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Early experience affects adult personality in the red junglefowl: A role for cognitive stimulation?

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ABSTRACT

Despite intense research efforts, biologists are still puzzled by the existence of animal personality. While recent studies support a link between cognition and personality, the directionality of this relationship still needs to be clarified. Early-life experiences can affect adult behaviour, and among these, cognitive stimulation has been suggested theoretically to influence personality. Yet, the influence of early cognitive stimulation has rarely been explored in empirical investigations of animal behaviour and personality. We investigated the effect of early cognitive stimulation on adult personality in the red junglefowl (*Gallus gallus*). To this end, we assessed adult behaviour across a number of personality assays and compared behaviour of individuals previously exposed to a series of learning tasks as chicks, with that of control individuals lacking this experience. We found that individuals exposed to early stimulation were, as adults, more vigilant and performed fewer escape attempts in personality assays. Other behaviours describing personality traits in the fowl were not affected. We conclude that our results support the hypothesis that early stimulation can affect aspects of adult behaviour and personality, suggesting a hitherto underappreciated causality link between cognition and personality. Future research should aim to confirm these findings and resolve their underlying dynamics and proximate mechanisms.

Contents

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1. Introduction

The last two decades have witnessed a rapid increase in research interest surrounding consistent individual differences in behaviour, also known as animal personality (Gosling, 2001; Dall et al., 2004; Sih et al., 2004; Réale et al., 2007). Personality has been described in a broad range of species (Gosling, 2001; Carere and Maestripieri, 2013) and demonstrated to have important ecological and evolutionary consequences (Dall et al., 2004; Sih et al., 2004; Smith and Blumstein, 2008; Carere and Maestripieri, 2013). Despite this, the factors shaping variation in animal personality are still poorly understood. While genetic mechanisms have been demonstrated in a number of species, their contribution to personality variation is generally limited (e.g. van Oers et al., 2005; van Oers and Sinn, 2011; Dochtermann et al., 2015). This leaves ample scope for environmental effects to contribute to personality (Stamps and Groothuis, 2010; Groothuis and Trillmich, 2011). Early life experiences in particular are predicted to have far-reaching consequences for the development of individual personality traits (Stamps and Groothuis, 2010), yet such effects have rarely been empirically explored (but see e.g. Naguib et al., 2011; Schuett et al., 2013; Krause and Naguib, 2014; van Oers et al., 2015). Further studies of the developmental processes affecting personality are therefore needed to improve our understanding of both the proximate mechanisms underlying personality variation and its evolutionary consequences (Stamps and Groothuis, 2010; Groothuis and Trillmich, 2011).

There are several studies demonstrating that early experiences can influence adult behaviour, suggesting that personality traits may also be affected. However, most of the evidence is limited to laboratory studies of mammals. Deprivation of maternal care has been shown to increase anxiety-like behaviour in rodents and primates (Papaioannou et al., 2002; Barr et al., 2003; Neto et al., 2012), while early handling can have the opposite effect and reduce anxiety (reviewed in Chapillon et al., 2002). Similarly, early environmental enrichment can have profound effects on behaviour (e.g. review by van Praag et al., 2000; Christensen and Nielsen, 2004; Lazic et al., 2007; Patzke et al., 2009), for example by reducing stress reactivity (Chapillon et al., 2002) and by enhancing explorative behaviour later in life (e.g. Joseph, 1979; Christensen and Nielsen, 2004). These effects likely occur due to changes in the developing neuronal and physiological systems. For example, early experiences can modify the development of central neuronal systems involved in regulation of stress and emotion (Levine et al., 1957; Meaney et al., 1991; van Praag et al., 2000). Early experiences can thus have critical effects on brain development, physiology and behaviour, and may also have long-lasting consequences affecting personality.

