Neuroscience and Biobehavioral Reviews 150 (2023) 105194

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

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

The epigenetics of animal personality

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ARTICLE INFO

Keywords:
Personality
Adaptation
Reaction norm
Plasticity
DNA methylation

ABSTRACT

Animal personality, consistent individual differences in behaviour, is an important concept for understanding how individuals vary in how they cope with environmental challenges. In order to understand the evolutionary significance of animal personality, it is crucial to understand the underlying regulatory mechanisms. Epigenetic marks such as DNA methylation are hypothesised to play a major role in explaining variation in phenotypic changes in response to environmental alterations. Several characteristics of DNA methylation also align well with the concept of animal personality. In this review paper, we summarise the current literature on the role that molecular epigenetic mechanisms may have in explaining personality variation. We elaborate on the potential for epigenetic mechanisms to explain behavioural variation, behavioural development and temporal consistency in behaviour. We then suggest future routes for this emerging field and point to potential pitfalls that may be encountered. We conclude that a more inclusive approach is needed for studying the epigenetics of animal personality and that epigenetic mechanisms cannot be studied without considering the genetic background.

1. Introduction

Behaviour lies at the heart of how individuals respond to environmental challenges (Bateson, 2003). It is now generally recognised that a great amount of within-population variation in behaviour consists of adaptive individual variation rather than only being non-adaptive variation around an adaptive mean (Wilson, 1998). Individual differences in ecologically important behaviours, such as foraging behaviour (Harfmann Short and Petren, 2008; Osborne et al., 1997), courtship behaviour (Wheeler et al., 1991) and dispersal (Dingemanse et al., 2003; Duckworth and Badyaev, 2007) contribute to individual survival and reproduction (Smith and Blumstein, 2008). Hence, animals tend to show consistent responses when experiencing environmental variation in a range of contexts (Bell et al., 2009; Brodie and Russel, 1999) and behavioural responses across contexts tend to be correlated (Bell, 2007; Sih et al., 2004). This phenomenon is now widely referred to as animal personality (Carere and Maestripieri, 2013). Where we know that both heritable (van Oers et al., 2005) and developmental effects (Stamps and Groothuis, 2010) are driving personality trait variation, we lack good knowledge on the molecular regulatory mechanisms that underlie this interplay of genes and environment in creating personality types during development and beyond (Trillmich et al., 2018). Understanding these mechanisms, however, is decisive for understanding the evolutionary outcome of selection on such traits (van den Berg and Weissing, 2015). This again is crucial for estimating the rate at which individuals and populations can behaviourally adapt to changing environmental conditions, such as climate change and urbanisation (Both et al., 2006; Reed et al., 2013).

One promising group of potential mechanisms explaining the way the environment shapes the phenotype via an interaction with the genetic predisposition, are epigenetic mechanisms. A number of excellent views have been formulated on the potential value of epigenetic mechanisms for studies in animal behaviour (Jensen, 2015; Kilvitis et al., 2014; Ledon-Rettig et al., 2013; Schrey et al., 2013; Seebacher and Krause, 2019; Vogt, 2021). These have described the potential for epigenetic mechanisms for helping to answer several outstanding questions in the ecology and evolution of behaviour, often focussing on the potential for epigenetic mechanisms for responding to environmental influences. Recently, empirical studies have started to investigate how epigenetic processes relate to the expression of personality traits. In this review paper, we specifically discuss how epigenetic mechanisms may play a role in the emergence and maintenance of animal personality differences within populations. We will do this by reviewing recent published evidence of relationships between epigenetic mechanisms and individual behavioural differences. We acknowledge the vast body of literature, including several influential

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https://doi.org/10.1016/j.neubiorev.2023.105194
Received 29 October 2022; Received in revised form 12 April 2023; Accepted 21 April 2023
Available online 23 April 2023

reviews on the role of epigenetic mechanisms for explaining behavioural variation in model species (e.g. Weaver et al., 2004). A number of excellent papers have also introduced the hypothesis that both heritable and environmental effects on behavioural and personality traits may be mediated by epigenetic changes (Ledón-Rettig et al., 2013; Romano et al., 2017). In this review we used examples of such reviews to link the fields that study the neurobiology of behaviour to fields that study animal personality in an ecological and evolutionary context. Apart from reviewing the literature, we elaborate on the origin of epigenetic variation and we thereby argue that studies on epigenetic mechanisms should not solely focus on non-genetic, environmental factors. We emphasise that the interplay between genetic and non-genetic mechanisms should be considered when aiming to investigate the role for epigenetics in explaining variation and consistency in personality traits.

2. Animal personality

Several definitions of animal personality exist, but in this review we refer to the concept as the presence of individual differences in behavioural tendencies and how these can be more or less consistent across situations and time (Stamps and Groothuis, 2010). Personality in non-human animals is typically measured via behavioural traits that are related to ecological relevant situations, such as exploration for food, avoidance of risks, competition or social life (Réale et al., 2007; van Oers, 2008). Animal personality traits influence reproductive success and survival, are under natural- and sexual selection (Dingemanse and Réale, 2005; Schuett et al., 2010; Smith and Blumstein, 2008) and therefore have both ecological and evolutionary significance. The maintenance of personality variation can be explained by fluctuating selection pressures on temporal (Quinn et al., 2009; Thys et al., 2021) and spatial scales (Mouchet et al., 2021) with varying environmental and social conditions such as food availability (Dingemanse et al., 2004; Quinn et al., 2009), density (Cote et al., 2008; Nicolaus et al., 2016) and social niche (Montiglio et al., 2013; Pearish et al., 2019) as drivers for selection.

Apart from the fact that individuals differ in their behaviour, the most striking characteristic of personality traits is the extent to which these individual differences are consistent over time or context (Kaiser and Müller, 2021). Early work on animal personality has focussed on assessing how repeatable the behavioural traits of interest were (Bell et al., 2009; Kaiser and Müller, 2021). In other words, how much of the observed phenotypic variation in behaviour is due to between-individual variation. With this proof of principle, researchers have shown that there is a repeatable component in many behaviours. In more recent years, predominantly in behavioural ecology, the emphasis has shifted towards studying the among-individual component of behaviour as a measure of personality, rather than the total phenotypic variation (see e.g. Niemelä and Dingemanse, 2018). For studying how epigenetic variation associates with behavioural variation in personality traits, it is interesting to investigate behaviour both at the phenotypic- as well as at the among-individual level. Therefore, for this review, we focus on the questions to what extent molecular epigenetic mechanisms could explain behavioural variation in general, what contribution it may have for behavioural consistency, and why behaviour and consistency may vary across age, between sexes and over time, but also how individuals might differ in plasticity. To better understand the potential role of epigenetics for explaining variation in personality at all these levels, it is important to first consider the origin of individual behavioural differences.

