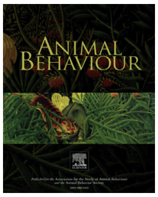
Animal Behaviour 111 (2016) 251–260

Contents lists available at ScienceDirect

Animal Behaviour

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



Associative learning is inversely related to reversal learning and varies with nestling corticosterone exposure

Sara E. Bebus*, Thomas W. Small, Blake C. Jones, Emily K. Elderbrock, Stephan J. Schoech

Department of Biological Sciences, University of Memphis, Memphis, TN, U.S.A.

ARTICLE INFO

Article history:
Received 6 May 2015
Initial acceptance 3 June 2015
Final acceptance 22 September 2015
Available online
MS. number: A15-00371R

Keywords:
behavioural flexibility
cognitive style
coping style
corticosterone
exploratory behaviour
glucocorticoid
learning
neophobia
personality

Intraspecies differences are fundamental to natural selection, yet individual differences in cognition in free-living populations have received little attention. Proactive and reactive coping styles describe individual differences in personality and related stress physiology; however, the coping style model can be extended to include predictions regarding measures of cognition. We compared two measures of personality (neophobia and exploratory behaviour) included in the coping style model to cognitive performance on colour-based associative and reversal learning tests in adult Florida scrub-jays, *Aphelocoma coerulescens*. Also, as exogenous glucocorticoid treatment can affect cognitive performance, we examined whether an individual's naturally occurring physiological phenotype, reflected by corticosterone measures obtained during development and at the time of the learning tests, covaried with learning performance. Performance on associative and reversal learning tests were inversely related. Scrub-jays with low levels of corticosterone as 11-day-old nestlings performed better on an associative learning test as adults, and there was a marginally nonsignificant trend for nestlings with high levels of corticosterone to perform better on a reversal learning test. There was also a marginally nonsignificant trend for neophobic birds to perform better on reversal learning tests. There were no relationships either between adult stress-induced corticosterone levels and learning, or between exploratory behaviour and learning. Our findings provide evidence that variation in sensitivity to environmental conditions, as reflected by an individual's coping style, underlie the specific strategy by which individuals perform cognitive tasks (i.e. cognitive style). Florida scrub-jays experience a trade-off in performance between types of learning that covary with early corticosterone exposure.

In recent years, individual differences within species have received considerable attention (Cockrem & Silverin, 2002; Cole, Cram, & Quinn, 2011; Dingemanse, Both, Drent, & Tinbergen, 2004). Personality, behavioural syndrome, coping style and temperament are among the terms commonly used to describe consistent individual differences in behaviour (Gosling, 2001; Koolhaas et al., 1999; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004). Additionally, recent studies have shown that individuals commonly display consistency in their performance on cognitive tests (e.g. problem solving in great tits, *Parus major*: Cole et al., 2011; association and discrimination tasks in black-capped chickadees, *Poecile atricapillus*: Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015). Shettleworth (1998, page 5) defined cognition as ‘the mechanisms by which animals acquire, process, store, and act on information from the environment’. As such, cognition cannot be directly measured, but psychologists have devised a number of tests to assess certain cognitive abilities, often by assessing learning ability. For example, the Morris water maze is a well-known laboratory test used to assess spatial learning in rodents (Vorhees & Williams, 2006). Modifications of protocols and testing conditions allow for insight into a subject's cognitive processes. However, in such tests only behaviour can be measured not cognition per se. In this way, our understanding of cognition is directly influenced by an individual's behaviour. It can be argued that cognitive performance is actually a combination of cognitive ability and cognitive style. Cognitive ability is an individual's capability to acquire, process, store and use information, whereas cognitive style is the specific strategy by which the individual acquires, processes, stores and uses the information (Carere & Locurto, 2011; Griffin, Guillette, & Healy, 2015; Sih & Del Giudice, 2012).

---

* Correspondence: S. E. Bebus, Department of Biological Sciences, University of Memphis, 201 Life Sciences, 3774 Walker Avenue, Memphis, TN 38152, U.S.A.
E-mail address: sarabebus@gmail.com (S. E. Bebus).

http://dx.doi.org/10.1016/j.anbehav.2015.10.027

Influences of Cognitive Style on Cognition

To illustrate, during a test in which an award can be obtained by pushing a red lever, a test subject may have the cognitive ability to discriminate different colours, make the connection between red and the reward, remember this information and then recall it when presented with a selection of levers. However, the subject's cognitive style (e.g. how the individual focuses its attention) may influence performance on a standardized laboratory test. One individual may continue to push the red lever to obtain a reward while ignoring other stimuli that may also allow him/her to obtain a reward (e.g. different coloured levers), whereas a second individual with the same cognitive abilities may continue to collect information from the environment (e.g. push other levers). Sih and Del Giudice (2012) describe this as a type of cognitive style that is based on a speed–accuracy trade-off. The first subject quickly makes a decision to obtain the reward from pushing the red lever (‘speed’), whereas the second individual may be slower at mastering the test, but makes a more complete and ‘accurate’ assessment of the environment. In an associative task, as described above, the first subject will perform better. However, in a reversal learning test, a measure of behavioural flexibility, the second subject will perform better due to more thorough sampling of the environment by trying other levers.

