



Cortisol during adolescence organises personality traits and behavioural syndromes



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ABSTRACT

Despite the growing evidence for the importance of developmental experiences shaping consistent individual differences in behaviour and physiology, the role of endocrine factors underlying the development and maintenance of such differences across multiple traits, remains poorly understood. Here, we investigated how an experimental manipulation of circulating glucocorticoids during early adolescence affects behavioural and physiological variation and covariation later in life in the precocial cavy (*Cavia aperea*). Plasma cortisol concentrations were experimentally elevated by administering cortisol via food for 3 weeks. Struggle docility, escape latency, boldness, exploration and social behaviour were then tested three times after individuals attained sexual maturity. In addition, blood samples were taken repeatedly to monitor circulating cortisol concentrations. Exogenous cortisol affected mean trait expression of plasma cortisol levels, struggle docility and escape latency. Repeatability of cortisol and escape latency was increased and repeatability of struggle docility tended to be higher (approaching significance) in treated individuals. Increased repeatability was mainly caused by an increase of among-individual variance. Correlations among docility, escape latency and cortisol were stronger in treated animals compared to control animals. These results suggest that exposure to elevated levels of cortisol during adolescence can alter animal personality traits as well as behavioural syndromes. Social and risk-taking traits showed no correlation with cortisol levels and were unaffected by the experimental manipulation, indicating behavioural modularity. Taken together, our data highlight that cortisol can have organising effects during adolescence on the development of personality traits and behavioural syndromes, adding to the increasing evidence that not only early life but also adolescence is an important sensitive period for behavioural development.

1. Introduction

While consistent among-individual differences in behaviour, i.e., animal personality (Dingemanse and Wolf, 2010; Wolf and Weissing, 2010), are common across taxa, our knowledge about the mechanisms driving and maintaining these differences is still rather limited (Dingemanse and Wolf, 2010; Groothuis and Trillmich, 2011; Koolhaas et al., 2010; Stamps and Groothuis, 2010a, b). Variation in personality arises from the combined influence of genetic and environmental factors (Dingemanse and Dochtermann, 2014; Dobzhansky et al., 1977; Han and Dingemanse, 2015). Hence, understanding the contribution of developmental experiences in shaping adult personality traits is fundamental to a comprehensive understanding of the generation of consistent individual differences (Groothuis and Trillmich, 2011; Stamps and Groothuis, 2010a, 2010b).

Because phenotypic plasticity may involve costs (Snell-Rood, 2013), the adjustment of personality traits may potentially be limited to sensitive windows during development (Bateson, 1979). Sensitive windows are defined as periods or developmental stages in which experiences shape phenotypic characteristics to a larger extent than in other periods or stages (Fawcett and Frankenhuis, 2015). The canalisation of behaviour within sensitive windows may represent an evolutionary adaptation when the costs and benefits of sampling and reacting to information vary between life stages (Panchanathan and Frankenhuis, 2016). So far, most attention has been given to early life periods, usually the pre-natal and early post-natal life (Bateson, 1979; Curley and Branchi, 2010; Fawcett and Frankenhuis, 2015) while recently, also the early adolescent period has been identified as one such sensitive window in which many species adjust to their environment (Blakemore and Mills, 2014; Ellis et al., 2012; Sachser et al., 2013; Sebastian et al., 2010).

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Across taxa, there is strong evidence that glucocorticoids (GCs) mediate environmental challenges including stressors through pleiotropic effects on multiple neurological, physiological and behavioural traits (Hau et al., 2016). Brain circuits involving the prefrontal cortex and parts of the limbic system, such as the hippocampus and amygdala, play a central role in stress reactivity as they contain high densities of gluco- and mineralocorticoid receptors, which bind adrenal steroids that are regulated by the hypothalamic–pituitary–adrenal (HPA) axis (Herman et al., 1997). During adolescence, all these brain structures undergo structural and functional maturation (Brydges, 2016; Uematsu et al., 2012), which is likely to be affected by variation in the main glucocorticoids, cortisol and corticosterone (Lupien et al., 2009; McEwen, 2007).

Environmental effects such as predation pressure, population density, food availability or environmental predictability that are experienced throughout development, can have canalising effects on the hormonal phenotype that last into adulthood, thereby altering behaviour and fitness across the life span (Brown and Spencer, 2013; Kapoor et al., 2006; Love et al., 2005; Monaghan and Haussmann, 2015). Hence, glucocorticoids are prime candidates by which environmental conditions experienced during early adolescence create differences in adult personality traits among individuals.

Most studies investigating effects of GCs on personality traits to date focus on the comparison of the mean phenotypic response of a trait in control versus experimentally stressed animals. Exposure to corticosterone during development, for example, leads to increased activity and novel environment exploration in adult Japanese quail (*Coturnix coturnix japonica*) (Zimmer et al., 2013). In small rodents, stress or direct exposure to stress hormones during adolescence generally leads to more anxious adults (for review see McCormick and Green, 2013).