Like many other phenotypic characteristics, variation in personality traits is explained by both genetic and environmental factors (Groothuis and Trillmich, 2011; Pigliucci, 2001; Trillmich et al., 2018). Personality traits have a substantial heritable component, which implies that at least part of the behavioural trait variation is transmitted across generations (Laine and van Oers, 2017; van Oers et al., 2005). Although the demonstration of the presence of heritable variation does not elucidate the mechanisms that allow for such transmission, the terms heritable variation, genetic variation and genomic variation have been interchangeably used in the past (Bell and Dochtermann, 2015). However, only part of the heritable variation is explained by genomic variation, such as single nucleotide polymorphisms (SNPs) or other structural variants (Laine and van Oers, 2017). The additive genetic effect of such genomic polymorphisms explains only the narrow-sense heritability (Dochtermann et al., 2015), while the broad-sense heritability includes genomic inheritance and other factors, such as the interaction between genes, transmission of information from one generation to the other (i.e. cultural inheritance, see Whiten, 2005), or via consistent environmental variance (Danchin et al., 2011; Lynch and Walsh, 1998). Epigenetic factors are expected to play a role in all these different modes of inheritance. Indeed, the evolution of behaviour is known to also be affected by non-genetic inheritance (see e.g. Jablonka and Lamb, 2014). Especially conditions during early development, in so-called sensitive windows (Fawcett and Frankenhuis, 2015), seem to affect personality traits (Trillmich et al., 2018). Consequently, the environment that offspring experience can increase the heritability of personality traits if the parental environment resembles that of the offspring, or if the parent modulates the offspring environment in response to their own environment. Such inter-generational effects may shape much of the repeatable individual differences in their offspring (Meaney, 2001; Trillmich et al., 2018).

In conclusion, the expression, ecological relevance, inheritance and evolutionary potential of personality traits relies on both genetic and non-genetic factors, but even more by the interplay between these two. Genetic inheritance is, for example, known to vary over age (Class et al., 2019) and non-genetic inheritance is not functionally independent from the DNA sequence (Adrian-Kalchhauser et al., 2020). This explains why studies looking at solely genomic or environmental mechanisms are able to only explain a small fraction of the observed phenotypic variation, plastic changes and heritability of personality traits. More promising are factors that directly connect information from genomic origin with the early environment and that are able to plastically change over age. Since not only the availability but also the uncertainty of information available to an organisms will determine how much they will use of this information (Fawcett and Frankenhuis, 2015), the relative contribution of genes and the environment also changes over age (Class et al., 2019; Kandler et al., 2021).

3. Epigenetic mechanisms

A promising group of mechanisms explaining the way the environment shapes the personality phenotype via an interaction with a genetic predisposition, are epigenetic mechanisms. The word epigenetics has been used in an ambiguous way in the past (Greally, 2018). In this review, we define epigenetics as the biochemical mechanisms that can stably alter gene expression by affecting transcription or translation without changing the primary nucleotide sequence of the genome (Richards, 2006). Since changes in gene expression are precursors or direct causes of changes in phenotypic traits, it is generally accepted that changes within epigenetic mechanisms alter phenotypic characteristics (Law and Jacobsen, 2010).

The most-studied of these biochemical mechanisms is DNA methylation, a molecular process by which a methyl group (-CH_3) is added to a DNA nucleotide, which is usually a cytosine (Korochkin, 2006). Although DNA methylation is present in many organisms, its patterns and functionality cannot be generalised across and within taxa. Differences exist even among animal genomes, as in invertebrates DNA methylation is commonly sporadic, while vertebrates show genome-wide DNA methylation (Albalat et al., 2012; Bird et al., 1995; Gardiner-Garden and Frommer, 1987; Tweedie et al., 1997). Interestingly, also within-genome differences exist. In the vertebrate genome, DNA methylation levels are typically high, but there is variation in promoter regions of genes and transposable elements (TEs; Suzuki and

Bird, 2008). Furthermore, cytosine methylation can occur in three different contexts: CpG, CHG and CHH, where G is a guanine and H is an adenine, thymine or cytosine. However, in vertebrate genomes, cytosines in CpG dinucleotide context are a major target of DNA methylation (Bernstein et al., 2007; Bird, 2002; Derks et al., 2016). There are regions in the genome that contain larger numbers of CpGs, also called CpG islands (CGIs). These CpG islands can predominantly be found in promoter and transcription start site (TSS) regions. Methylation in these regulatory regions is negatively associated with gene expression (Bird, 2002; Laine et al., 2016; Li et al., 2011; Moore et al., 2013) as it can interfere with the binding of transcription factors (Yin et al., 2017). There are several ways of measuring DNA methylation in animals, for which pros and cons have been described in detail elsewhere (see e.g. Feng and Lou, 2019; Laine et al., 2022). The specific characteristics of these methods need to be taken into account for the specific questions. For example, for an exploratory scan of DNA methylation across the genome, genome-wide methods give sufficient resolution. However, when aiming at measuring DNA methylation at the candidate gene level, a more targeted approach is needed (Laine et al., 2022).

Variation in DNA methylation originates from three different sources: genetic variation (Richards, 2006), epimutations (Becker et al., 2011) and environmental induction (Pertille et al., 2017; Weaver et al., 2004; Zimmer et al., 2017). The first source of variation in DNA methylation is genetic variation, indicating that DNA methylation can be dependent on underlying genomic variation. This is also referred to as obligatory epigenetic variation (Richards, 2006). Studies on plants, fish, birds and humans have shown that the DNA methylation landscape is largely genotypically controlled (Czamara et al., 2021; Dubin et al., 2015; Höglund et al., 2020; Hu et al., 2021; Sepers et al., 2023a, 2023b; Villicaña and Bell, 2021). The second origin of variation in DNA methylation lies in epimutations. Epimutations are spontaneously and randomly arising epigenetic variations (Becker et al., 2011). In rare occasions epimutations may inherit stably over generations in plants (Becker et al., 2011), but they also inherit from cell to cell without being stably inherited over generations. Epimutations are expected to be as frequent as DNA mutations (Becker et al., 2011), although epimutations have been found to be more common than genetic mutations in wild Darwin's finches (Skinner et al., 2014), indicating that epigenetic marks are less stable compared to nucleotides. It is difficult, however, to separate genetically and environmentally induced epigenetic marks from true epimutations, where true epimutations might not even exist in vertebrates as they often turn out to be dependent on genetic variation (Heard and Martienssen, 2014). Variation in DNA methylation can also be induced by the environment. Several studies in vertebrates have shown that DNA methylation is (likely) affected by environmental influences such as habitat quality (Hu et al., 2019), parasites (Hu et al., 2018; McNew et al., 2021; Wenzel and Piertney, 2014), pH (Massicotte and Angers, 2012), contaminants (Laine et al., 2021; Mäkinen et al., 2021; McNew et al., 2021; Nilsen et al., 2016; Pierron et al., 2014; Romano et al., 2017) and urbanisation (Caizergues et al., 2022; Garcia et al., 2019; McNew et al., 2017; Riyahi et al., 2015; Watson et al., 2021). When variation in DNA methylation is induced in response to environmental changes, DNA methylation may allow for an adaptive behavioural response via phenotypic plasticity (Bossdorf et al., 2008; Jablonka and Lamb, 2006; Verhoeven et al., 2016). Thus, DNA methylation might be one of the mechanisms that underlies phenotypic plasticity of behavioural traits and if it is indeed true that such environmentally induced epigenetic change can be inherited mitotically from cell to cell, this epigenetic response to changing ecological circumstances may affect an individual's behaviour consistently throughout its lifetime (Verhoeven et al., 2016). Hence, epigenetic mechanisms possess all those characteristics for explaining the mechanisms underlying adaptive and consistent individual differences in personality.

