on the perception of their offspring of the early environment. Also other factors, like siblings, are important parts of the early environment. Although I'm not quite sure it is possible to make a correct distinction between parental and other early effect on the environment. The other early factors, as described in the results, might be influenced by the parents as well and therefore qualify as a parental effect. For instance the nest composition could very well be manipulated by the parents, whether they can do this actively or if it happens more subconsciously. The effect of the parental effects depends on the environment during the parents' life and on their personalities. Therefore I conclude that the development of the personality of an individual already indirectly starts during the life of its parents.

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