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Does early stress prepare individuals for a stressful future? Stress during adolescence improves foraging under threat

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Adolescent exposure to adverse environmental conditions can cause lasting changes in behaviour, cognition and physiology. One explanation for why such changes occur is that they allow organisms to adjust aspects of their phenotype to enhance function in an unfavourable environment. This concept has been investigated for stress during gestation (e.g. thrifty phenotype hypothesis, maternal mismatch hypothesis). Here, we apply these ideas within an individual's lifetime as a possible explanation for long-term phenotypic changes in response to stress during adolescence. To test whether stress during adolescence can cause phenotypic changes that prepare an animal for future threat, we exposed laboratory rats to either chronic stress or unstressed control conditions during adolescent development. After a 5-week delay, rats were assessed in a timed-foraging task under both low-threat and high-threat conditions. Chronic stress during adolescence caused long-term changes in foraging behaviours and foraging performance. In low-threat conditions, stress-exposed rats had a longer latency to begin foraging but consumed the same number of rewards as unstressed rats. However, under high-threat conditions, rats exposed to stress during adolescence began foraging sooner, made more transitions between foraging patches and consumed more rewards than unstressed rats. These results indicate that stress exposure enabled rats to forage more effectively under later novel threat, and that phenotypic changes resulting from stressful experiences during adolescence may enhance function in future high-threat environments.

Stress has long been recognized as a transformative force in many taxa (Selye & Albert, 1942; reviewed in: Armario, Escorihuela, & Nadal, 2008; Francis et al., 1996). The effects of stress depend on intensity, duration and the developmental stage at exposure (Ariza Traslaviña, de Oliveira, & Franci, 2014; Park, Zoladz, Conrad, Fleshner, & Diamond, 2008; Wingfield et al., 1998; reviewed in Lupien, McEwen, Gunnar, & Heim, 2009). For example, exposure to predation threat during early development can cause lasting phenotypic changes in wood frogs (e.g. large limbs, narrower bodies; Relyea, 2001) and song sparrows (e.g. body size; Travers, Clinchy, Zanette, Boonstra, & Williams, 2010). In laboratory rats, a single encounter with a cat can decrease later exploratory behaviour (Adamec, Blundell, & Collins, 2001), interfere with memory consolidation and retrieval (Diamond et al., 2006) and change the shape of dendrites in brain cells (Mitra, Adamec, & Sapolsky, 2009).

The experience of stress during adolescent development, an inherently plastic time when regions in the brain that regulate the hypothalamic–pituitary–adrenal (HPA) axis mature, can cause lasting changes in behaviour, cognition and physiology (Caruso, McClintock, & Cavigelli, 2014; McCormick, Mathews, Thomas, & Waters, 2010; Sterlemann et al., 2008; Weintraub, Singaravelu, & Bhatnagar, 2010; reviewed in: Lupien et al., 2009; Romeo, 2010). Evidence for lasting changes following stress during adolescence is growing (reviewed in McCormick & Green, 2012). Studies of laboratory rodents have found that adolescent stress can affect spatial navigation (via changes in the hippocampus; Isgor, Kabbaj, Akil, & Watson, 2004; McCormick et al., 2010; Sterlemann et al., 2008), enhance novelty-seeking and risk-taking behaviour (Arrant,

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Schramm-Sapyta, & Kuhn, 2013; Toledo-Rodriguez & Sandi, 2011), alter decision making (Chaby, Cavigelli, White, Wang, & Braithwaite, 2013; Irwin, 1989; Torregrossa, Xie, & Taylor, 2012), change HPA axis function (McCormick et al., 2010) and increase anxiety (Green, Barnes, & McCormick, 2012; Schmidt et al., 2007).

Several studies of the lasting effects of stress during adolescence have reported negative functional outcomes, such as impairments to memory of object locations (McCormick et al., 2012) and poor reversal learning (Han, Wang, Xue, Shao, & Li, 2011). These changes have been attributed to disruptions of development and subsequent abnormal functioning of brain regions that mature during adolescence (Toledo-Rodreguiz & Sandi, 2007). However, other studies have reported phenotypic responses to adolescent stress that appear to be beneficial, including enhanced auditory fear conditioning (Toledo-Rodreguiz & Sandi, 2007) and accelerated decision making (Chaby et al., 2015). To understand the alternative outcomes from these studies, it is important to consider the context in which these responses were assessed.

