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Unfolding Personalities: The Importance of Studying Ontogeny

ABSTRACT: We aim to stimulate an ontogenetic approach to personalities. We explain the importance of studying development for understanding proximate and ultimate aspects of personality and critically discuss, partly by perhaps provocative statements, our current lack of knowledge and potential approaches to the study of personality development. We first clarify some terminology and argue for a difference between behavioral profiles (BP; at the descriptive level) and personality (at the explanatory level). We then focus on the issue of temporal stability of personality, arguing that based on evolutionary theory, neurophysiological knowledge, and recent findings, personality is probably less stable than often thought. Next we consider the potential influence of genes, discussing gene by environment correlations and interactions and argue that developmental changes in the regulation of DNA expression are probably more relevant than individual differences in DNA sequence. We end by suggesting perspectives for future research. © 2011 Wiley Periodicals, Inc. *Dev Psychobiol* 53: 641–655, 2011.

Keywords: animal personalities; temperament; coping styles; behavioral syndromes; development; self-organization; epigenesis; evolution

INTRODUCTION

The Importance of the Ontogenetic Approach to Personality

The presence of consistent individual differences in behavior and physiology has now become firmly established in the field of behavioral biology, including behavioral ecology, and comparative psychology. Such differences are not considered as measurement noise anymore, but as relevant sources of biological information. Several substantial reviews and special issues of international journals have been published on the topic over the past 10 years (e.g., Bell, 2007; Dall, Houston,

& McNamara, 2004; Gosling, 2001; Groothuis & Carere, 2005; Koolhaas, de Boer, Buwalda, & von Reenen, 2007; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, Johnson, & Ziemba, 2004; Stamps & Groothuis, 2010a,b; other reviews in *Phil Trans Royal Soc B*, 365, 2010). The majority of studies in this field either describe the existence of individual behavioral consistencies in a particular species, or use a functional and evolutionary approach. Fewer reviews, mainly from the field of stress physiology, take a more mechanistic 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.

However, the evolution of phenotypic traits and complexes can be regarded as the evolution of development for two reasons: first, mutations occur during the life time of an animal and evolution is therefore modified ontogeny. Second, developmental plasticity leading to adult traits is shaped by selection (West-Eberhard, 2003). This consideration suggests that the standard approaches to personality neglect several important points:

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Dedicated by F.T. to W. Wickler on the occasion of his 80th birthday.

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- First, young animals are not just incomplete and inadequate copies of adults. Young animals need to be adapted to their particular niches in order to survive to and reproduce in adulthood. A wide array of ontogenetic adaptations take care of this, including behavioral adaptations that are specifically tuned for the early life stage and which often disappear later in life. It has been argued that personalities are linked to life history traits such as metabolism and growth (Biro & Stamps, 2008) and these may change considerably with age. The ecological niche of young animals may be very different from those of adults, not only in insects where the larva (say a caterpillar) is often a completely different animal than the adult (say a butterfly), but also in many altricial and even precocial species of other taxa. Therefore, it is to be expected that if the organization of behavior in personalities is beneficial for survival, young animals may have different ones than adult animals. Moreover, the presence of complex adaptive behavior early in ontogeny indicates that behavior does not necessarily require a long and gradual process of building up the behavioral organization.
- Second, the emphasis on stability of personality may underestimate life time changes in personalities that would have strong repercussions for the evolutionary explanation of personalities. Stable consistencies in linkages between behavioral traits are thought to constrain evolutionary processes that tend to optimize behavior since adaptive changes in one trait would also induce a change in the other that might be maladaptive (Sih et al., 2004). Several models explore potentially adaptive consequences of such behavioral inflexibility (e.g., Dall, Houston, & McNamara, 2004; Wolf, van Doorn, Leimar, & Weissing, 2007; Wolf & Weissing, 2010). However, if personalities are more flexible over life time than currently thought, this may change our evolutionary perspective substantially. Depending on the relative strength of selection on the juvenile versus adult phenotype selection may even uncouple different axes of personality to achieve sufficient adaptation at different stages of the life history. Alternatively, if personalities were stable from early life, the selection pressure for such personalities may act mostly in early life and not in the adult stage where selection on survival is often less intense, yet the study of adaptation of personality mostly focuses on adult animals.
- Third, if personalities unfold gradually or change with age, tracing this developmental process may shed light on the proximate mechanisms underlying personalities. By documenting which neurobiological

and physiological variables change parallel to each other in close correlation with changes in observable behavior and by describing their mutual linkages, we might be able to reveal which systems are likely underlying differences in personality. Linking such knowledge to what is already known about the ontogeny of these systems may give insight into possibilities for developmental plasticity of personalities too.

- Fourth, there is a strong tendency to assume that personalities are genetically determined. Some authors have even stated that genetic determination is a prerequisite for labeling individual differences personality (Van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005). Such a focus on genes may partly come from the use of selection lines for studies on personality, coping style, and heritability. As we will argue below, the use of selection lines may create artefacts and the results of such studies as well as of heritability studies may not be due to genetic effects only. Such a focus neglects the potential strong influence of factors other than genes on development. Moreover, and more fundamental, genes, being structural biochemical units and not behavior, can only become expressed in behavior by a translational process in interaction with other genes and further internal and external factors. Due to this continuous interaction process behavior as an end product of such a translational process cannot be divided in how much is contributed by genes and how much by environmental factors. Manipulating genes tells us something about the influence of genes and can provide a powerful tool to unravel behavioral mechanisms, but as these always interact with other factors (genetic and otherwise) this can easily generate an incomplete picture of the developmental process as we will show below.