In animals, most epigenetic marks do not survive gametogenesis and early development, which are processes that involve DNA demethylation (Morgan et al., 2005; Richards, 2006) and restructuring of chromatin (Jablonka and Raz, 2009). Nevertheless evidence is accumulating (for an overview, see Skvortsova et al., 2018) that some epigenetic marks escape epigenetic resetting (Brykczynska et al., 2010) or are reconstructed (Gapp et al., 2014; Kasowski et al., 2013; Schaefer and Nadeau, 2015). If DNA methylation is stably inherited via the germline to subsequent generations this is referred to as transgenerational inheritance. Transgenerational inheritance would allow for DNA methylation to respond to selection directly and consequently, to have a direct impact on evolutionary processes (Bošković and Rando, 2018; Heard and Martienssen, 2014). It is important to note, however, that epigenetic reprogramming of DNA methylation is quite drastic in vertebrates (Feng et al., 2010; Morgan et al., 2005; Reik et al., 2001; Sasaki and Matsui, 2008). Often, observed inherited epigenetic variation has been induced through the persistence of the environmental effect. For example, in vertebrates, when pregnant females are exposed to environmental influences, also their fetus can be affected by the same environment as may be the germline of the fetus (Heard and Martienssen, 2014). This so-called intergenerational inheritance indicates that epigenetic information, instead of being inherited through the germline (Guerrero-Bosagna et al., 2018), is transmitted via persistent environmental influences over generations, with parental care being a classical example (Weaver et al., 2004). For a more elaborate discussion on the difference between inter- and transgenerational inheritance see e.g., (Bale, 2015; Heard and Martienssen, 2014; Perez and Lehner, 2019). To date, transgenerational inheritance has not been unequivocally shown in vertebrates and is therefore an ongoing subject of discussion (Burggren, 2016; Richards and Massimo Pigliucci, 2020; Guerrero-Bosagna et al., 2018; Heard and Martienssen, 2014; Laland et al., 2014, 2014; Liberman et al., 2019; Lind and Spagopoulou, 2018; Perez and Lehner, 2019; Sarkies, 2020; Vogt, 2021). Also, even in the case of intergenerational inheritance of DNA methylation, this is not independent from the genome (Vogt, 2021). This, therefore, calls for more research on the independent role for transgenerational inheritance of epigenetic marks for the evolution of personality traits.

4. Epigenetic effects on personality

In this section we will review the literature on the role of DNA methylation in mediating behavioural plasticity and consistency in animal personality traits. Although personality is often measured as the relative between-individual variance compared to the total phenotypic variance, the behaviour of an individual is expected to be plastic over time in response to environmental cues (West-Eberhard, 2003). Animal personality can therefore be seen as a concept with multiple layers; individuals might differ at the average personality trait level either being caused by genetic predisposition or developmental history, but also at the level of plasticity. Phenotypic plasticity, in the strict sense, is defined as the ability of a genotype to produce a range of phenotypes in response to different environments during ontogeny. The genotype-specific pattern that describes this phenotypic expression is defined as a reaction norm (Pigliucci, 2005, 2001). The term phenotypic plasticity is often more loosely used as all within-individual phenotypic changes in response to environmental variability (Ledon-Rettig et al., 2013). However, DNA methylation is expected to act differently according to whether these behavioural changes are permanent after development or whether they can flexibly change throughout an individual's lifetime. In order to be able to distinguish these different functions, we here refer to developmental plasticity for the irreversible phenotypic change during ontogeny and behavioural flexibility for any reversible plasticity in behaviour later in life (Piersma and Drent, 2003). When variation exists in the strength of phenotypic changes over development, time or in response to an environmental variable, individuals vary in the slope of the reaction norm (Dingemanse et al., 2010; van Oers et al., 2005). In the next section, we report studies that investigate how developmental plasticity may affect DNA methylation and personality traits, the role of

DNA methylation underlying between-individual variation in personality traits, and how DNA methylation may cause individual differences in behavioural flexibility, phenotypic plasticity and temporal consistency (Fig. 1).

4.1. Developmental plasticity

Within an individual, the phenotypic expression of personality traits shows to be plastic since behavioural expression changes in response to fluctuations in environmental conditions. Indeed, especially conditions during early development are known to affect behaviour (Fawcett and Frankenhuis, 2015; Gartstein and Skinner, 2018; Stamps and Groothuis, 2010; Trillmich et al., 2018). As epigenetic mechanisms are predominantly activated during early development (Jaenisch and Bird, 2003; Watson et al., 2019), respond to alterations in environmental factors (Richards, 2006), and can contribute to phenotypic variation, epigenetic mechanisms are good candidates for studying the mechanisms explaining developmental plasticity of personality traits. Various factors acting during development are known to be influential. Parents are central in affecting their offspring phenotypes and are known to transfer information about their environment to their offspring, likely to maximise their own fitness (Lindstrom, 1999; Mousseau and Fox, 1998). Also, offspring respond to the environment they are experiencing themselves in order to maximise their own fitness (Beldade et al., 2011). Below we specifically highlight the evidence that epigenetic mechanisms underlie behavioural responses to parental and environmental effects during development.

4.1.1. Parental effects

Studies on how parental effects alter both behaviour and DNA methylation are not necessarily focused on personality traits directly. Nonetheless, the studies described below assessed individual behaviour in situations that are often used to study personality traits, namely: risky situations, new situations, situations with conspecifics and general activity (Réale et al., 2007). Furthermore, behavioural and endocrinological responses to parental influences often reflect functional aspects of the hypothalamic-pituitary-adrenal (HPA) axis, which is known to also be a key facet underlying several personality traits (Baugh et al., 2017; Caro et al., 2019; Weaver et al., 2004).

Most of the published studies that focus on parental effects to date have been conducted on rodents. Especially the numerous studies on maternal effects in model species such as rodents (for an overview, see Jawahar et al., 2015), have provided a foundation for the field of behavioural epigenetics. High and low maternal care rats differ in the frequency of pup licking and grooming, but only in the only first week after giving birth. This induces striking differences in offspring behavioural and HPA responses to stress in adulthood (Weaver et al., 2004; for an overview, see Champagne et al., 2003). These effects are, at least partly, due to differences in the regulation of the glucocorticoid-mediated stress response. Glucocorticoids mediate the reaction to stress by inhibiting corticotrophin factor release, which results in inactivation of the pituitary-adrenal system and the tempering of the HPA response (De Kloet et al., 1998). Several reviews provide a detailed overview of the studies and the molecular basis for the effects on the HPA response (Anacker et al., 2014; Fish et al., 2006; Meaney and Szyf, 2005; Szyf et al., 2005; Zhang et al., 2013). In short, although offspring from high and low frequency care mothers (rats) initially do not differ in methylation level of the glucocorticoid receptor (*GR*) gene, differences appear when they are six days old (Weaver et al., 2004), In the hippocampi of offspring that received low nursing levels there appeared to be lower histone acetylation and increased *GR* promoter binding site methylation, which probably explained the decreased binding of a transcription factor (nerve-growth-factor-inducible protein A, *NGFI-A*), the low *GR* expression (Weaver et al., 2007) and the altered behavioural and HPA responses. Later studies suggest that the altered behaviour might also be mediated via epigenetic effects on the GABAergic system by altering DNA methylation and expression of glutamic acid decarboxylase 1 (*GAD1)* (Zhang et al., 2010) and glutamate metabotropic receptor 1 (*GRM1*) (Bagot et al., 2012). Many of the above-mentioned effects could be at least partly reversed with cross-fostering (Caldji et al., 2003; Francis et al., 1999; Weaver et al., 2004) and by administration of a methyl donor or a histone deacetylate inhibitor (Weaver, 2005; Weaver et al., 2006). This strongly suggests that maternal care causally affects behaviour of offspring that reached adulthood, at least partly, via epigenetic mechanisms.