Notably, already two decades ago, the importance of variation around the mean has been pointed out, as this variation provides the basis on which selection can operate (Boake, 1989; Hayes and Jenkins, 1997). Although this notion was for a long time somewhat neglected, researchers have now started to quantify the contribution of within-versus among individual variation in shaping behavioural variation (Dingemanse, Dochtermann, 2013; Westneat et al., 2015). Within-individual variation indicates flexibility and measurement error (Dingemanse, Dochtermann, 2013; Jenkins, 2011). Among-individual variation, on the other hand, indicates the extent to which individuals differ in their mean trait expression. Nutritional stress during the nestling stage of zebra finches (*Taeniopygia guttata*), for example, increases differences in exploration and activity between individuals (i.e. increasing among-individual variance) (Careau et al., 2014a). The proportion of among-individual variance divided by the total phenotypic variance is known as trait repeatability (Falconer and Mackay, 1996). Its quantification is one of the cornerstones of animal personality research as repeatability can set the upper boundary for heritability and thus indicates the evolutionary significance of a trait (Falconer and Mackay, 1996). Recent research indicates that the relative contributions of these two variance components and hence repeatability can show sex-specific and experience-specific variation within species (Briffa, 2013; Careau et al., 2014a; Han and Dingemanse, 2017; Jenkins, 2011; Royauté and Dochtermann, 2017). For example, hermit crabs (*Pagurus bernhardus*) exposed to a perceived predation threat show increased repeatability by decreasing within-individual variation (Briffa, 2013). Similarly, dietary stress increases repeatability in anti-predator behaviour of house crickets (*Acheta domesticus*) by decreasing within-individual variation (Royauté and Dochtermann, 2017).

In addition to effects on single personality traits, exposure to stressful environments during development has the potential to alter the covariance between traits and hence affect behavioural syndrome structure (Killen et al., 2013). Pesticide exposure has been shown to weaken correlations between personality traits in jumping spiders (*Eris militaris*) (Royauté et al., 2015). Similarly, dietary stress during development uncoupled correlations between different personality traits in

great tits (*Parus major*) (Carere et al., 2005) and between activity, metabolic rate and stress-induced corticosterone in zebra finches (Careau et al., 2014b). On the other hand, food deprivation of European bass (*Dicentrarchus labrax*) led to a stronger correlation between risk-taking and metabolic rate (Burton et al., 2011) and unpredictable food conditions revealed an association between metabolic rate and territory acquisition in Atlantic salmon not being present in controls (*Salmo salar*) (Reid et al., 2011). Despite the existing evidence that environmental characteristics can influence the covariance structure, the developmental mechanisms that shape the emergence or break up the existence of behavioural syndromes are poorly understood so far (Groothuis and Trillmich, 2011; Han and Dingemanse, 2015).

Here we propose that circulating glucocorticoids during early adolescence (also called pre-puberty) represent a key mechanism by which stressful experiences shape personality traits, levels of among- and within individual variation as well as among-individual covariation between personality traits (i.e. behavioural syndromes, structural consistency). To test this, we manipulated levels of circulating cortisol (CORT) for a period of 3 weeks during early adolescence to simulate chronic stress in wild cavies (*Cavia aperea*). After the end of the treatment, behaviours indicating stress-coping, risk-taking and social tendencies as well as baseline cortisol levels were measured three times throughout life. We then compared mean trait expression, trait variances and correlations among traits between treated animals and control animals.

We hypothesise based on the literature (1) that a three-week CORT elevation modifies the developmental trajectory resulting in more anxious, less risk-taking and potentially less social individuals. We further hypothesise (2) that the CORT manipulation leads to an increased repeatability compared to untreated animals. We hence investigate if changes in repeatability estimates arise due to effects on among- or within-individual variance components. In addition to changes in among-individual variation, elevated stress-hormone levels may affect within-individual variation, i.e. individual flexibility (Briffa, 2013; Careau et al., 2014a; Royauté and Dochtermann, 2017). Finally, (3) we test if the manipulation of CORT during development has the potential to alter behavioural syndromes up into adulthood (Careau et al., 2014b).

2. Material and methods

2.1. Animals and maintenance

Experimental animals were bred in outdoor enclosures during spring by adding one male to two females each. After weaning, juvenile cavies ($n_{\text{mothers}} = 24$; $n_{\text{juveniles}} = 60$; ♀26, ♂33) were individually marked with a pit tag (ID-100, TROVAN, passive transponder system; Euro ID, Weilerswist, Germany; dimensions: diameter: 2.12 mm; length 11.5 mm) inserted subcutaneously into the interscapular region and kept in 24 unrelated same sex groups throughout the experiment. Siblings were divided such that half of them were later assigned to the control group and the other half to the treatment group.

Group enclosures were located in two rooms directly adjacent to each other. Enclosures could be divided into multiple compartments by trap doors allowing a separation of individuals for behavioural testing. Each compartment measured 0.8 m² and contained a brick stone, a water bottle, a feeder, hay and an opaque shelter. Wood chips were used for bedding. Except for behavioural testing, the trap doors stayed open, allowing animals to move freely within the enclosure and interact with each other. Four males became aggressive when approaching adulthood and were thus separated prior to the last test phase. They had still visual, olfactory and auditory contact to their former group mates.

Animals were kept under natural light conditions with additional artificial light from 6 am to 7 pm, at constant temperatures of 20 ± 2 °C. Hay, guinea pig pellets (Höveler, Germany) and water were available ad libitum and supplemented with fresh greens (apples,

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