The aim of this study is to stimulate research on the ontogeny of personality by means of some, perhaps provocative, statements followed by short explanations. We will focus on proximate and ultimate aspects of (in)stability of personalities over the life time, and argue that the claim that personalities are stable over the life time after early gradual development is not well based on current theory or facts. We will then discuss the role of genes and epigenetic effects, arguing that we should focus more on the latter rather than the former. Before doing so, however, we will discuss some terminology, arguing that changes in behavioral phenotype are not necessarily the same as changes in personality, and that labeling of personalities needs caution.

Distinguishing “Personality” from “Behavioral Profile”

Consistent individual differences in behavior may encompass different aspects of the behavioral phenotype: individuals of the same sex and species may differ in the level of a particular behavior (e.g., aggression to a conspecific) at two time points such that those that are the most, intermediate, or least aggressive individuals retain their position relative to the others over a certain time span. This is called differential consistency (Stamps & Groothuis, 2010a) to indicate that personalities are defined relative to other individuals in the population. In addition, animals may show correlations among different behaviors, or among seemingly same behaviors in different contexts. For example animals being very aggressive (relative to others) towards conspecifics may also be the most (or the least) aggressive towards predators (same behavior in different context), or the most or least explorative in a novel environment (different behavior in a different context). This is called context generality, and when stable over time structural consistency (it tells us something about the underlying structure of behavior). We do not separate context generality for the same or different behaviors as it is difficult to establish whether the seemingly same behavior in different contexts (e.g., aggression towards conspecifics and predators) is really the same behavior or not. Nowadays most authors refer to personality when the behavior shows both differential and context generality (e.g., Stamps & Groothuis, 2010a,b) although evidence for one of them is frequently taken as evidence for the presence of personality too.

Stable individual differences have also been labeled as behavioral syndromes (mostly referring to differential consistency; Sih et al., 2004), coping styles (referring to differences in coping with stressors; Koolhaas et al., 1999), temperament (Capitanio, 2010; Gosling, 2001; mainly among psychologists with the connotation of a strong genetic component; also Réale et al., 2007), and BP (Groothuis & Carere, 2005). Although the use of the label personality (and coping styles as equivalent) has become prevalent we think it is important to realize that personality (and coping style) are *interpretations* of the observed patterns in behavior. Personality is often classified as bold versus shy, active versus passive, pro-active versus re-active, risk-taking or cautious, and these classifications are based on behaviors such as activity in an open field, approach to a novel object, or aggression to conspecifics. These behaviors can be objectively and adequately described as a certain BP (high level of activity in an open field and of aggression), but whether they reflect one underlying common causal factor needs further study.

This distinction between personality and BP is especially relevant in the study of personality development since young animals often express different behaviors than adult animals. In case the animals show differential and structural consistencies in both life stages, albeit with different behaviors (e.g., begging for food and proneness to sleep disturbances in early life and aggression and exploration as adults), we are faced with two different possibilities: (1) it reflects an age- or situation-dependent change in the *expression* of the *same* personality (which we cannot observe directly) and (2) it reflects truly a change in the personality itself. For example, begging for parental food by a young bird among its nest mates and aggression towards a conspecific both may be interpreted as an expression of competitive behavior and similarly, differences in sleep pattern and in open field behavior both may be interpreted as vulnerability to stressors. If so, it is the expression of personality, the BP, that changes, not personality itself. Only further testing can disentangle the two interpretations.

Personality and the Architecture of Behavior

One reason why personality may attract so much attention is that it evoked surprise among investigators of behavior, by showing that seemingly completely different behaviors were linked to each other (structural consistency). That very same phenomenon makes, in our opinion, personalities so interesting since it may shed new light on the architecture of behavior. Perhaps what we have classified as different behaviors, partly because of their different function, might actually share important common causal factors. Since the rise of Ethology in the second half of the previous century it was argued that behavior was organized in a hierarchical manner, with different motivational units for different functional classes of behavior, culminating in the landmark review by Baerends (1976) on the functional organization of behavior. However, different behaviors like aggression and sexual behavior activate a wide array of brain areas that largely overlap for both behaviors. Moreover, differences in behavior such as between femalelike males and more macho males in the gecko (that may be classified as differences in personality) are reflected in a wide array of overlapping brain areas (reviewed in Crews & Groothuis, 2005). This suggests that differences in personality may actually indicate differences in some fundamental aspect of the organization of behavior that affects more than one system, or, in the old terminology, more than one drive. The challenge is now to unravel such fundamental aspects without falling into the same pitfalls as those who classified behavior into different drives. Using

classifications such as bold versus shy, risk taking versus cautious, active versus passive, proactive versus re-active, or routine-formers versus flexible individuals, may be useful as they could stimulate further research into the organization of personality as long as these classifications are used to generate testable hypotheses. However, such classifications are often post hoc labels to characterize individuals in a convenient way without the necessary follow up of experimental testing of the adequateness of these labels. Such naming helps little to explain the phenomenon and may suggest understanding where it is really lacking. In addition, using labels borrowed from human psychology carries the danger of anthropomorphism (Weinstein, Capitanio, & Gosling, 2008). Ultimately, personalities should perhaps be labeled by their underlying neurobiological characteristics (a hypothetical example may be serotonin turnover), but this is as yet not within reach. Until then we recommend a critical attitude to personality labels and the use of more descriptive BPs.

THE QUEST FOR STABILITY

Life-Long Stability Is Difficult to Test and May Be Masked by Developmental Plasticity

The concept of personality presupposes a certain stability of the behavioral phenotype (Clarke & Boinski, 1995; Gosling, 2001) and we need to clarify how we can relate this to the dynamics of development over ontogeny. Therefore, we need to ask whether personality is something stable that characterizes the individual from birth to death or is better understood as something that unfolds and changes gradually or becomes reorganized through self-organization during early ontogeny or certain sensitive periods in continuous interaction with the social and nonsocial environment influenced by negative and positive feedbacks (see below).