Sih and Del Giudice (2012) proposed that the speed–accuracy trade-off cognitive style may closely align with individual differences in behaviour, such as those described by proactive and reactive coping styles. Proactive individuals are less sensitive to external stimuli and more ‘intrinsically driven’, whereas reactive individuals are more sensitive to external stimuli (i.e. they are more likely to assess and react to their environment) (Koolhaas et al., 1999). Consequently, when compared to reactive types, proactive individuals are quicker to approach a novel object, faster to explore a new place, more aggressive towards conspecifics, less flexible in behaviour and quicker to form routines (Cockrem, 2007; Koolhaas et al., 1999). Additionally, in examinations of physiological measures that covary across the proactive–reactive spectrum, proactive individuals generally have lower hypothalamic–pituitary–adrenal (HPA) axis activity, as exemplified by a reduced reactivity in response to stressors (Cockrem, 2007; Koolhaas et al., 1999).

Intrinsically driven proactive individuals and highly sensitive reactive individuals respond differently to environmental stimuli, which may drive differences in cognitive style and, subsequently, performance on cognitive tests (Sih & Del Giudice, 2012). Evidence indicates that individuals with proactive traits (e.g. bold, explorative, aggressive) learn associations better than individuals with reactive traits (guppy, *Poecilia reticulata*: Dugatkin & Alfieri, 2003; cavy, *Cavia aperea*: Guenther, Brust, Dersen, & Trillmich, 2014). Conversely, individuals with reactive traits (e.g. timid, less explorative, nonaggressive) perform reversal learning tasks better than individuals with proactive traits (black-capped chickadee: Guillette, Reddon, Hoeschele, & Sturdy, 2011; cavy: Guenther et al., 2014). However, the opposite relationship between coping style and learning performance has also been found (great tit: Amy, van Oers, & Naguib, 2012; Titulaer, van Oers, & Naguib, 2012; black-capped chickadee: Guillette et al., 2015).

Influences of Stress Physiology on Cognition

In addition to cognitive style, stress and glucocorticoids are known to influence cognitive performance, although the nature of the relationship is not always easy to predict (McEwen & Sapolsky, 1995). Corticosterone is the main glucocorticoid released by HPA axis activation in avian, herptile and rodent species, whereas cortisol is found in fish and most other mammals (hereafter, both to be termed ‘CORT’). Elevated CORT affects learning performance across taxa, although the degree to which learning is affected and whether exposure results in benefits or decrements depends on the extent and timing of CORT exposure, as well as the type of learning or cognitive measure in question (de Kloet, Oitzl, & Joëls, 1999; Lupien & McEwen, 1997; Pravosudov, Mendoza, & Clayton, 2003; Roozendaal, 2002). High CORT levels during development may be particularly significant and result in long-term effects on learning (reviewed in Schoech, Rensel, & Heiss, 2011). For instance, chronically elevated CORT levels early in development impair performance on associative and spatial learning tasks later in life (black-legged kittiwakes, *Rissa tridactyla*: Kitaysky, Kitaiskaia, Piatt, & Wingfield, 2003). However, reversal learning may be facilitated by exposure to stress (Japanese quail, *Coturnix japonica*: Calandreau et al., 2011; Norway rat, *Rattus norvegicus*: Thai, Zhang, & Howland, 2013). Similarly, rainbow trout, *Oncorhynchus mykiss*, selected for a high CORT response display greater flexibility in utilizing a new food patch than fish bred for a low CORT response (Ruiz-Gomez, Huntingford, Øverli, Thörnqvist, & Höglund, 2011). To the best of our knowledge, no one has reported a direct relationship between learning and naturally occurring individual differences in CORT response (i.e. in wild-type individuals that were not artificially selected for a trait).

Present Study

We investigated two factors that may have relationships with cognition: personality and CORT. We tested associative and reversal learning in Florida scrub-jays, *Aphelocoma coerulescens*, as measures of cognition and assessed whether learning performance varied with two personality traits (neophobia and exploratory behaviour). We also compared learning performance with stress physiology, assessed in nestlings and again just prior to learning tests as birds approached 1 year of age. While the coping style model includes predictions regarding personality and stress physiology, we did not examine those relationships here, as they were further investigated in a separate study of our population (Bebus, Jones, Elderbrock, Small, & Schoech, 2015).

Based upon descriptions of proactive–reactive coping styles, we predicted that less neophobic and faster exploring individuals would perform better in associative learning tests but worse in reversal learning tests. In addition, based on links between cognition and CORT, we predicted that individuals with low CORT levels during early development would perform better in associative learning tests but worse in reversal learning tests as adults, and that individuals with low stress-induced CORT responses would perform better in associative learning tests but worse in reversal learning tests.

METHODS

Study System

Florida scrub-jays are cooperative breeders that hold year-round territories (Woolfenden & Fitzpatrick, 1984). The birds live in family groups with a male and a female breeder and up to seven nonbreeding ‘helpers’ (Woolfenden & Fitzpatrick, 1984). Helpers aid in territory defence against conspecifics, in antipredator actions (detection, warning, mobbing) and in provisioning nestlings and fledglings. They are generally older offspring of the breeding pair that have stayed on their parents' territory, even though they are reproductively capable by 1 year of age (Schoech, Mumme, & Wingfield, 1996). Our study population resides in the southern portion of Archbold Biological Station, Highlands County, Florida (27°19′N, 81°2l′W, elevation 38–68 m). This population has been