Studies on the effects of maternal care in captive macaques have also provided many insights in behavioural epigenetics (for an overview, see Guerrero et al., 2020). In young rhesus (*Macaca mulatta*) and bonnet macaques (*Macaca radiata*), surrogate–peer rearing and exposure to unpredictable foraging conditions during infancy increase anxiousness, impulsiveness, and aggression in adulthood. Furthermore, it induces a more reactive stress response and alters neurotransmitter functioning (for an overview, see Stevens et al., 2009). In addition, differential (hydroxy)methylation in the blood and brain between maternally-reared and surrogate–peer reared rhesus macaques were found (Massart et al., 2016, 2014; Nieratschker et al., 2014; Provencal et al., 2012), suggesting that DNA methylation might facilitate stable behavioural responses the early life conditions. Alternatively, DNA methylation might buffer or exacerbate the effects of early life stress. In rhesus macaques, the effects of maternal separation on activity behaviour were intensified (i.e. enhanced behavioural reactivity to stress) in individuals with higher methylation (Kinnally et al., 2010). Similar

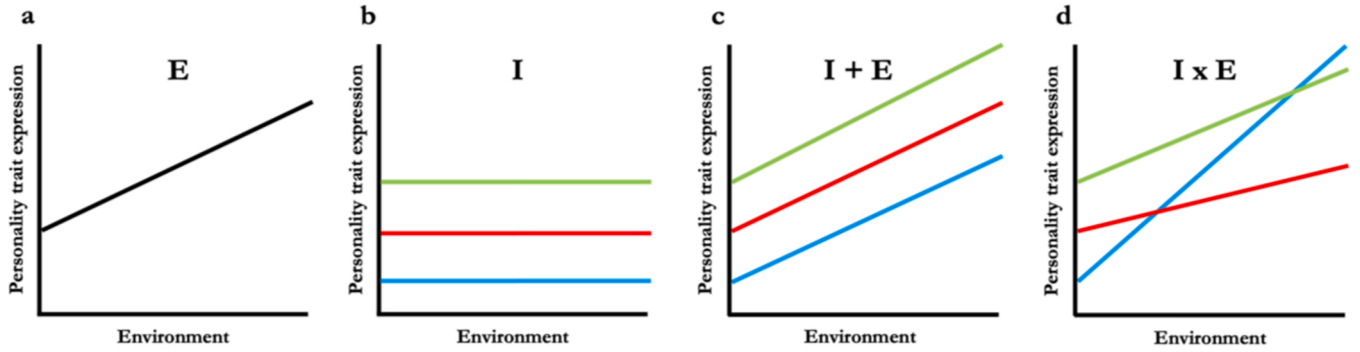

Fig. 1. Phenotypic plasticity. The expression of a personality trait in response to environmental variation. Each colour representing one individual. E in the figure reflects an environmental influence and I consistent individual differences. (**a**) No between-individual differences in average trait expression, but trait expression changes in response to environmental changes (E), hence, there is phenotypic plasticity. (**b**) Trait expression does not change in response to environmental changes, hence, there is no phenotypic plasticity. Between-individual differences (I) exist, but remain constant over time. (**c**) Trait expression changes in response to environmental (E) changes, hence, there is phenotypic plasticity. In addition, individuals remain consistently different from each other (I). (**d**) The individuals respond differently to environmental changes, resulting in between-individual differences in phenotypic plasticity (I x E).

results were found in adult female bonnet macaques exposed to unpredictable foraging conditions during infancy (Kinnally et al., 2011). In these females, higher behavioural stress reactivity was associated with both higher whole genome methylation and higher serotonin transporter gene (*5-HTT*) methylation, while this association was not observed in control females (Kinnally et al., 2011). In both studies, methylation level or behavioural stress reactivity did not differ between the control and the stressed group (Kinnally et al., 2011, 2010). Therefore, these results indicate that maternal effects do not necessarily induce a certain behavioural phenotype via effects on DNA methylation, but the intensity of the behavioural response to postnatal conditions might depend on the methylation status of certain genes.

Besides postnatal effects, several studies have focused on preconceptional or prenatal parental effects on DNA methylation and/or behaviour. For example, in rats, fathers that were stressed preconception, sire more anxious pups with higher levels of serum corticosterone compared to pups from control fathers (Niknazar et al., 2017). Pups from stressed fathers also showed higher levels of methylation in the hippocampus, suggesting that these effects might be mediated via methylation (Mychasiuk et al., 2013; Niknazar et al., 2017). Also, maternal stress during pregnancy increased anxiety-like behaviour and serum corticosterone levels in rat pups and altered their corticotrophin releasing hormone methylation and expression in the hypothalamus (Xu et al., 2014). However, especially in species with postnatal care, it is hard to determine whether such prenatal stressors have a direct effect on the offspring or whether the effects are induced indirectly postnatally as prenatal stress also reduces maternal care (St-Cyr and McGowan, 2015).

In oviparous species, the embryo develops outside the female's body, making it possible to separate prenatal from postnatal effects. Nonetheless, there are only few studies linking DNA methylation variation to behaviour in non-mammalian species. One of these exposed female sticklebacks (*Gasterosteus aculeatus*) to predators and found that they sire offspring that perform less well in learning tasks and show increased anti-predator behaviour compared to offspring from control females (Mommer and Bell, 2014). Furthermore, biological pathways in epigenetic inheritance differed between embryos of predator-exposed mothers and embryos of control mothers (Mommer and Bell, 2014), which suggests that the behavioural effects are mediated via epigenetic mechanisms. In male zebra finches (*Taeniopygia guttata*), experimentally elevated yolk testosterone increased aggression and induced differential methylation and expression in the amygdala and hypothalamus of adult males that had hatched from those eggs (Bentz et al., 2021). As there is no maternal care in sticklebacks (Mommer and Bell, 2014) and yolk testosterone was directly manipulated (Bentz et al., 2021), these findings evidently show that preconceptional and prenatal maternal factors or conditions induce changes in DNA methylation and behaviour. Overall, this indicates that parents have a wide window to affect offspring behaviour via molecular epigenetic mechanisms. Functional validation of these findings is supplied by a study in which prenatal methyl donor deficiency was accompanied by increased anxiety in the adult offspring and differential methylation of candidate genes related to brain development and glucocorticoid metabolism (Konycheva et al., 2011).

Since several studies found parental effects on DNA methylation and behaviour in adult offspring (see e.g. Bentz et al., 2021; Franklin et al., 2010; Provencal et al., 2012; St-Cyr and McGowan, 2015), these findings also suggest that epigenetic mechanisms facilitate stable behavioural responses via early life conditions. When personality traits are subject to developmental plasticity via epigenetic mechanisms, this does not necessarily mean that epigenetic mechanisms increase the within-individual variation in expression of these traits and, as a result, decrease the repeatable variation. If functional epigenetic marks are induced by conditions during early development and are subsequently stably mitotically inherited, they contribute to the stasis of the stable expression of personality traits or stable individual differences in personality traits once an individual is able to express these personality traits after early development. Such a stable response is especially well demonstrated in a study in mice where maternal separation increased offspring immobility (stress coping behaviour) and affected methylation and expression of the arginine vasopressin gene at the age of six weeks, three months and one year (Murgatroyd et al., 2009).