To measure stability makes most sense relative to the life history and life expectancy of the organism under consideration. As explained above, developing organisms go through a series of ecological and social niches and each may require different adaptations. This makes it not unlikely that the BP of an individual changes over time by developmental plasticity (see below). However, the challenge is to disentangle changes in the expression of personality (BPs) from changes in personality itself. One possibility might be to deduce a basic aspect that all components of the adult profile may share (such as risk taking or routine formation) and then design behavioral tests to investigate the presence of such a common aspect in the behavior of the juvenile. Another and even better approach might be to

bring this black box analysis a step further and test a physiological parameter that may have similar pleiotropic effects at different ages. An example would be the early and late effects of testosterone on the behavior, growth, and immunocompetence of young black-headed gulls (Ros, Groothuis, & Apanius, 1997). This is obviously not an easy task.

In order to evaluate the stability of a personality we need to be able to measure a significant repeatability of behaviors over a substantial part of the organism's life cycle. What degree of repeatability and over which time span is required, needs to be judged in relation to the length and nature of the species' life cycle and the changes over ontogeny involved. However, in testing repeatability of behavior we have to realize that the outcome of later tests may be influenced by previous tests. A classical example is the winner effect, in which winning or losing a fight strongly determines winning chances in subsequent fights (Hsu, Earley, & Wolf, 2006; Rutte, Taborsky, & Brinkhof, 2006). Similarly, an explorative animal in an open field test may experience no effective risk in that test and explore even more in the next test, in contrast to an animal that hardly explored. Such interactions between repeated measurements and personality are worth further study.

At this stage we should again clarify some labeling. Differential consistency refers, as explained above, to the extent to which scores for a certain behavior in a certain context at a certain time correlates among individuals with scores for the same behavior in the same context at another time (Stamps & Groothuis, 2010a). A high differential consistency does not exclude that animals change their behavior over time. Individuals may show plasticity over time, but as long as this reaction norm is the same for all individuals the differential consistency remains high. This individual plasticity may depend on the genotype, and if animals despite the same genotype show different plasticity because of differences in previous experience then this is called developmental plasticity. The latter is an ideal tool to adjust the phenotype to prevailing environmental circumstances and it has been suggested that natural selection may directly act on genes for phenotypic plasticity thereby influencing the reaction norm. This might explain why some species and some individuals within species are more susceptible to experience than others (for an elaborate discussion see Ellis, Boyce, Belsky, Bakermans-Kranenburg, & van Ijzendoorn, 2011). The value of developmental plasticity might be illustrated for the case of begging for parental food provisioning in chicks. In most species, chicks from the same parents (similar genetic background) find themselves in different social niches since they hatch asynchronously so that older chicks have an advantage in

the sibling hierarchy. Chicks might therefore adjust their begging strategies according to their position in the hierarchy. That even highly altricial young indeed quickly learn about begging strategies has been shown for passerines (Kedar, Rodriguez-Girones, Yedvab, Winkler, & Lotem, 2000). That early begging may be part of personality or BP was demonstrated in selection lines for two types of BPs in great tits (*Parus major*). There, proactive individuals tend to beg more intensely than reactive chicks (Carere, Drent, Koolhaas, & Groothuis, 2005).

To describe variation within individuals the term flexibility has also been used. We propose that this should not be confused with the term plasticity nor with that of contextual plasticity (the extent to which the behavior of an animal varies across contexts, relative to that of other animals of the same age, in the same context and at the same time; Stamps & Groothuis, 2010a). The latter term may describe differences between animals showing a high versus low degree of routine formation. Flexibility should be used for describing to what extent the animal responds with variation in behavior in a given context (e.g., just overt aggression or also different kinds of threat displays in an agonistic situation).

Proximate Mechanisms Suggest no Lifelong Stability

From a physiological point of view these functional arguments for change can be supported. Brain structures, that is, the CNS, the hypothalamo-pituitary axis (HPA) and the sympathetic-adreno-medullary axis (SAM) develop at a different pace. For example, the prefrontal cortex develops relatively late in life. As it is responsible for planning and behavioral inhibition, the latter being implied in personality (Koolhaas et al., 2007) we would expect these traits and their part in personality also to show up later in life. Furthermore, development of the brain consists to a large extent of pruning of neuronal connections and along with this slow structural shaping of the brain one would expect brain functioning to emerge equally slowly. Indeed the prefrontal cortex finishes development only in adolescence (Giedd et al., 1999) and this questions the expectation to find the same personality early and late in ontogeny. Moreover, the last two decades have shown that the brain retains much more plasticity later in life than previously thought (Gage, 2002).

One idea for explaining the development of a potentially important aspect of personality, is that early reward sensitivity mediated by the limbic system can influence the building and functioning of higher structures such as the prefrontal cortex by determining

evaluation of stimuli and consequent behavioral output. If these higher centers function in accordance with underlying physiological and neurobiological mechanisms that constitute or influence emotional reactivity and its development, then the early basic limbic functions may represent a foundation on which personality structures are built. In other words, mechanisms determining emotional reactivity (sometimes called temperament) and their coupling to HPA and SAM might be primary and their workings may determine through positive and negative feedbacks (emotional rewards) how personality becomes structured during development through self-organizing processes. Capitanio (2010) describes such processes in which, for example, the physiology of the dopamine system interacts with effects of the HPA- and cortico-medullary axis (CMA) to structure the reaction norm for the development of an individual's personality. This system has been called the emotional reactivity axis. However, we are still in the early stages of defining and understanding this system and its role in development.

