Animal Behaviour 86 (2013) 127–138

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Hand rearing affects emotional responses but not basic cognitive performance in European starlings☆

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ARTICLE INFO

Article history:
Received 27 September 2012
Initial acceptance 12 December 2012
Final acceptance 9 April 2013
Available online 10 June 2013
MS. number: 12-00741

Keywords:
animal welfare
behavioural disinhibition
early life stress
European starling
impulsivity
maternal deprivation
perseveration
Sturnus vulgaris

Hand rearing is a common procedure in behavioural research on birds. While likely to produce tamer experimental animals, there is a risk that it could induce pathological changes in brain and behaviour similar to those seen in mammals that have experienced maternal separation. We explored the effects of hand rearing on the cognitive and behavioural development of European starlings, *Sturnus vulgaris*, to assess the generality of results obtained from hand-reared animals. Two groups of age-matched birds were created from the same wild population: one hand-reared from 10 days posthatch and one brought into the laboratory as independent juveniles. These groups were compared on a battery of neuropsychological tasks designed to probe different aspects of cognitive function including learning, perseverative cognition, interval timing, neophobia and impulsivity. There was no evidence for cognitive impairment in the hand-reared birds. They did not have reduced learning speed, impairments in accuracy or precision of interval timing or pathological perseverative cognition compared to the wild-caught birds. Additionally, there was no evidence that birds that developed stereotypies in laboratory cages (predominantly the wild-caught birds) had any cognitive impairments, although this may be because no birds had severe, crystallized stereotypies. There was some evidence that hand-reared birds were less neophobic and less impulsive than wild-caught birds, suggesting that hand rearing might alter emotionally mediated decision making in a direction usually associated with reduced developmental stress in mammals. This study therefore supports the use of hand rearing as an experimental procedure in behavioural research on passerine birds.

Hand rearing experimental animals is a common procedure in behavioural research. Reasons for hand rearing include control of maternal effects (e.g. Madruga et al. 2006; Hulshof et al. 2011), manipulation of experience or diet during development (Thorpe 1958; Nowicki et al. 2002; Exnerova et al. 2006) and, via extensive human handling, habituation of animals to humans and laboratory procedures (e.g. Jones & Waddington 1992; Bilko & Altbacker 2000). The latter motivation for hand rearing is particularly prevalent in recent studies of nondomesticated passerine bird species that rely on well-habituated experimental subjects (e.g. Clayton & Dickinson 1998; Seed et al. 2007; Hoffmann et al. 2011; Schwab et al. 2012). In support of the practice, there is evidence that early handling reduces fear of humans and the stress reaction to restraint in parrots (Aengus & Millam 1999; Collette et al. 2000), and recent experimental studies have confirmed that hand-reared starlings are less fearful of humans and novel environments compared to birds caught from the wild as adults (Feenders & Bateson 2011; Feenders et al. 2011; Jayne et al. 2013). While hand rearing is undoubtedly a valuable experimental tool, there is reason to believe that it could have profound effects on the cognition and behaviour of adult animals, some of which are potentially indicative of pathological changes in the brain. Therefore, to assess the generality of scientific findings from hand-reared birds, it is important to understand how hand rearing affects behavioural development, and specifically whether the cognitive and behavioural phenotypes of adult hand-reared birds are abnormal. We addressed this question by conducting a neuropsychological investigation of the effects of hand rearing in the European starling, *Sturnus vulgaris*, the wild passerine most commonly used in laboratory research (Bateson & Feenders 2010).

Hand rearing usually involves removal of the young animals from their parents, and often also from the wild, shortly after birth or hatching. The young animals are subsequently housed in the laboratory, either in isolation or in peer groups, and are reared by human care-givers using replacement diets (e.g. Feenders & Bateson 2011). Hand rearing therefore alters several aspects of early life experience, including the quantity and quality of maternal care, the physical and social environment and the developmental diet.

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http://dx.doi.org/10.1016/j.anbehav.2013.05.002

In humans, poor parenting and adverse experiences during early development are associated with impairments in adult cognitive ability and an increased risk for developing psychiatric disorders such as anxiety, depression and psychoses (Kaufman et al. 2000; Heim & Nemeroff 2001; McEwen 2003). There have been numerous attempts to model these effects in nonhuman animals. In mammals, many studies have explored how manipulating specific aspects of maternal care shapes the adult physiological, neurobiological and behavioural phenotype. In rats, *Rattus norvegicus*, maternal separation produces long-lasting changes in emotional behaviour and impaired responses to stress (Anisman et al. 1998; Meaney 2001; Pryce & Feldon 2003; Macrì & Würbel 2006). Maternal separation also induces reduced neurogenesis in the adult hippocampus and consequential impairments in learning and memory (Korosi et al. 2012). In rhesus monkeys, *Macaca mulatta*, removal from the mother followed by peer rearing or rearing by mothers experiencing variable foraging conditions produces adults with more reactive stress physiology, increased anxiety, impulsivity and aggression and behavioural abnormalities such as motor stereotypies (e.g. Hennessy 1997; Cirulli et al. 2009; Nelson et al. 2009; Stevens et al. 2009; Prescott et al. 2012). Furthermore, adverse events during early development have been shown to increase the likelihood of developing abnormal behaviour, and specifically motor stereotypies, in a range of species. For example, animals removed from their mother at an earlier age, and animals born in captive as opposed to natural environments, show a higher incidence of stereotypic behaviour (Mason 2006; Latham & Mason 2008; Jones et al. 2011). Stereotypies are of concern because they are associated with executive dysfunction involving inappropriate repetition of responses (perseveration) and pathological changes in the underlying basal ganglia circuitry (Sandson & Albert 1984; Garner 2006; Langen et al. 2011).