In theory, early developmental conditions can induce epigenetic marks that may engender an adaptive phenotype throughout an individual's lifetime (Jablonka and Raz, 2009; Richards, 2006). To increase parental fitness, it would, therefore, be advantageous to 'prepare' offspring for the environmental conditions they have to grow-up in. Fitness increases if developing organisms are able to produce behaviours that are most appropriate for future environments. Epigenetic mechanisms might provide the parents with the perfect opportunity to alter gene expression in the offspring and make the offspring's phenotype more suitable for the current local environment (Lachmann and Jablonka, 1996). This hypothesis has been supported by a study, in which mouse offspring exposed to a predator odour during pregnancy showed increased anti-predator behaviour and a predator-odour induced decrease in activity after birth (St-Cyr and McGowan, 2015). Methylation and expression of brain-derived neurotrophic factor (*BDNF*) were also affected, although assessed in adult female offspring only (St-Cyr and McGowan, 2015). Whether such changes are indeed adaptive, remains speculative in this study, since lifetime reproductive success could not be measured. In three-spined sticklebacks (*G. aculeatus*), paternal care reduced offspring anxiety and did increase offspring survival (McGhee and Bell, 2014). since parental care also affected expression of one of the DNA methyltransferases (*DNMT3a*), which are known to catalyse methylation (Cheng and Blumenthal, 1999; Robertson and Wolffe, 2000), it is likely that DNA methylation was also affected by paternal care (McGhee and Bell, 2014). Therefore, the two studies above indicate that parents can impact offspring behaviour and subsequently survival through epigenetic alterations. Nevertheless, the exact functional causal mechanisms remain unclear until experiments are conducted that directly manipulate DNA methylation associated with personality related gene expression.

Although the studies described above often found clear parental effects on offspring DNA methylation, behaviour and sometimes survival, it is important to acknowledge that the effects might not be general across offspring. As DNA methylation patterns (Gatev et al., 2021; Liu et al., 2010; McCarthy et al., 2014; Natt et al., 2014; Solomon et al., 2022; Teranishi et al., 2001; Yousefi et al., 2015) and personality trait expression or consistency (see e.g. Buirski et al., 1978; Michelangeli et al., 2020; Schuett and Dall, 2009) might (at least partly) depend on offspring sex, this opens up the possibility of a sex-dependent relationship between offspring behaviour and DNA methylation. Indeed, preconceptional, prenatal and postnatal stress affected stress responsivity and reward seeking behaviour in rodent offspring in a sex-dependent way (prenatal: Mueller and Bale, 2008; preconception: Mychasiuk et al., 2013; postnatal: Sasagawa et al., 2017). These changes were accompanied by altered *DRD1* (Sasagawa et al., 2017) and glucocorticoid receptor and central corticotropin-releasing factor gene expression and methylation in brain tissue of either males or females (Mueller and Bale, 2008), although methylation was only assessed in either one of the sexes. Furthermore, preconceptional paternal stress reduced methylation in brain tissue of female offspring only (Mychasiuk et al., 2013), while prenatal stress induced differential gene expression in the placenta, among which increased *DNMT1* expression in female placentas only (Mueller and Bale, 2008), and increased levels of *DNMT1* and corticosterone in the adult female brain (Benoit et al., 2015). In rhesus macaques, postnatal stress induced sex-dependent methylation patterns until at least two years after birth (Massart et al., 2016). Such results suggest that epigenetic mechanisms allow sex-dependent sensitivity to prenatal stress or sex-dependent buffering of prenatal stress, which allows parents to prenatally modulate offspring behaviour in a sex-dependent way. This might lead to personality differences between the sexes, explained by epigenetic mechanisms. However, such patterns

might be very species specific as sex differences in personality have not been found in all species (see e.g. Michelangeli et al., 2020; Naguib et al., 2013) and the existence is an ongoing point of discussion (see e.g. Harrison et al., 2022; Michelangeli et al., 2016).

4.1.2. Early environmental effects

The parental environment might not necessarily be the same as the offspring environment as environmental conditions can fluctuate between and within generations. In such a case, offspring can increase their fitness more if they behaviourally respond more strongly to the current local conditions rather than to the parental conditions. Also, if these environments are not very stable, there might be a conflict in what maximises parent fitness and what maximises offspring fitness (Trivers, 1974). DNA methylation might allow offspring such a flexible response to the experienced environment. To our knowledge, there is only one study that simultaneously assessed the effect of early environmental effects on DNA methylation and behaviour while taking the parental environment into account. In this study, mangrove killifish (*Kryptolebias marmoratus*) reared in enriched or barren environments differed in methylation in 1854 cytosines (Berbel-Filho et al., 2020). Furthermore, the enriched environment induced higher activity and neophobia and lower cortisol levels. Out of the 1854 sites, 724 changed in methylation status if the offspring environment did not match the parental environment, while only 98 more or less maintained the parental methylation pattern (Berbel-Filho et al., 2020).

4.2. Epigenetic causes of individual variation

Personality traits are by definition approached from an individual rather than a population perspective. If we measure a personality trait multiple times in several individuals, we see that individuals tend to differ more from each other than between subsequent measurements. This so-called repeatability is often measured as the intraclass correlation coefficient, a statistic assessing the relative amount of between-individual variation compared to the total phenotypic variation (Bell et al., 2009). This rather strict statistical definition of animal personality (Sánchez-Tójar et al., 2022), however, does not take into consideration whether and which molecular mechanisms are underlying behavioural consistency. At the molecular level, these individual differences can potentially be explained by both genetic and epigenetic effects (Bengston et al., 2018) and an emerging hypothesis is that behavioural repeatability can be explained by individual differences in DNA methylation.

A number of studies have shown that personality traits are polygenic and likely many genes of small effect, affect personality trait variation (Santure et al., 2015). Several candidate genes have been identified where genetic polymorphisms seem to underlie heritable variation in personality traits (Grunst et al., 2021; van Oers and Mueller, 2010). Often the associations between personality and polymorphisms in these genes are low and vary among studies and therefore seem to be context dependent (Bubac et al., 2020). If DNA methylation modulates these genetic predispositions, such epigenetic variation could explain these ambiguous findings. Even in the presence of these genetic polymorphisms, DNA methylation can override genetic differences, by preventing gene expression.

The best-studied candidate genes belong to the dopaminergic signalling pathway, predominantly dopamine receptors D4 (*DRD4*) and D2 (*DRD2*). Dopamine is a neurotransmitter involved in reward regulation processes and was initially generally associated with human personality (Savitz and Ramesar, 2004). In great tits (*Parus major*), a commonly used operational measure of a personality trait is exploratory behaviour, which is measured as the reaction to a novel environment (Dingemanse et al., 2002). In both wild and captive great tits, exploratory behaviour is heritable (Dingemanse et al., 2002; Drent et al., 2003; Quinn et al., 2009) and *DRD4* has been suggested as a candidate gene for great tit personality in some, but not all populations (Fidler et al., 2007; Korsten et al., 2010; Mueller et al., 2013).