It is long known that behavioral development can be strongly influenced by environmental factors during early sensitive phases (Bateson, 1979). More recently it was detected that during later sensitive periods in specific life history stages, like adolescence or first reproduction, a consolidation phase may occur in which either the information gained earlier is confirmed, or in which the behavior is adjusted on the basis of new information. These later sensitive periods may provide a point of predictable instability in the life cycle when remodeling of the personality is possible (Bischof, 2007). At such a stage, a change in personality and the behavioral correlation structure underlying it may well prove adaptive by adjusting the individual to its prevailing social and other environmental circumstances. It is quite conceivable that selection has favored such sensitive periods in order to allow re-adjustment of phenotypes to circumstances which may not be predictable in the long-term. The flexible way of DNA expression by environmentally induced DNA silencing that may also produce stability is discussed below in the section Regulation of DNA Expression Is More Relevant Than DNA Sequence.

Data Suggest Correlations among Behaviors Can Be Broken

Due to the emphasis on stability of personality, not much research has been done to experimentally test the potential plasticity of animal personalities. However, in the few cases where this has been addressed, considerable plasticity has been found. Postnatal cross-fostering of offspring from selection lines for what is called

pro-active and reactive mice diminished the differences in behavioral flexibility, while leaving other aspects of the personality intact (Benus & Henkelmann, 1998). Food deprivation of chicks of selection lines for what is called bold and shy personalities in great tits strongly affected exploration behavior in one line and aggression in the other (two traits that are linked in this personality), a clear illustration of gene by environment interactions (see below; Carere et al., 2005; Groothuis & Carere, 2005). Exposure to predation generated the correlation between aggression and exploration in sticklebacks (Bell & Sih, 2007). Transportation diminished and even reversed personality differences among two selection lines of trout, changing the relation between physiology (cortisol response) and behavior (Ruiz-Gomez et al., 2008).

These findings may shed light on the underlying causation of personality. They indicate that the linkage between traits can be decoupled. This in turn indicates that the different traits each have their own regulation. The idea that pleiotropic effects of physiological mechanisms may impose far fewer constraints on the flexibility of behavioral linkages and their evolution than sometimes assumed is in line with recent developments in behavioral endocrinology. It has long been thought that the behavioral regulation by hormones, exerting pleiotropic effects on different behavioral domains, may limit behavioral and evolutionary flexibility but given the complexity and flexibility of such hormonal regulation at many different levels this is unlikely (e.g., Hau, 2007).

Several models may explain the above-mentioned decoupling. First, if a physiological/neurobiological/genetic factor affects only one trait directly, and the others are influenced only indirectly via traits affecting each other (Fig. 1-I), then a factor causing a change in one particular trait may have consequences for those traits that were affected by that one particular trait but not by the others. In contrast, when the physiological/neurobiological/genetic factor affects all traits directly, then an effect on one trait may affect only that particular trait (Fig. 1-II). Finally, if two or more physiological/neurobiological/genetic factors affect the traits, for example, in the case of multi-dimensional personalities as has been investigated mostly in humans but hardly in animals (but see Koolhaas, de Boer, Coppens, & Buwalda, 2010), then again a decoupling can occur when the factor only affects one dimension (Fig. 1-III). For example, different steroid hormones have different pleiotropic effects and individuals can show consistent individual differences in hormone production or sensitivity (Williams, 2008), due to early social or hormonal experience (Ros, Dieleman, & Groothuis, 2002; Ros, Franco, & Groothuis, 2009). Later in life experience

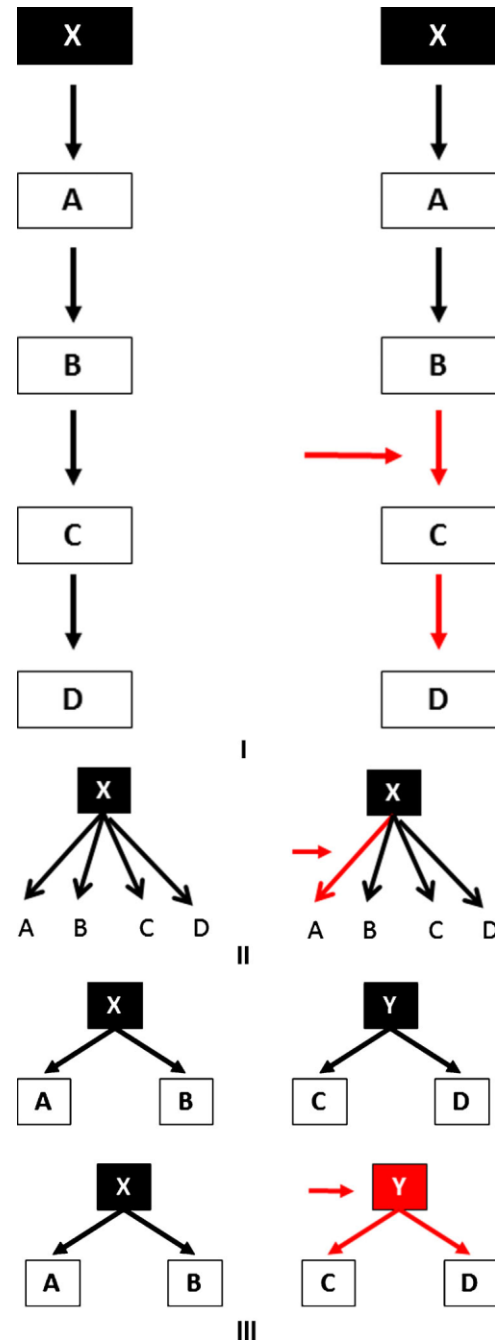


FIGURE 1 Three models explaining decoupling of structural consistency. (I) Left: Linkages between traits A, B, C, and D are due to one direct effect of physiology (X) on A and three indirect effects: A influences B, which in turn influences C which in turn influences D. Right: in such a case an effect on one particular trait (B) only affects downstream traits. (II) Left: All factors are directly influenced by the same physiological factor. Consequently, an effect on A (right) only changes that trait. (III) The rest of the 4 schemes illustrates an alternative model, in which different traits are caused by different common causal factors. Bottom: A common influence on the physiology (Y) underlying traits C and D only affects those two traits.

may modulate production or reception of one of these hormones, but not the other.

