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Essay

Evidence for the role of personality in stereotypy predisposition

Carrie L. Ijichi*, Lisa M. Collins, Robert W. Elwood

School of Biological Sciences, Queen's University Belfast, Belfast, U.K.

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It is often suggested that stereotypic behaviour represents a coping response to suboptimal environmental conditions. However, individuals of many species show different coping styles depending on their personality type. Therefore, personality is an important consideration when investigating why only certain individuals become stereotypic under suboptimal conditions. Thus, the aim of this review is to explore the possibility that personality, in particular coping style, may explain why certain individuals are predisposed to stereotypy. We review behavioural and physiological similarities between proactive and stereotypic individuals and suggest that they may in fact be the same phenotype. We also explore how these characteristics might predispose proactive individuals to stereotypy and how this is triggered by the environment. We conclude that personality factors relating to proactivity may mediate whether an animal expresses stereotypic behaviour and that the alternative strategy in such conditions is depression and emotional blunting. We conclude by outlining the animal welfare implications if this hypothesis is correct.

Stereotypic behaviour is repetitive, invariant and has no obvious goal or function (Mason 1991). Many of the causal factors and neurobiological mechanisms in the development of such behaviour are now known (reviewed in Mason & Rushen 2006). Yet despite an ever increasing understanding of how and why stereotypies develop, an explanation for why only certain individuals are affected by such factors remains elusive. That is, there are individual differences in how animals respond to suboptimal conditions. Individual differences in behaviour that are consistent across time and contexts are called 'personality' (Gosling & John 1999) or 'behavioural syndromes' (Sih et al. 2004) and are known to have a physiological basis (Koolhaas et al. 1999). Personality research is the study and quantification of such differences and may provide useful insight here. One method of quantifying personality is through the assessment of coping styles which define how an animal attempts to minimize the impact of environmental stress on affective and physiological homeostasis (Koolhaas et al. 1999). Because stereotypic behaviour is the result of such stress and may be an attempt to cope, coping style may be relevant to questions concerning differences in stereotypy development (Wechsler 1995; Koolhaas et al. 1999). Fortunately, the biological mechanisms involved in coping strategies are particularly well understood and so can be compared with those mediating stereotypic behaviour.

LINKING PERSONALITY AND STEREOTYPIC BEHAVIOUR

Individuals react to stress (defined here as any challenge to an individual's homeostasis that results in poor welfare) in different ways which can be described along two independent axes: (1) how stress sensitive an animal is and (2) how they minimize stress once a critical threshold has been reached (reviewed in Koolhaas et al. 2010). Stress sensitivity is associated with scoring highly for the personality factor neuroticism and is often proposed to be a causal factor in stereotypic behaviour. This is intuitive because stereotypy represents a response to stress. However, stereotypic and non-stereotypic animals kept in the same conditions show the same basal hypothalamic–pituitary axis (HPA) activity and heart rate (e.g. Pell & McGreevy 1999; McBride & Cuddeford 2001; Clegg et al. 2008; Engel et al. 2011), which implies differences in stress sensitivity may not adequately explain stereotypic behaviour. Stress sensitivity mediates the threshold at which a coping response is required but coping style facilitates which response is used once this threshold is reached (Koolhaas et al. 1999). We propose that stereotypic behaviour reflects a proactive coping response to stress but, in reactive individuals, there is an equal and opposite response, namely depression. Of course, not all proactive animals will express stereotypic behaviour because not all individuals will experience the relevant triggers. Furthermore, more stress-resilient animals will need a much greater stressor before either of these coping strategies is expressed but in theory, with a great enough stressor, all animals will adopt one or the other strategy.

* Correspondence: C. L. Ijichi, School of Biological Sciences, Medical Biology Centre, 97 Lisburn Road, Belfast BT9 7BL, U.K.
E-mail address: cijichi01@qub.ac.uk (C. L. Ijichi).

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Here, we address how proactive and reactive strategies may link with stereotypic behaviour and depression under stressful conditions. Proactive animals are categorized as having active responses to stress (Benus et al. 1989; Driscoll et al. 1990) such as high incidence of defensive burying in a shock probe test (Sluyter et al. 1996), active swimming in a forced swim test (Veenema et al. 2005) and low levels of immobility (Benus et al. 1987). They also show high restraint resistance (Hessing et al. 1993; Korte et al. 1997; Bolhuis et al. 2005). Their reactive counterparts show opposite reactions largely relating to a freeze response to stressors. These findings indicate that proactive animals try to exert control over environmental stressors through aggression, removal of the stressor or, if those responses are not successful or possible, by removing themselves from the context in which the stressors are presented. By contrast, reactive animals adopt passive responses to stressors and show few, if any, attempts to control them. This passive strategy results in emotional blunting and has depressive-like symptoms (Porsolt et al. 1977).

Suboptimal environmental conditions such as unnatural weaning (Würbel & Stauffacher 1997; Würbel & Stauffacher 1998), social isolation (Jeppesen et al. 2000) and food restriction (Bildsøe et al. 1991; Mason et al. 2001) have been implicated in the development of stereotypic behaviour. There are currently two hypotheses concerning the potential benefit of stereotypy under such suboptimal conditions: (1) the 'reward function' serving to keep the animal within an affective homeostasis (Hughes & Duncan 1988) and (2) the behavioural needs function maintaining motivational and physiological homeostasis (Jensen & Toates 1993). Both hypotheses involve the individual attempting to exert control in a suboptimal environment in order to maintain its stress levels within a tolerable limit, in other words, a proactive response.