These candidate genes were the first candidates for exploring epigenetic associations with personality related genetic variation. For example, when comparing individuals originating from lines artificially selected for fast and slow exploratory behaviour, Verhulst et al. (2016) found small differences in the levels of DNA methylation in a CpG island in the promoter region of *DRD4*. These differences were not present at CpG islands downstream in the gene body, indicating a functional link between DNA methylation in this gene and the phenotype (Verhulst et al., 2016). Remarkedly, differential methylation ranged from 3% to 10%. Such small differences can only be picked up with targeted techniques such as pyrosequencing, as was used in this study. In another study on great tits, behaviour and DNA methylation in *DRD4* were compared between forest and urban great tits. In this study, Riyahi et al. (2015) found that overall, urban great tits showed higher levels of exploration and novelty seeking behaviour than forest great tits. In line with this, the urban greats tits had higher levels of *DRD4* methylation compared to forest great tits (Riyahi et al., 2015). More evidence that there is such a relationship between candidate gene DNA methylation variation and personality was found in a study where DNA methylation in *DRD2* was investigated in relation to five rating-based personality traits in chimpanzees (*Pan troglodytes*). When all 16 sequenced CpG sites of *DRD2* were merged into four PCAs, *DRD2* methylation in these four PCAs was found to be associated with extraversion and to a lesser extent with openness (Staes et al., 2022). Another candidate gene that has been widely associated with personality variation is the Serotonin Receptor gene (*SERT*). *SERT* is a member of the *SLC* group (also called *SLC6A4*), which protein transports serotonin that has been linked to adverse early life conditions and stress responses in both humans and animals models (see Non et al., 2016; Parade et al., 2021). Serotonin has been found to be associated with the expression of exploratory behaviour in several animal studies (Grunst et al., 2021; Riyahi et al., 2015; Timm et al., 2018). Only one study to date, has investigated DNA methylation in *SERT* in relation to animal personality in an urban forest comparison. Urban birds are known to be faster explorers compared to forest-dwelling birds (Charmantier et al., 2017; Riyahi et al., 2017). Therefore, the result that methylation levels in *SERT* were found to be lower in forest-dwelling compared with urban great tits (Riyahi et al., 2015) is in line with the expectation. However, when directly associating DNA methylation with exploratory behaviour the relationship was not straightforward (Riyahi et al., 2015).

These studies form the basis of investigating the functional role of DNA methylation in candidate genes and provide us with a functional mechanism why such candidate genes relate to personality differences. Next steps, apart from including more and multiple candidate genes in association studies, is to include measures of gene expression and to investigate the origin of this variation in DNA methylation. The expectation is that much of this variation is actually present as cis-acting DNA sequence variation in the form of genetic polymorphisms within the gene or promoter region. For example, in a study on humans, five of such cis located SNPs explained variation in DNA methylation in the promoter of the *DRD4* gene. Since these SNPs were synonymous, these results provide us with a functional reason for associations between synonymous mutations and phenotypes found in earlier studies (Docherty et al., 2012; Fidler et al., 2007).

In systems where genetic variation is absent, epigenetic marks have also shown to be responsible for distinct differences between individuals. For example, in the ant *Camponotus floridanus* epigenetic programming including methylation changes, cause caste-specific behaviour to be expressed. When such modifications are experimentally altered, also the behaviour changes, indicating a direct causal relationship between methylation and individual differences in behaviour (Simola et al., 2016). A similar phenomenon is observed in honeybees (*Apis mellifera*), more than 550 genes showed DNA methylation differences between queen and worker female castes (Lyko et al., 2010). Normally, larvae that have not been feeding on royal jelly do not become

queens, but down-regulation of DNA methyltransferase in these larvae resulted in the development into queens (Kucharski et al., 2008).

An intriguing question is if selection acts on DNA methylation, there will be a response to selection, either directly and independent on genetic variation or indirectly, dependent on the underlying genetic variation. Evidence exists that indeed DNA methylation is involved in genomic evolution. For example, in the great tit, an increased CpG methylation was observed in genes that were present in regions that had been under recent selection, so called sweep regions (Laine et al., 2016). These genes turned out to be involved in learning, cognition and neuronal functions. This thus suggests that epigenetic mechanisms might have an impact on the evolution of behaviour of learning, cognition and neuronal functions. The alternative explanation is that of reversed causation, where methylation changes may be the consequence of selection on genes coding for these traits. This so-called reverse causation, is something that needs specific attention (Relton and Davey Smith, 2012), since often the route from DNA methylation, via expression to phenotype is assumed, but epigenetic marks such as DNA methylation are prone to be affected by gene expression as well (Höglund et al., 2020). For example in a study on olive flounder (*Paralichthys olivaceus*), genes that were differentially expressed in bold and shy flounders were not always negatively corelated with a change in methylation, but also positive associations between gene expression and DNA methylation were detected (Zou et al., 2021).

The search for structural genomic variants underlying the heritable component of behavioural traits has only revealed a fraction of the heritable variation in behavioural traits (Alison M Bell and Dochtermann, 2015; Laine and van Oers, 2017). Other hereditary molecular mechanisms, such as DNA methylation, might therefore explain part of the heritability of behavioural traits (Groothuis and Trillmich, 2011; Stamps and Groothuis, 2010; Trillmich and Hudson, 2011). If this is the case, selection on a behavioural trait results in co-selection on genetic variants that affect DNA methylation (Verhoeven et al., 2016). However, whether the heritable fraction of behavioural variation is affected by stably inherited DNA methylation is largely unknown, and only few examples exist where coinheritance of DNA methylation variation and genetic variation has been investigated. One study on great tits, specifically looked at whether DNA methylation variation could be co-selected after artificial phenotypic selection, by comparing genome-wide DNA methylation levels between F4 individuals from fast and slow early exploratory behaviour selection lines. In this study, van Oers et al. (2020) found no DNA methylation marks that were different between unrelated individuals from the two lines. This revealed the absence of stably inherited epigenetic marks for this population and a lack of a response of DNA methylation to selection on phenotypic variation. Therefore, variation in DNA methylation related to exploratory behaviour has likely a very low evolutionary potential itself (Herrel et al., 2020; Verhoeven et al., 2016), at least in this species.

Overall, the results of studies linking genotypic variation in personality traits with DNA methylation suggest that there is relatively little scope for an influence of DNA methylation on animal personality traits that is independent from genetic variation. DNA methylation likely associates with genomic variation in or near the genes that code for personality variation, demonstrating that DNA methylation related to genetic personality variation is genetically controlled in itself. However, genome-wide studies are needed to locate epigenetic marks that are more distant from genes, or that are even unrelated to genetic variation. Eventually, methylation levels need to be manipulated, in order to test causality between DNA methylation, gene expression and phenotypic expression, which might be challenging in many wild animals.

4.3. Temporal consistency and reaction norms

4.3.1. Epigenetic control of temporal consistency

Repeatability of behaviour can also be assessed by measuring behaviour between set time points. An individual behaves consistently through time, when repeatabilities are high and the within-individual change over time is relatively low compared to the between-individual change. Since DNA methylation patterns inherit from cell to cell, DNA methylation patterns that emerged during development, either of genetic or environmental origin, can potentially stably affect gene expression and hence cause personality differences to maintain throughout an individual's life. When epigenetic marks of genetic origin are relatively stable over time, but also when epigenetic marks change plastically in response to the environment, personality differences may persist over time in relatively stable environments (Fig. 1b), or when individuals show similar responses to environmental changes (Fig. 1c).