THE QUEST FOR GENETIC EFFECTS

We Should Shift Focus in the Study of the Role of Genetics

To understand genetic effects on personality and its development we need to determine what kind of information about genetics is necessary to address particular major questions. Arguments in favor of an important role of genes in determining differences among personalities come from the following: (1) there are genes with major effects on many aspects of personality in animals and humans (Van Oers & Müller, 2010). However, as pointed out below, this concerns only a minority of cases; (2) selection can influence personality (and its development?) over few generations (e.g., Drent, van Oers, & van Noordwijk, 2003), (3) personality has a heritable component (Van Oers et al., 2005). However, both artificial selection with postnatal cross-fostering and heritability measurements do not necessarily control for prenatal maternal effects and gene-environment interactions, a topic discussed below, and (4) genetic influences, perhaps through pleiotropic effects, could explain limits of plasticity in personality but this needs more substantial empirical evidence (Van Oers et al., 2005).

Given the complexity of gene regulation and interactions among genes, and between genes and other internal and external factors there are also many arguments against the attempt to understand personality from an analysis of its genetics. The human genome project has yielded surprisingly few results with respect to the discovery of correlations between adult traits and specific genes. Perhaps such an approach is indeed naïve given the complexity of interactions mentioned above. Examples for this will be given below. In other words, one may argue that genetics only produce the structure that allows to build brain modules which then in self-organization produce the personality we observe. So arguments against a major role of genetics would be: (1) indeed, the same phenotype may be produced by different underlying genes (Uller, Pen, Wapstra, Beukeboom, & Komdeur, 2007). In addition, there are likely so many genes of minor effects involved in setting up the brain (which then self-organizes) that no major effects of single genes on personality are to be expected. Furthermore, gene by environment correlations, induced by maternal effects and genotype-dependent niche picking, and gene by environment interactions, including epigenetic effects obscure the evidence for genetic

effects (see also Sullivan, Mendoza, & Capitanio, in press).

Limits of plasticity later in life and the stability of personality need not be based on genetic determination but equally likely may come about through early brain organizational processes and learning. This is open to experimental study, by determining whether cloned animals show much variation in BPs (which is surprisingly often the case, Lewejohann, Zipser, and Sachser, 2011; Schuett et al., 2011; Stamps & Groothuis, 2010a) and how this variation compares to that of wild-type organisms. Such an approach could demonstrate nongenetic processes of self-organization that may be just as or even more important than underlying genetics.

In the following we briefly discuss single gene effects and outline the potential importance of the genetic complexities and interactions as well as regulatory effects.

Major Single Gene Effects Are Not Always Straight Forward

The results of the search for *candidate genes* exerting large effects on behavior is limited to only a few cases in which repeatedly the same candidate genes have been found to play a role in the regulation of behavior. For example, 5-HTT, the serotonin transporter (often called the depression gene), and DRD4, the dopamine receptor D4 (related to novelty seeking and the efficiency of handling conflict) influence several behaviors in different contexts. It is obviously worthwhile to continue study of these major genes and their regulation. Work by Koolhaas and coworkers on the importance of the serotonin system for aggression and violence has been amply described and reviewed (Koolhaas et al., 1999, 2007; Natarajan, de Vries, Saaltink, de Boer, & Koolhaas, 2009). Work on the DRD4 gene polymorphism suggested that this variation correlates with personality in the great tit. However, the initial results on the selection lines for personality in this species could not be replicated in other populations (Korsten et al., 2010) and the authors suggested a more complex relationship between this polymorphism in genes and behavior.

A convincing case, amply supported by experimental data, is the following. Arginine vasopressin (AVP) and the site and intensity of expression of its receptor (V1aR) cause male prairie voles (*Microtus ochrogaster*) to bond strongly to a female and to behave paternally to offspring (Lim et al., 2004; Young, Nilsen, Waymire, MacGregor, & Insel, 1999). The change in V1aR expression not only influences bonding to a female and social recognition, but also reduces aggressiveness and

increases the male's response to offspring stimuli inducing paternal care (Numan & Insel, 2003). This was convincingly shown by transfer of the gene to meadow voles (*M. pennsylvanicus*) which are normally promiscuous and solitary, but show partner preferences and huddling upon increased expression of the V1aR-gene in the ventral forebrain (Lim et al., 2004). Thus, a change in the expression of a single gene influences personality in a major way by changing covariance among a series of behaviors across contexts including mating, bonding, partner recognition, and parental care. Interestingly, a similar behavioral and physiological change can be obtained by cross-fostering between species with a similar difference in social system, showing that the result of genetic manipulation does not mean at all that nongenetic factors are unimportant. Cross-fostering of pups from the California mouse (*Peromyscus californicus*) in which males are aggressive and take part in parental care, to the white-footed mouse (*P. leucopus*) that does not show these behaviors, not only reduced these behaviors in the cross-fostered pups but also AVP content in the brain (Bester-Meredith & Marler, 2003).

Coloration by melanin is frequently associated with differences in physiological and behavioral traits of vertebrates. Ducrest, Keller, and Roulin (2008) reviewed the associations of the melanocortin receptor (MCR) types and their regulators with physiology and behavior. They suggest that darker individuals are generally more aggressive, sexually active, and stress-resistant than lighter conspecifics. This effect comes about by interaction of MCRs with the various endocrinologically active products of the proopiomelanocortin (POMC) gene like melanocyte-stimulating hormone (MSH), adreno-corticotropic hormone (ACTH), and endorphins and the antagonist, agouti-signaling protein. The interaction of the level of expression of the various MCRs and the (multiple) products of the POMC locus strongly influence behavioral phenotype and due to the coupling of effects may lead to different personalities.