In birds, there is some evidence that manipulations that involve elements of hand rearing affect the adult phenotypes similarly to the effects observed in mammals. For example, zebra finches, *Taeniopygia guttata*, fed corticosterone as chicks exhibit exaggerated and prolonged responses to acute stress as adults (Spencer et al. 2009), and in various passerine models reducing the quantity or quality of food fed to chicks impairs learning (Nowicki et al. 2002; Fisher et al. 2006). The picture in relation to stereotypies is less clear. In parrots, like mammals, early maternal separation leads to an increase in stereotypic behaviour (Schmid et al. 2006), and in blue jays, *Cyanocitta cristata*, hand-reared birds perform more spot-pecking stereotypies but less route tracing than wild-caught conspecifics (Keiper 1969). In contrast, hand-reared European starlings exhibit higher activity but less stereotypic route tracing and somersaulting compared with wild-caught conspecifics (Feenders & Bateson 2012). There is some evidence that motor stereotypies are associated with perseverative cognition indicative of basal ganglia pathology in both parrots and passerines (Garner et al. 2003a, b).

In summary, there is a body of evidence suggesting that manipulations that include one or more elements of the hand-rearing procedure result in adult animals with more reactive stress physiology, impaired cognitive performance, increased anxiety and impulsivity and a higher incidence of abnormal stereotypic behaviour. However, there have been few studies of the effects of hand rearing per se in birds. Our aim in this study was to establish the impact of hand rearing on cognitive performance in European starlings. We created two groups of age-matched birds from the same wild population: a hand-reared group brought into the laboratory 10 days posthatch and reared in peer groups by humans and a wild-caught group reared by their parents in the wild and subsequently caught and brought into the laboratory as independent juveniles. We used a battery of established neuropsychological tests to compare the two groups. In addition, we quantified the incidence of stereotypic behaviour in both groups of birds to establish whether behavioural stereotypies (in this case route tracing and stereotypic somersaulting) are associated with perseverative cognition or other cognitive impairments. Below we briefly describe the neuropsychological tests that we chose and outline our predictions.

Autoshaping

Autoshaping can be used to measure the speed of associative learning. During an autoshaping procedure, a novel conditioned stimulus (CS, in this case a key light) predicts unconditional delivery of a food reward (US; e.g. Bateson & Kacelnik 1995). The learning of an association between the CS and US is evidenced by appetitive responses (pecking) directed at the CS. We predicted that hand-reared birds would show impaired speed of learning due to early maternal separation or deficits in early nutrition.

Novel Stimulus

Response to a novel object or stimulus is a measure of neophobia and anxiety (e.g. Meehan & Mench 2002; Drent et al. 2003; Forkman et al. 2007; Feenders et al. 2011). In this study the task was implemented by changing the colour of the stimulus (key light) used for autoshaping. We predicted that if hand-reared birds are more anxious as a result of early stress, they would be more neophobic and slower to peck the novel colour.

Extinction

Extinction of a previously learnt association is a measure of cognitive perseveration. During extinction learning, the subject is first rewarded for responding to a CS, for example pecking an illuminated key; then, the reward is ceased and persistence in responding is measured. Subjects with cognitive perseveration tend to persist longer than normal subjects (Garner et al. 2003a). We predicted higher levels of perseveration in birds performing more stereotypic behaviour.

Two-choice Guessing Task

The two-choice guessing (or gambling) task is a standard test of cognitive perseveration. In this task, the subject is presented with a choice of two operanda and challenged to find the 'correct' (i.e. rewarded) option. In reality, the reward is randomly assigned to the two options meaning that there is no correct response. Normal subjects will explore both options, randomly alternating between them, whereas perseverative subjects persist in responding on one alternative (e.g. continue to press the left key) for extended periods (Frith & Done 1983; Garner 2006). As for extinction, we predicted higher levels of perseveration in those birds performing higher levels of stereotypic behaviour.

Sensitivity to Risk in Delay to Reward

Decision making when a subject is presented with a choice between a fixed delay to reward versus a risky delay (that is either shorter or longer with equal probability) provides a measure of impulsivity (Bateson & Kacelnik 1996, 1997; Kacelnik & Bateson 1997). When given a choice between a fixed delay to reward and a risky delay with the same arithmetic mean, animals universally prefer the risky option (Kacelnik & Bateson 1996). This preference occurs because animals discount delayed rewards hyperbolically with time; the risky option has a higher value due to the short delays to reward it contains. The fixed delay can be titrated until the subject is indifferent to obtain a quantitative estimate of how