Proactive individuals share multiple common behavioural and physiological traits with stereotypic individuals (for a summary see Fig. 1) suggesting they may be linked. For example, proactive animals show behavioural patterns that are largely independent of actual external stimuli (Benus et al. 1988) and are highly routine forming (Benus et al. 1987; Benus & Daas 1990; Bolhuis et al. 2004). Proactive animals also have much lower cue dependency than reactive animals (Benus et al. 1987; Sluyter et al. 1996). In an open maze test proactive mice, *Mus musculus*, learn a response (e.g. always turn left for food reward), which they continue even if entering through a different arm of the maze. By contrast, reactive mice use their greater cue dependency to alter their response to enter the correct arm of the maze (Benus et al. 1987). Like proactive animals, stereotypic animals quickly adopt response strategies (Garner et al. 2003; Parker et al. 2009). Once this strategy is established, they show limited exploration (Parker et al. 2009) and poor extinction/reversal learning (Garner et al. 2003; Vickery & Mason 2005; Parker et al. 2008) indicative of stimulus response learning (Parker et al. 2008; Tanimura et al. 2008), more commonly

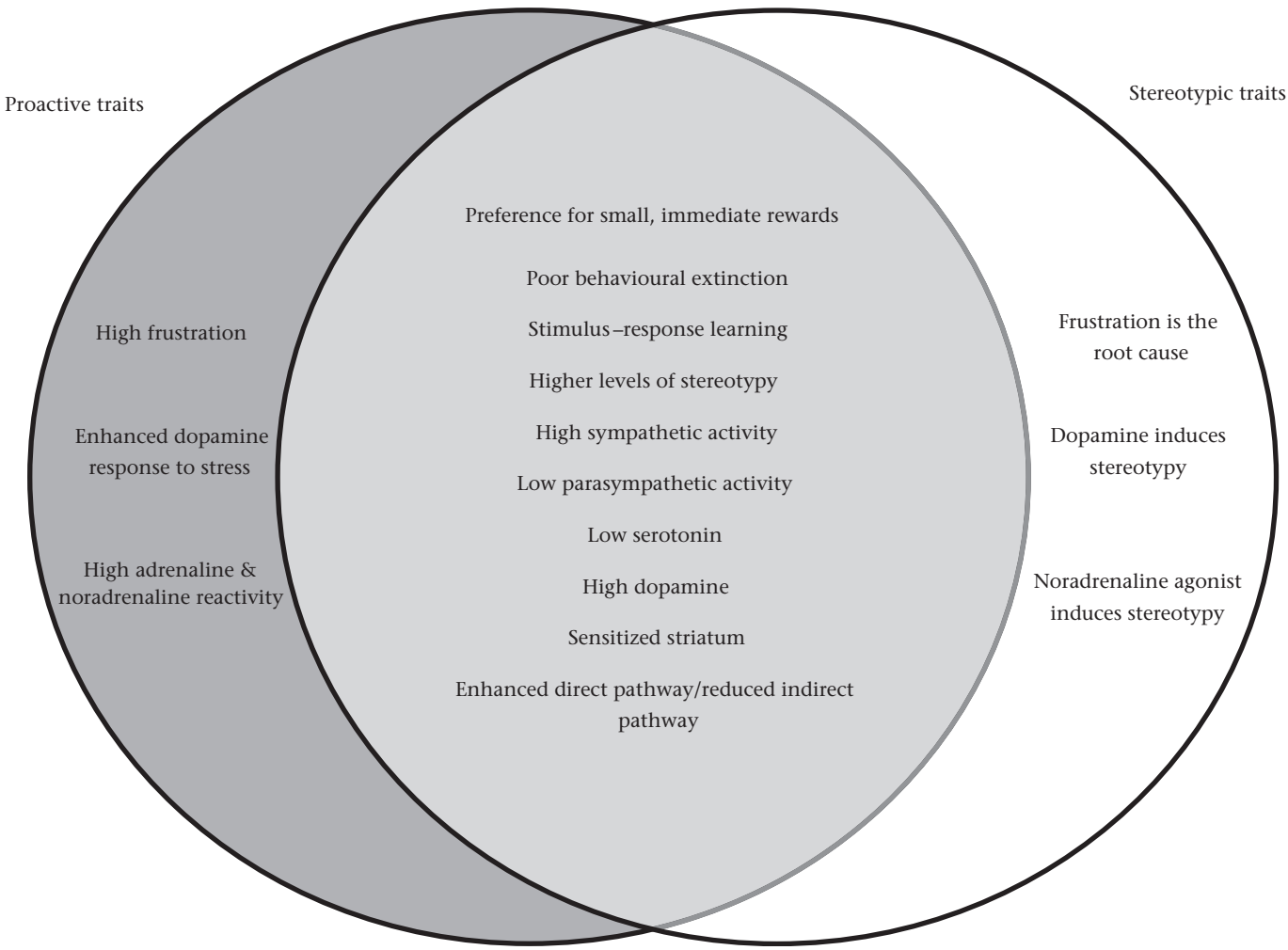

Figure 1. Venn diagram illustrating similarities between proactive and stereotypic individuals, suggesting they are overlapping phenotypes.

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