Even in this relatively well-characterized system exceptions are easily found. The work of Boerner & Krueger (2009) on the common buzzard (*Buteo buteo*) demonstrates that dark pigmentation does not always correlate with higher aggression. Buzzards occur in three-color morphs, light, dark, and intermediate. The authors demonstrated a major effect of color morph on aggressiveness in this species. However, in contrast to other studies, where usually the dark morph is found to be more aggressive, they found the dark buzzard less aggressive against a predator (the eagle owl, *Bubo bubo*). In males, aggressiveness against the predator correlated with aggressiveness against buzzards, but in the latter case was modulated by the morph of the

presented dummy. All three types tended to respond stronger to their own color morph than to the other two. Here, as in other species (Ducrest et al., 2008), there is obviously a relationship between melanin-based coloration and aggressiveness.

In the case of such differences in behavioral and other phenotypes, caused by the differential expression of single genes, we would expect lifelong stable differences in personality. If so, we then need to search for an explanation of the long-term coexistence of the different behavioral phenotypes. However, some systems show strong effects of major candidate genes, others do not. An explanation for this variation has not yet been forthcoming. Many of these large effect genes tend to be monomorphic in the population so that phenotypic differences in behavioral traits may not depend on these major genes, but rather on their regulation by other factors, genetic or environmental. Moreover, it needs to be remembered that these major effect genes, though sometimes spectacular in their effects, explain (e.g., in the case of the DRD4 gene) only 10% of the variation in novelty seeking in humans (Van Oers et al., 2005).

Selection Lines Have Disadvantages

Perhaps the focus on genetic influences on personality development has come from the work with genetic selection lines. This work has been very important and influential for establishing the field of animal personality, especially the work on outbred rat lines and mouse lines selected for short and long attack latency (De Boer, van der Veegt, & Koolhaas, 2003; Koolhaas et al., 1999), and on great tit lines for bold and shy personalities (Groothuis & Carere, 2005). However, further use of such selection lines may be of limited use for the study of personalities (Stamps & Groothuis, 2010a,b). For example, replicate selection lines show inconsistent patterns of QTLs (Quantitative Trait Loci) for behavior. This suggests that there are just too many genes involved in the development of particular traits, making this approach of little help in understanding the architecture of the traits. Such inconsistent results may partly be a problem caused by artificial coselection, that is, replicate selection lines may carry different genes along with the traits selected for (Mackay, 2009). This may also artificially induce different personalities among different lines, calling for the need to have a substantial number of selection replicates that is only rarely the case. In many cases such selection lines may not change much of the architecture underlying a personality trait, but they may primarily change the threshold for the expression of a trait perhaps by changing the threshold for environmental sensitivity (Groothuis & Stamps, 2010a). Also, selection lines get established

for extreme traits which may not be representative of the traits expressed at the center of the distribution and may therefore bias our view of the phenomenon. The work with selection lines may have suggested bimodal distributions of personality traits while in unselected populations such a distribution is rarely found. Moreover, even if heritability is being established by showing that selection leads to a shift in trait distribution, this may not tell us much about the underlying genetic architecture. It may not even take gene–environment correlations and interactions into account, as heritability estimates may strongly depend on the environment in which the study was performed and may not account for (prenatal) maternal effects. Finally, even if selection indicates genetic effects when trait changes are replicated in multiple lines, in different environments and taking maternal effects into account, even this does not exclude important environmental effects. Studies in the great tit selection lines have shown that an early competitive environment in the nest may shift individuals of selection lines away from the trait expression predicted from their genetic makeup. Great tit chicks from slow lines raised under food restriction became faster explorers (Carere et al., 2005) and similarly, shifts in the sex ratio in mouse litters strongly affected the expression of aggressive behavior of mouse lines similar to the effect of selection (Benus & Henkelmann, 1998; Mendl & Paul, 1991). These examples show that early ontogenetic conditions can greatly change the expression of behavioral traits in the adult. In effect, the reaction norm may be shifted but it may be as broad as before selection.

Different Genetics for the Same Traits

There is no one to one relation between genes and behavior. The sex determination system can serve as a particularly clear example of the finding that different genetic systems may underlie a similar phenotype. Sex can be determined environmentally, that is, by environmental conditions influencing the developmental trajectory, or by genetic determination as for example in humans and mammals in general. Both ways of sex determination have evolved repeatedly and it is easy to select for either one within one species, for example, the house fly *Musca domestica* (Kozielska, Pen, Beukeboom, & Weissing, 2006). In this system, selection for sex ratio shifts may cause a change in the underlying sex determining mechanism even without changing the sex ratio (e.g., from several genes, as in the house fly, to sex chromosomal determination; Kozielska et al., 2006). Thus, differences in the mechanism of sex determination do not permit conclusions about the underlying genetic architecture since selection lines produce

the same sex ratios based on very different underlying genetic architecture. Interestingly, this finding suggests that a genetic constraint may evolve from a system that is free to vary the sex ratio rather than the other way around as usually assumed (Uller et al., 2007). However, selection may also drive the system from fixed genetic sex determination to one where environmental conditions are more important. Even there, we will mostly find stable sex ratios, again suggesting that genetics adjusts to the ecological situation and the selective regime it causes rather than determining the phenotype. Individual plasticity (e.g., in condition) also is expected to influence the outcome of such selective regimes in a major way (Sheldon & West, 2005).

