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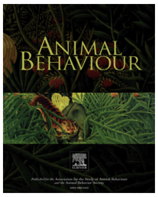

Are you what you eat? Micronutritional deficiencies during development influence adult personality-related traits

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Stressful environmental conditions such as periods of poor nutrition have been shown to affect a variety of life history traits. Although nutrition-induced effects on the phenotype can appear through the entire life of an individual, it is becoming evident that there are sensitive periods during development when phenotypic traits have heightened sensitivity to nutritional conditions. Very few studies have investigated how nutrition can affect an important aspect of an organism's phenotype: the development of its ‘personality’. In this study we manipulated the availability of the main micronutrients (i.e. vitamins and essential minerals) present in the diet of zebra finches, *Taeniopygia guttata*, during their postnatal development and/or during their sexual maturation. Later, once the birds were fully adult, we assessed a series of behavioural traits previously used to assess personality in birds. We found that low availability of dietary micronutrients during the postnatal period resulted in reduced boldness in males once they reached adulthood, but had no effect on adult stress responses or neophobic behaviour. No such effects were found in females. In contrast, a low micronutrient diet during sexual maturation led in both sexes to reduced stress responses and neophobic behaviours in adulthood. Interestingly, we also found that females became more aggressive as adults if they had received a low micronutrient diet during development, irrespective of when the availability of micronutrients was modified. Overall, our results demonstrate substantial effects of diet on the development of behavioural traits, and that these effects differ both between the sexes and over different developmental periods.

Exposure to stressful circumstances has pervasive effects on the phenotype, affecting behaviour, morphology and physiology (Lindström, 1999; Metcalfe & Monaghan, 2001; Monaghan, 2014; Noguera, Kim, & Velando, 2012; Spencer & Verhulst, 2007). Many of these effects are negative, shifting the phenotype from its optimal state (Lippmann, Bress, Nemeroff, Plotsky, & Monteggia, 2007; Lupien, McEwen, Gunnar, & Heim, 2009; Meerlo, Horvath, Nagy, Bohus, & Koolhaas, 1999; Weinstock, 1997). Other changes might, however, be adaptive, enabling the individual to better cope if faced with similar situations in the future (Bateson, 2001; Gluckman, Hanson, & Beedle, 2007; Monaghan, 2008). Although stress-induced effects on the phenotype can appear through the entire life of an individual, it is becoming evident that there are sensitive periods during development when phenotypic traits have heightened sensitivity to environmental stressors. Well-known examples of this include the influence that stress exposure during early development and adolescence has in shaping neural circuits that profoundly affect brain functioning and behaviour for the rest of the animal's life (Coppens, de Boer, & Koolhaas, 2010; Heim & Binder, 2012; Lupien et al., 2009; Saul et al., 2012).

Individuals of many taxa exhibit suites of correlated behavioural differences that are consistent over time and/or situations, usually referred to as ‘personality’ traits (Bell, Hankison, & Laskowski, 2009; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Personalities vary along a continuum, but individuals are usually classified as proactive or reactive (Cockrem, 2007), with proactive individuals being bolder, faster to explore, more prone to risk taking and more aggressive, while reactive individuals are shy, more risk averse and are less exploratory and aggressive. Personality-related traits may be correlated with physiological traits (Koolhaas, 2008) and may have important fitness consequences (Gutiérrez et al., 2013; Réale et al., 2007; Seyfarth, Silk, & Cheney, 2012; Smith & Blumstein, 2008). Importantly, although behavioural patterns are known to be partially genetic in origin (Dingemanse & Réale, 2005; Drent, van Oers, & van Noordwijk,

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2003; Réale et al., 2007; Van Oers, Drent, De Goede, & Van Noordwijk, 2004), personality exhibits phenotypic plasticity and can be influenced by environmental stressors during development (Arnold, Ramsay, Donaldson, & Adam, 2007; Carere & Maestripieri, 2013; Caspi & Roberts, 2001; Stamps & Groothuis, 2010). For instance, in several species of passerine birds, chicks experiencing periods of food scarcity (Carere, Drent, Koolhaas, & Groothuis, 2005), a low-quality diet (Krause, Honarmand, Wetzel, & Naguib, 2009) or a higher level of physiological stress (Spencer & Verhulst, 2007) tend to become more aggressive and explorative, and less neophobic, later in life. It has been suggested that the development of such behavioural traits, typical of more proactive personalities (Cockrem, 2007), could be beneficial when/if the individuals face unfavourable and poor environmental conditions. More proactive individuals, for instance, show higher motivation to feed. This might be a behavioural mechanism favouring greater, and possibly more opportunistic, food intake (David, Auclair, Giraldeau, & Cezilly, 2012), which in turn could favour survival during periods of food scarcity (Dingemanse, Both, Drent, & Tinbergen, 2004; but see also Naguib, Flörcke, & van Oers, 2011 for similar arguments about social stress).