Studies investigating the consistency of DNA methylation patterns within individuals over time, indeed find that within-individual changes in methylation are small (Viitaniemi et al., 2019), with only a small fraction of CpG sites actually changing over time (Lindner et al., 2021b). Genome-wide repeatabilities of DNA methylation are therefore generally substantial, with intra class correlations ranging between 0.59 and 0.80 in human tissues (Yu et al., 2021) to even 0.97 in human sperm cells (Cortessis et al., 2011). This leads to the hypothesis that the consistency in DNA methylation contributes to a relatively high within-individual consistency in behaviour, explaining at least part of the existence of personality differences. Up to date, no study has explored this idea in animals. However, in a study on humans, Tabassum and co-workers (2015), measured longitudinal profiles of gene expression and DNA methylation in 12 individuals in order to measure genomic individual consistency. They found that 67% of the variance in gene expression and up to 88% in DNA methylation was explained by between-individual differences. From this the authors concluded that such baseline omics data, including DNA methylation, show that personality is also measurable at the epigenomic level (Tabassum et al., 2015). An important factor that needs to be taken into account is that the repeatability of technical replicates in several methods is only moderate (Dugué et al., 2015), causing a limit to which methods can be used for investigating this interesting question. Future studies should therefore focus on using highly repeatable methods when studying how temporal changes and stability in DNA methylation relates to the relative contribution of between-individual variation in behaviour. On the other hand, this calls for measuring technical replicates when assessing repeatabilities of DNA methylation data in studies on animal personality.

To assess the stability of DNA methylation within an individual's lifetime, a very promising direction for future research would be to study if the repeatability of DNA methylation is causally related to the repeatability of personality traits. For example, individuals could be sampled and behaviourally tested multiple times. This way, repeatabilities of both DNA methylation and the personality trait could be calculated and within- and between-individual correlations between DNA methylation and the personality trait can be assessed (Dingemanse and Dochtermann, 2013). Second, to assess if environmentally induced variation in DNA methylation can explain repeatability of personality traits, individuals can be behaviourally measured for personality before and multiple times after exposure to a certain environmental factor. Such an environmental factor should be an ecologically relevant factor that is expected to affect both behaviour and DNA methylation, such as nutrition (Konycheva et al., 2011; Sullivan et al., 2010; Vucetic et al., 2010) or brood size (Sepers et al., 2023b, 2021; Sheldon et al., 2018). The repeatabilities should be compared to those of a control group to rule out a change in repeatability due to for example aging (Christensen et al., 2009). At the same time, such an approach would also allow the assessment of within-individual changes in DNA methylation and behaviour. This alternative procedure of assessing personality has been suggested before (Dall and Griffith, 2014; Dingemanse and Dochtermann, 2013). Furthermore, such an approach would also allow to investigate whether the relative influence of genes and environment changes over a lifetime and whether DNA methylation might explain age-related changes in heritability of personality traits (Class et al., 2019).

4.3.2. Individual differences in reaction norms

Individuals or genotypes may also differ in the plastic expression of behavioural traits along an environmental gradient (Dingemanse et al., 2010; van Oers et al., 2005). The molecular mechanisms by which environmental cues are translated into a plastic response are still largely unknown, especially in wild animals (Aubin-Horth and Renn, 2009), and that is even more so for individual differences in these mechanisms (Bengston et al., 2018). Such individual differences in the slope of this response, may be caused by individual variation in the susceptibility to gene expression changes, caused by epigenetic modifications. An example where individual differences in reaction norms are explained by epigenetic factors is in high- and low novelty seeking rats. High novelty seeking rats are more vulnerable to depressive-like symptoms and avoidance of conspecifics after social defeat compared to low novelty seeking rats (Duclot and Kabbaj, 2013). This is caused by an increase in hippocampal *BDNF* expression in low novelty seeking rats after social defeat, while this up-regulation was not found in high novelty seeking rats. These differences in the susceptibility to social stress were likely caused by epigenetic factors regulating stress resilience via *BDNF* expression, since differences in histone acetylation and methylation were detected between the two groups (Duclot and Kabbaj, 2013). A study in Senegalese house sparrows shows how individual differences in reactions norms might be mediated by environmentally dependent epigenetic effects. Corticosterone (the major avian glucocorticosteroid) positively covaried with hippocampal *DNMT* expression in a more recently established population at the range-edge, whereas this covariation was negative in the oldest population at the range-core (Kilvitis et al., 2018). Since hippocampal *DNMT* expression is required for synaptic plasticity as well as learning and memory (Feng et al., 2010), a positive covariation possibly enhances resilience to stressors through neurogenesis, whereas a negative covariation potentially leads to higher hippocampal plasticity in the absence of stressors. In the range-edge, where individuals are also more exploratory (Liebl and Martin, 2012), individuals might therefore show more behavioural flexibility under stress conditions, whereas in the range core, individuals might be more flexible under baseline conditions.

Individuals are known to not only vary consistently in their mean trait value or in their reaction norm, but also in the predictability of the trait (Stamps et al., 2012). This means that certain individuals might be more flexible in their behaviour compared to others. Recently it has been shown that this within-individual behavioural flexibility around the mean value also has a quantitative and molecular genetic basis (Henriksen et al., 2020; Martin et al., 2017). Between-individual differences in wideness in range of achieved phenotypes may be due to differences in epigenetic potential, quantified as the number of CpG sites an individual maintains, since a higher number of CpGs might enable them to adjust gene expression more rapidly (Kilvitis et al., 2017). Epigenetic potential in the promoter region was predictive of expression levels of the immune gene *TLR4* in blood, but high epigenetic potential predicted gene expression reversibility only in females and not males (Hanson et al., 2021).

A special case of how epigenetic variation may underlie reaction norms is in life-cycle staging, when phenotypes change reversibly, but predictably, for example when phenotypes are seasonally plastic (Piersma and Drent, 2003). Such predictable phenotypic changes can be under epigenetic control, if genotypes are responding to fluctuations in cues that have a temporal predictability, such as the fraction of hours of light per day (Dawson et al., 2001), seasonally fluctuations in temperature (Bonamour et al., 2019), precipitation (Feng et al., 2013), or the moon cycle (Prugh and Golden, 2014). One example where within individual changes in DNA methylation have received attention, is in studies on seasonal timing (Alvarado et al., 2015; Baerwald et al., 2016; Lindner et al., 2021a; Saino et al., 2017; Viitaniemi et al., 2019). By creating datasets of individuals that are repeatedly sampled over a range of time periods, stability and repeatability of such marks can be studied (Mäkinen et al., 2019), and the association with one of the environmental cues. For example, a clear pattern of seasonality has been found in DNA methylation of promoters when sampling females multiple times during the reproductive season (Lindner et al., 2021a; Viitaniemi et al., 2019), indicating that the timing of sampling is very important. Individuals (Caro et al., 2019) and genotypes (Visser et al., 2011) have been shown to differ in such norms of reaction along a reproductive increase, indicating that the patterns of change over the reproductive season are expected to relate to individual differences in personality. An interesting example of possible future research on the importance of methylation in cyclic temporal changes in behaviour related to the moon cycle, is that of the glass eel (*Anguilla* Anguilla). Several behavioural patterns, such as locomotor activity, migration behaviour and pulses in recruitment are known to be dependent on the moon cycle (Cresci et al., 2019). More recently, also the orientation of migration was found to be dependent on the moon cycle (Cresci et al., 2019). Since the orientation of migration was found to not be explained by visual mechanisms, a likely role for DNA methylation has been speculated upon (Liu et al., 2022).