Same Genes for Different Traits

Evo-Devo results for the plasticity in the development of butterfly wing patterns provide another interesting example of the extreme flexibility of the regulation and multiple use of genes (Beldade & Brakefield, 2002). There is a clear Nymphalid ground plan of modular units of pattern that is modified widely in different species and within a species under different ecological conditions. The same genes are repeatedly and flexibly involved at several stages of module building for example in positioning and controlling the extent of wing patterning. This leads to staggeringly high plasticity of phenotypes across and within species, the latter being expressed as seasonal phenotypes, that is, the same species expressing a very different wing pattern in the summer and autumn generation. Obviously, environmental signals at certain stages in development lead to the emergence of different wing patterns. In these cases it is clearly not different genes that effect the structuring of pattern, but the differences emerge through changes in the regulatory network switching these genes on and off.

In this context it is very important to keep in mind that genes are part of the environment of other genes and will influence their expression. Therefore, it appears more fruitful to study the regulation of gene activity (provided genes are identified) rather than genes per se. Such a study is more likely to help understanding the contribution of genetic factors to personality development.

Regulation of DNA Expression Is More Relevant Than DNA Sequence

DNA-methylation and histone modification by methylation and acetylation influencing DNA packing potentially contribute to plasticity and changes in personality over a lifetime. Such changes may occur in response to the environmental conditions encountered and can

thereby allow adjustment to changing conditions within a lifetime (Angers, Castonguay, & Massicotte, 2010). We know that DNA-methylation changes at random over an individual's lifetime due to a 5% error rate during mitotic transmission. Such slow changes may contribute to changes in personality with age. More importantly, differences in BP may arise by maternal influences on methylation patterns. One of the most drastic influences reported is the case of bee development into queen versus worker. Here, diet-induced DNA-methylation changes were shown to be responsible for the enormous differentiation between a worker and a queen phenotype with all the accompanying behavioral differences (Kucharski, Maleszka, Foret, & Maleszka, 2008). The critical change from the developmental trajectory of a worker into that of a queen is due to differential feeding with royal jelly. The feeding regime influences the developmental trajectory during the L2–L3 larval transition demonstrating a sort of sensitive period for this maternal effect. The resulting phenotypes differ dramatically in life span, physiology, and behavior. The underlying cause is the silencing of or reduction in the activity of Dnmt3 (DNA cytosine-5-methyltransferase).

Another prominent example closer to the question of personality concerns systematic influences of maternal behavior on the expression of maternal behavior in offspring (Weaver et al., 2004). Mother rats that lick and groom (LG) their pups a lot and do much arched-backed nursing (ABN) induce no methylation at a specific promotor site important for binding of a transcription factor to induce transcription of the glucocorticoid receptor (GR) in the hippocampus. This leads to a lower stress response since the GR leads to negative feedback on the hypothalamic release of the corticotropin releasing factor (CRF). This behaviorally induced modification by differential methylation persists into adulthood and reduces stress sensitivity, exploration and later parental behavior of individuals with a high LG and ABN mother, thereby changing personality. The effect arises during the first postnatal week. Once more, there appears to be a sensitive period here similar to imprinting phenomena. Cross-fostering experiments have shown that the effect depends on maternal behavior experienced and not on the mother of origin thereby proving the epigenetic nature of the change in phenotype. Similar effects of early stress on, for example, coping and avoidance learning have been documented in mice. They were found to be related to altered AVP expression via hypo-methylation of a key regulatory region of the *Avp* gene in the paraventricular nucleus. This leads to persistent up-regulation of the *Avp* gene (Murgatroyd et al., 2008). Similarly, altered histone acetylation was shown to be associated with age-

dependent memory impairment in mice (Peleg et al., 2010). Such epigenetic effects can thus be trans-generational, and even trans-populational and transferred by fathers (Crews et al., 2007).

Nutritional conditions during the slow growth period in humans in one generation have also been reported to influence development in later generations (Pembrey et al., 2006) thereby suggesting the potential for lasting effects of poor seasons on development of later generations. Thus fluctuating environments and an animal's dispersal into another habitat may well influence its own as well as its progeny's traits. If specific food contents important for methylation can influence the level of methylation of CpG islands (Cropley, Suter, Beckman, & Martin, 2007), this may also lead to changes in personality whenever relevant promoters or binding sites are changed. So we must even consider that changing food preferences as potentially happens when an animal settles in a new habitat may influence the development of its BP and that of its offspring. These changes in BP would be expected to be of intermediate stability. However, given their dependence on the stability of methylation or rapid de-methylation, traits influenced by these epigenetic processes may change as environmental conditions change or else even be transmitted across generations (Angers et al., 2010).

The above-described examples are parental effects, in which the mother or father affects the offspring by influencing its environment, either directly by, for example, parental care, or indirectly by rearing the offspring in a certain environment. Over the past decade this has become a flourishing field of research in behavioral biology. Recent research has also documented long-term consequences of maternal effects mediated by egg quality such as the deposition of maternal hormones, which may affect both behavior and physiology of the offspring (reviewed in Groothuis, von Engelhardt, Müller, Carere, & Eising, 2005; Von Engelhardt & Groothuis, 2011), suggesting an effect on personality development. Moreover, selection lines for personality seem to differ in egg hormone levels of maternal origin, suggesting a role for these hormones in personality development. Parental effects on personality development are extensively reviewed by Groothuis & Maestripiere (2011).

Niche Picking and Niche Construction

The amazing observation that within families siblings often differ much in personality (Plomin, Ashbury, Dip, & Dunn, 2001) and that conjoint Siamese twins might even be extremely different in their personality (Smith, 1988) suggests that individuals living in the same external environment may use developmental plasticity to

utilize different aspects of that environment to avoid competition as much as possible. Competition within a family is necessarily very intense since individuals are genetically similar and share the same environmental resources, so that differentiation in niche utilization and personality might be adaptive. Sulloway (2010) has suggested that one major force leading to such differential development of personality is character displacement as observed in different closely related species such as the Darwin's finches. In this sense then niche construction is a very active process that is most likely to occur in closed social systems like children within one family, chicks in a nest or young within one litter (Hudson, Bautista, Reyes-Meza, Morales-Montor, & Rödel, 2011). In such a situation where competition for the same resources becomes extreme any small differentiation in use of the environment will diminish competitive and potentially agonistic interactions and reward social differentiation. If circumstances do not permit such differentiation, deadly competition will occur as often observed in siblicidal species (Drummond, 2006; Hudson & Trillmich, 2008). The influence of social niche differentiation on personality differentiation in cooperatively breeding fish has shown that early differentiation among helpers can indeed lead to lifelong stable differences in behavior (Bergmüller & Taborsky, 2010).