Despite this, exploration of the implications of early experience on the development of animal personality is still largely limited to theoretical models (e.g. Wolf et al., 2008; Bergmüller and Taborsky, 2010; Dingemanse and Wolf, 2010; Duckworth, 2010). Among the growing number of empirical studies conducted to date, there is increasing evidence for effects of early experience on adult personality. For example, in guppies (*Poecilia reticulata*), unpredictable feeding regimes increased boldness and exploration later in life (Chapman et al., 2010). In zebra finches (*Taeniopygia guttata*), reduced dietary micronutrients reduced adult boldness (Noguera et al., 2015), while the personality of foster parents (Schuett et al., 2013), and the condition of parents (Krause and Naguib, 2014) influenced exploration in offspring as adults. These behavioural changes may arise through effects on the developing central neural system. For example, in marsh tits (*Parus palustris*, Clayton and Krebs, 1994), and in domestic chicks (*Gallus gallus domesticus*, Freire and Cheng, 2004), early stimulation generates changes in the hippocampus and activation of monoaminergic pathways.

Among the early life experiences potentially affecting adult personality, cognitive stimulation has been suggested to have important effects (Carere and Locurto, 2011). Complex interplays between personality and cognition have been recently suggested, mainly based on theoretical grounds (Carere and Locurto, 2011; Sih and Del Giudice, 2012; Griffin et al., 2015), but also by some empirical studies (e.g. Guillette et al., 2009, 2011, 2015; Exnerová et al., 2010; Light et al., 2011; Amy et al., 2012; Titulaer et al., 2012). Nevertheless, the directionality of any causal link between personality and cognition is still largely unresolved (Carere and Locurto, 2011; Sih and Del Giudice, 2012; Griffin et al., 2015). Theoretically, any relationship can be due to one of three scenarios; (i) personality and cognition may share a common underlying mechanism, (ii) personality may affect cognition, or (iii) cognition may affect personality (Matzel et al., 2003; Light et al., 2008). Examples of shared underlying factors include variation in speed-accuracy trade-offs (Sih and Del Giudice, 2012), or shared underlying control structures (Coppens et al., 2010). The latter has been suggested by artificial selection experiments showing that selection for personality traits can affect performance in cognitive tasks (Groothuis and Carere, 2005), most likely by influencing the shared HPA-axis control of behaviours (reviewed in Groothuis and Carere, 2005; Mathot et al., 2012). On the other hand, individual differences in personality traits, like exploration and boldness, could affect individual cognitive abilities if, for example, explorative individuals interact more with their environment and therefore acquire more information (Light et al., 2008). However, as far as we know, this scenario has not been experimentally supported. On the contrary, while mice exposed to novel environments showed increased exploration tendency, there was no effect on learning (Matzel et al., 2003). Finally, variation in individual cognitive abilities and experiences may affect personality. For example, individuals that can process information faster may as a consequence explore faster, while slow individuals would be constrained in doing so (Light et al., 2011; Carere and Locuto, 2011). In experiments on mice, individuals with higher performance across several learning tests habituated faster to a novel environment and were more explorative, which was interpreted as support for cognition affecting behaviour and not vice versa (Light et al., 2011).

In fact, few studies have explicitly tested the hypothesis that cognition can affect personality (but see Light et al., 2011), and we are not aware of any specifically testing whether early cognitive stimulation may have long-lasting effects on personality traits. We therefore explored this possibility in the red junglefowl (*Gallus gallus*), a species for which we have developed behavioural assays that capture variation in personality (Favati et al., 2014a, b; Favati et al., 2015), where personality stabilises after ontogeny (Favati et al., 2015), and can be affected by the social environment (Favati et al., 2014b). Here, we investigated how early stimulation, aimed to stimulate cognition, affects adult personality, by exposing young chicks to a series of tasks involving learning, an important cognitive process (Shettleworth, 2010). We hypothesised that cognitive stimulation would most likely affect behaviour linked to information processing, such as vigilance and/or exploration of novel environments. On the other hand, we predicted that if early stress, rather than cognitive stimulation, is affecting adult behaviour, fear-related behaviour (such as latency to move after induction of tonic immobility, Forkman et al., 2007) would be affected the most.

2. Methods

2.1. Animals and housing

We used a total of 175 red junglefowl ($n_{males} = 95$, $n_{females} = 80$) from a captive, pedigree-bred population kept at Linköping Uni-

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