5. Future directions and conclusion

5.1. Functional validation

Although the suggestions described above would aid our understanding of the existence and evolutionary potential of animal personality, we should not forget that ecological studies are often based on generalisations related to the functionality of DNA methylation (Greally, 2018; Laine et al., 2022). Such generalisations come with limitations, of which several are described in Sepers et al. (2019). Some other limitations include that often DNA methylation levels are studied in blood cells, as this is an accessible tissue that allows for repeated sampling. However, whether blood DNA methylation levels can be used as a proxy or biomarker for DNA methylation in other tissues is still under discussion (Husby, 2020). For example, in contrast to blood, non-CpG methylation occurs in vertebrate brain cells only (de Mendoza et al., 2021; Derks et al., 2016; Laine et al., 2016; Pinney, 2014). Given the functional relationship between the brain and behaviour, non-CpG methylation might contribute to variation in personality traits in different ways compared to CpG methylation. This extends to the fact that epigenetic changes may only be apparent in the specific tissues where they target gene expression (Lindner et al., 2021b).

Lastly, although methylation of single sites can affect gene expression (see e.g. Pogribny et al., 2000), we do not know how large the difference needs to be to result in differences in gene expression. Furthermore, we cannot exclude the possibility that gene expression changes depend on regional changes instead of single sites (Laine et al., 2022). How many CpG sites have to be changed before a phenotypic effect arises, is something that needs more study. This indicates that laboratory studies are still needed to functionally validate whether changes in DNA methylation causally affect gene expression and whether changes in gene expression causally affect personality traits. This could be done by administering dietary methyl donors, such as choline, betaine, folate and methionine (Dominguez-Salas et al., 2013; Obeid, 2013; Weaver, 2005), or hypomethylating agents, such as decitabine or azacytidine (Derissen et al., 2013; Hollenbach et al., 2010). A CRISPR-based approach could be used for targeted DNA methylation or demethylation in certain model systems (Xu et al., 2016).

5.2. Other epigenetic mechanisms

In this paper we mainly focussed on DNA methylation as an epigenetic mechanism. This is mainly caused by the fact that studies often focus on DNA methylation. This often reflects the ease at which DNA methylation can be measured, but not its relative importance. However, not only DNA methylation, but the combined effects of different epigenetic processes are critical for inter-individual differences (David

Sweatt, 2019). In addition to DNA methylation, there are at least two other major epigenetic mechanisms that play an important role in variation in behavioural traits: post-translational histone modifications (Jaenisch and Bird, 2003) and non-coding RNAs (Champagne, 2018; Rahman and McGowan, 2022).

Whereas DNA methylation is relatively stable after development, histone modifications are more reversible (Reik, 2007). Modifications to histone tails can change the transcriptional state by influencing the accessibility of DNA to transcription factors or enzymes that regulate DNA methylation (Wilson and Merkenschlager, 2006). DNA methylation and post-translational histone modifications are therefore molecularly linked (Hashimoto et al., 2010). For example, histone deacetylation and DNA methylation coexist at silenced loci and can both be the initial epigenetic event that initiates silencing (Vaissière et al., 2008). DNA methylation readers interact with histone modification erasers to suppress transcription. Vice-versa, DNA methyltransferases contain chromatin recognition domains and may induce DNA methylation upon recognition of certain histone modifications (Bohnsack and Pandey, 2021). Interindividual difference in stress responsiveness and cognitive abilities are now known to be mediated by interdependent epigenetic alterations. In rats, higher stress sensitivity is accompanied by H3K9me3-mediated modification of DNA methylation at FGF2 promoter sites (Chaudhury et al., 2014). Maternal care-dependent behavioural changes that lead to differential corticotrophin-releasing hormone gene expression require both DNA methylation and histone modifications (Singh-Taylor et al., 2018; Wang et al., 2014).

Also non-coding RNAs, such as micro-RNAs and long non-coding RNAs, play a role in gene regulation (Champagne, 2018; Rahman and McGowan, 2022). Micro-RNAs repress gene expression post-transcriptionally, as their binding to mRNA prompt it's degradation, and they have been implicated in susceptibility to behavioural changes following early life stress (Allen and Dwivedi, 2020; Xu et al., 2017; Zhang et al., 2015). Long non-coding RNAs are involved in chromatin remodelling and histone modifications (Rahman and McGowan, 2022; Statello et al., 2021). They are poorly studied in relation to behaviour, but they are widely expressed in neural tissues and there are indications that they play a role in nervous system development and maintenance, stress responses and plasticity (Arzua et al., 2021; Qureshi et al., 2010).

Importantly, heritable epigenetic alterations in response to environmental factors require integration of all these, and other epigenetic processes. A bidirectional relationship exists between genetic variation and histone modifications, since histone modifications depend on certain regulatory DNA motifs (Ngo et al., 2019), but also maintain DNA sequence integrity (Aristizabal et al., 2020). The latter is specifically important in relation to transgenerational inheritance, as are non-coding RNAs. Non-coding RNAs likely underlie transgenerational epigenetic inheritance via the male germline (Gapp et al., 2014; Jawaid and Mansuy, 2019), as they direct DNA methylation. Non-coding RNA in the sperm from male F1 offspring from gestating female rats that were transiently exposed to a fungicide (vinclozolin) or pesticide (DDT), overlapped with F1 sperm differentially methylated regions, which also had significant overlap with differential histone retention, suggesting DNA methylation-directed histone retention. A high percentage of those induced differentially methylated regions in the F1 generation sperm were maintained in subsequent generations (Beck et al., 2021).

These findings suggest that not only DNA methylation, but a whole suit of epigenetic mechanisms can underlie behavioural consistency and plasticity. Moreover, those different mechanisms cannot be seen as acting independently. Ultimately to understand and predict epigenetic effects on animal personality we will have to put effort in studying multiple of these mechanisms as interdependent regulatory systems. Since they often rely on genetic variation, this thereby clearly has to be taken into consideration.

6. Concluding remarks

Here, we reviewed studies that show that epigenetics is an important factor when studying the molecular mechanisms underlying animal personality, at various levels. We increasingly know more about the multifaceted role that molecular epigenetic mechanisms play in regulating behavioural phenotypes and how they may play a role in explaining individual differences in behavioural at the level of the behavioural trait variation, their developmental trajectory and their consistency. Still the field is in its infancy and to date, most studies that investigated relationships between epigenetic mechanisms and personality are conducted in controlled non-natural settings. Since both genetic and environmental effects on behaviour may be mediated by epigenetic changes (Laine et al., 2022; Ledon-Rettig et al., 2013), studies in natural settings are becoming more important, in particular when investigating the interaction between genetic and environmental effects. There is enough evidence that these two cannot be considered independently. Epigenetic mechanisms are therefore not a way to contrast nature and nurture, but an intriguing way of organisms to find a way to integrate both heritable and transient factors to maximise fitness.

Acknowledgements

The authors thank the Ettore Majorana Foundation and Centre for Scientific Culture for hosting a stimulating symposium that led to the development of many of the ideas in this paper. We also thank Claudio Carere and Dario Maestripieri for hosting this workshop and for initiating and editing this special issue. During the writing of this manuscript Bernice Sepers (BS) was funded by NWO grant ALWOP.314 and Krista van den Heuvel (KvdH) was funded by a KNAW Research grant, both of which were granted to Kees van Oers (KVO). We would like to thank Melanie Lindner, Koen Verhoeven and Veronika Laine for fruitful discussions.

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