How does such differentiation come about? As pointed out above the brain influenced by prenatal and postnatal feedback mediated by the SAM, HPA, and hypothalamo-pituitary-gonadal axis (HPG) causes the individual to acquire a propensity to react in particular ways, that is, it develops a disposition to evaluate stimuli and react to them that can serve as a foundation to its personality. When this is combined with the organism's tendency to choose an environment suited to its needs and predispositions this leads to a positive feedback which under most circumstances will stabilize an individual's way to interact with its environment. Only if the individual gets into situations where it cannot choose its niche such an adaptation might prove to be maladaptive. Since in the laboratory environmental heterogeneity is often much less than in the field, personality differentiation may be less strong and less adaptive under such artificial circumstances (Stamps & Groothuis, 2010b).

Small differences in initial tendencies to interact with others within a social unit may lead through positive feedback to separate roles. That the modulation of BPs by the early social environment is possible has been shown convincingly for male mice growing up in litters of different sex composition (Benus & Henkelmann, 1998) and for birds growing up under food restriction (Carere et al., 2005). Once differentiation of

the nervous and endocrine system has taken place it will become increasingly difficult for an individual to change its dispositions as it will have learned to be successful in a particular role and changing to another one may be costly. Learning in early ontogeny has been shown to be very influential in choosing the habitat and the foraging mode an individual will use over its lifetime. Dispersing brush mice (*Peromyscus boylii*) preferred the habitat in which they had grown up (Mabry & Stamps, 2008) and great tits reared in blue tit (*Cyanistes caeruleus*) nests foraged for life in a way more similar to blue than to normal great tits (Slagsvold & Wiebe, 2007).

Such differences in the ontogenetic differentiation of the underlying mechanisms may explain long-term behavioral consistency across contexts. Organizing effects of hormonal mechanisms (Ketterson & Nolan, 1999), neural mechanisms, and neurotransmitter regulation (Capitanio, Mendoza, Lerche, & Mason, 1998; Koolhaas et al., 1999, 2007) and the emotional disposition caused by such underlying processes (Capitanio, 2010) and even simple heuristics (Todd & Gigerenzer, 2000) as well as pleiotropic gene effects (see below) can affect such consistencies.

CONCLUSION AND OUTLOOK

Better understanding of the development of personalities will shed light on their plasticity, causation, function, and evolution. However, our understanding of the ontogeny of personality is rather meager. What seems most needed now is an integration of different disciplines, including those that study pleiotropic effects of the early environment (such as maternal stress) currently outside the context of personality. First, we ought to be more open-minded about the potential plasticity of personalities during life. Second, to understand how different BPs are related to different personalities we need a more comprehensive approach than post hoc labeling of personalities based on a limited number of behavioral tests. Rather, a more extensive behavioral approach should be integrated with knowledge about the development of neurophysiological mechanisms. Third, it will be fruitful to integrate the ontogenetic approach with the study of the function and evolution of personality. To what extent does natural or sexual selection act independently on single aspects of the BP, for example, risk taking during foraging and during aggression, and to what extent may this constrain evolutionary adaptation or induce plasticity in underlying mechanisms? Further, a lifetime perspective on personality should determine at which life history stages selection acts most intensely on BPs or personality. Differences

in the action of selection on different life stages have indeed been found for North American squirrels (Boon, Réale, & Boutin, 2007) and bighorn ewes (Réale & Festa-Bianchet, 2003) as well as for great tits (Fucikova, 2010). In addition, it is important to investigate the influence of the social environment on consistency in BPs (Wolf, van Doorn, & Weissing, 2011). To study these questions more comprehensively we urgently need more theory that produces specific predictions on the importance of BPs at different stages of the life cycle which can be empirically tested. Even though much new theory is being developed (Dall et al., 2004; Dingemanse & Wolf, 2010; McNamara, Barta, & Houston, 2004; McNamara & Houston, 2009; Wolf, van Doorn, & Weissing, 2008; Wolf & Weissing, 2010) it hardly addresses the question of the ontogeny of personality.

A more direct interplay of theory and empirical research on behavior may be achievable once we have identified key state-behavior feedbacks. These might be found in the influences on BPs by: (1) the interplay of genetic effects with brain, HPA and SAM development where a slightly higher stress response may feed back on BP development by, for example, changing HPA sensitivity and incorporating experience related to stress; (2) metabolic physiology and condition dependency, that may change priorities of risk aversion and foraging which in turn will feed back on condition, (3) situation choice (niche picking) and social feedbacks that may, via cognition and learning, influence the situations into which animals get themselves, thereby exposing individuals of different BPs to different environmental and social feedback; finally, (5) life histories that may differ for animals born into different population densities (e.g., Eccard & Rödel, 2011) or into a season where immediate reproduction is possible versus the ones that have to survive an initial nonreproductive period. Several of these mechanisms have been characterized quite well, but have as yet not been brought in productive connection with the theory of behavioral ecology and evolution. Here, we see a wide open field for a fruitful connection between the study of developmental mechanisms, ontogeny, ecology, and evolution of BPs. Finally, the evidence presented above for the effect of the environment on gene expression should make us realize that standardized laboratory conditions, lacking environmental heterogeneity, or the use of inbred or selection lines, may yield artificial effects.

NOTES

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