The overall availability of food during development has long been recognized as having important influences on the adult phenotype (Kasumovic, 2013). There is, however, a growing interest in how the availability of specific micronutrients, which are only present in small amounts in the diet, can also underpin long-term phenotypic changes (e.g. Ashworth & Antipatis, 2001; Catoni, Peters, & Martin Schaefer, 2008; McGraw, 2007; McGraw, Adkins-Regan, & Parker, 2005) including adult personality traits (Arnold et al., 2007; Carere & Maestripieri, 2013). In contrast to macronutrients (i.e. carbohydrates, proteins and lipids), micronutrients such as vitamins (e.g. E, A, C, B) and minerals (e.g. Mg, Zn, Se, Ca) are normally only needed in small amounts but none the less play essential roles in the regulation of cellular metabolism or stress responsiveness and in providing components of the antioxidant defence system (Benton, 2008; Bhaskaram, 2002; Jiménez-Chillarón et al., 2012; McArdle & Ashworth, 1999; Surai, 2002). Consequently, micronutrient deficiencies may act as an important environmental stressor. Micronutrient deficiencies are not rare in nature and have been described in different taxa (i.e. Fisher, Fitzsimons, Combs, & Spitsbergen, 1996), including humans (Diaz, De las Cagigas, & Rodriguez, 2003). Furthermore, this phenomenon might be even more common than previously thought, especially in natural populations exposed to anthropogenic pollutants which may interfere with the normal absorption and metabolic routes of these nutritional components (Murvoll, Skaare, Jensen, & Jenssen, 2007).

Importantly, recent evidence suggests that dietary micronutrients may also exert effects on the development of behavioural traits (reviewed by Kaplan, Fisher, Crawford, Field, & Kolb, 2004). In humans and laboratory rodents, for instance, nutritional deficiencies of micronutrients can induce a higher level of aggressiveness (Kaplan, Crawford, Field, & Simpson, 2007; Kaplan et al., 2004; Rucklidge, Taylor, & Whitehead, 2011), a higher propensity to violence (Benton, 2008) and/or promote different types of antisocial and rule-breaking behaviour (Frensham, Bryan, & Parletta, 2012; Popper, 2001). The effects seem to vary according to the period of life when the micronutrient deficiency was experienced (Kaplan et al., 2007). It is therefore conceivable that micronutrient availability could also be mediating the development of personality traits in other vertebrate species, although as far as we know no studies have yet explored this possibility.

Here we investigated this possibility using zebra finches, *Taeniopygia guttata*. In the wild, zebra finches live in unpredictable habitats characterized by their dryness and with short breeding seasons, so that birds may have to compete to gain access to limited resources (i.e. food, water, mates or nest sites; Caryl, 1975; Zann & Bamford, 1996). In these habitats, the grass species on which zebra finch feed are often exposed to hydric stress which might alter the normal production and accumulation of different vitamins in the seeds (Watts et al., 2014). Importantly, nutritional conditions during zebra finch development have been shown to influence a range of traits related to physiology (Blount, Metcalfe, Arnold, Surai, & Monaghan, 2006; Criscuolo, Monaghan, Nasir, & Metcalfe, 2008; Kriengwatana, Wada, Macmillan, & MacDougall-Shackleton, 2013) and behaviour (Krause et al., 2009; Krause & Naguib, 2011). In a two by two factorial design, we manipulated the intake of micronutrients within the normal range of variation in captive conditions during both the postnatal period (first 40 days of life) and the timing of sexual maturation (40–90 days old). Once the birds were fully adult (6–8 months old), we assessed how the availability of micronutrients during these two periods of development affected the consistency across time and the direction of a suite of traits previously used as proxies of personality in birds: the degree of docility, aggressiveness, boldness, stress responses and neophobia.

METHODS

Animals and Housing

Fifty female and male adult zebra finches, all experienced breeders, were taken from our stock population (see Rehling et al., 2012 for further details), paired randomly and allowed to breed under standardized conditions in our facilities at the University of Glasgow, U.K. On the day of pairing the average age (months) of the males and the females was 16.37 ± 0.07 SE (range 14.40–17.23) and 5.88 ± 0.03 SE (range 5.33–6.16), respectively. Pairs were housed in individual breeding cages (60×50 cm and 50 cm high) with nesting material and an external, cage-mounted nestbox, in a room maintained at 20.5 ± 2 °C under full spectrum, artificial light (16:8 h light:dark cycle). The birds' diet prior to the hatching of their chicks comprised an ad libitum supply of mixed seeds (common millet, yellow millet and canary seed in an approximate ratio of 3:1:1; Johnson & Jeff, U.K.), oyster shell grit, cuttlefish and water. Once a week the birds also received Calcivet calcium supplement (Vetafarm, Wagga Wagga, NSW, Australia), a protein conditioning supplement (J.E. Haith, Cleethorpes, U.K.) and fresh vegetables. One day after the chicks hatched, all pairs continued receiving an ad libitum supply of mixed seeds (see below), oyster shell grit, cuttlefish and green vegetables but without any calcium or protein supplement.

Experimental Design and Nutritional Manipulation

Breeding pairs were monitored daily until clutches were completed, with the laying date of each egg and clutch size being recorded. In the wild, chicks tend to hatch fairly synchronously, but longer periods are also common (approximately 2–4 days; Zann & Bamford, 1996). Nests were therefore checked daily starting 3 days before the expected hatching date (13 days after clutch completion) to record the exact hatching date. At hatching, all chicks ($N = 126$) were weighed using an electronic balance (±0.01 g) and marked with a unique nest colour and individual colour combination by dyeing their toes with permanent marker pens. Each breeding pair was matched to another with a similar hatching date (±1 day) and clutch size; one of the two pairs was then assigned to follow a ‘High’ dietary micronutrient treatment and the other a ‘Low’ treatment (hereafter ‘H’ or ‘L’, respectively; details below). One day after the last chick in the nest hatched (mean hatching asynchrony = 2.3 days ± 0.2 SE), half of the chicks within each brood were cross-fostered between the two nests to account for family (genetic)