The concept that organisms can adjust aspects of their phenotype to enhance function in an unfavourable environment has been investigated for stress during gestation (e.g. thrifty phenotype: Hales & Barker, 1992; maternal mismatch hypothesis: Sheriff & Love, 2013). According to the thrifty phenotype and mismatch hypotheses, early exposure to an adverse environment will prepare individuals for a high-threat environment, but may detract from performance under low-threat conditions. The disadvantages of a mismatch between gestational and later life environment have been demonstrated using cross-fostering designs (Hales & Ozanne, 2003; reviewed in Hales, 1997), natural population cycles in snowshoe hares, *Lepus americanus* (Sheriff, Krebs, & Boonstra, 2009, 2010), and manipulations of glucocorticoid exposure during embryonic development (Love, Chin, Wynne-Edwards, & Williams, 2005; Love & Williams, 2008). Here we apply these ideas within the span of an individual lifetime as a possible explanation for long-term phenotypic changes resulting from exposure to stress during adolescence (Fig. 1). We hypothesized that adolescent-stress exposure would shape adult phenotype in a context-dependent way, by preparing animals to perform better under future threat, but decreasing performance in a mismatched, low-threat environment when compared to animals reared without stress. To our knowledge this is the first study to test the effects of early exposure to stress on performance using the same assay in different environmental conditions.

To test these ideas we exposed laboratory rats to stress during adolescence or to unstressed control conditions. After a 5-week delay, we screened adult foraging behaviours (latency to engage in foraging, number of patch visits) and foraging performance (number of rewards eaten) in both low-threat and high-threat conditions. Wild rodents adjust forging behaviours when cues of predators are present (Orrock, Danielson, & Brinkerhoff, 2004), and foraging performance can be influenced by predation conditions (Pintor & Sih, 2009; Sih, 1982; Werner & Hall, 1988). Foraging performance can affect fitness through the ability to mitigate exposure to threat (Morris & Davidson, 2000), attract mates (Keagy, Savard, & Borgia, 2009, 2011) and provision offspring (Schwagmeyer & Mock, 2008). Foraging was evaluated both with and without cues of predation, using a foraging task that permitted animals to access a familiar reward by manipulating a novel object; similar assays have been used with captive and wild animals (e.g. humans and chimpanzees, *Pan troglodytes*: Herrmann, Hernández-Lloreda, Call, Hare, & Tomasello, 2009; spotted hyaenas, *Crocuta crocuta*: Benson-Amram, Weldele, & Holekamp, 2013; satin bowerbirds, *Ptilonorhynchus violaceus*: Keagy et al., 2009; house sparrows, *Passer domesticus*: Bókony et al., 2013).

We predicted that stress during adolescence would prepare animals for future threat in a context-dependent way such that, under high-threat conditions, adolescent-stressed rats would show more active foraging behaviours (begin foraging faster, move between patches more) and enhanced foraging performance (consume more rewards) relative to unstressed rats, whereas under low-threat conditions, adolescent-stressed rats would show reduced foraging behaviours and performance. Alternatively, if stress during adolescence results in a negative functional phenotype, adolescent-stressed rats should show reduced foraging behaviours and performance under both high- and low-threat conditions.

METHODS

Animals and Housing

Male Sprague—Dawley rats ($N = 24$) were obtained at 21 days of age from Harlan Laboratory in Fredrick, Maryland, U.S.A. Following transport, rats were given 7 days to acclimate before handling and experimental procedures began. Animals were randomly assigned to pair-housing in plastic cages ($20 \times 26 \times 45$ cm) with wood chip

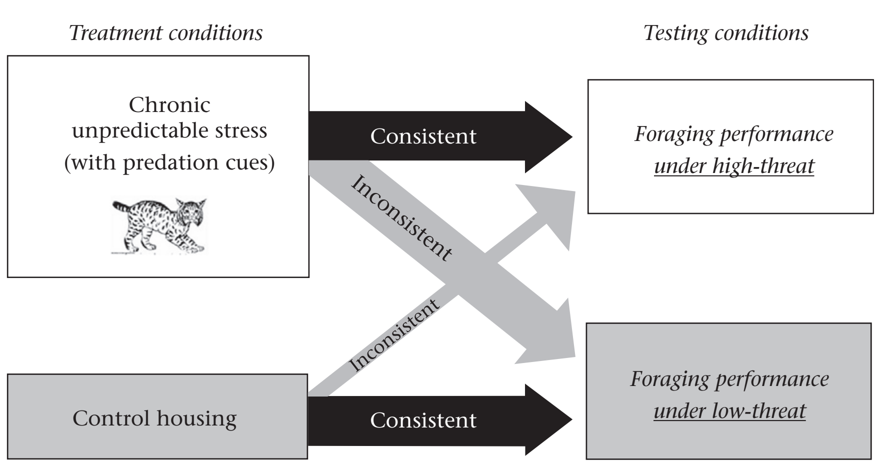

Figure 1. Framework of hypothesized performance in environmental conditions that were consistent and inconsistent with rearing (treatment) conditions. The effect of chronic unpredictable stress during adolescence on foraging performance of laboratory rats in adulthood was quantified using a seven-patch open arena foraging task under low-threat (standard conditions, under dim red light) and high-threat (visual and auditory cues of avian predation, bright white light). Stimuli used to create the high-threat testing environment were novel to both groups of rats.