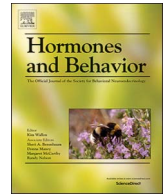




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Social information changes stress hormone receptor expression in the songbird brain



Jamie M. Cornelius^{a,*}, Gillian Perreau^b, Valerie R. Bishop^b, Jesse S. Krause^c, Rachael Smith^c, Thomas P. Hahn^c, Simone L. Meddle^b

^a Department of Biology, Eastern Michigan University, Ypsilanti, MI, USA

^b The Roslin Institute, The Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Easter Bush, UK

^c Animal Behavior Graduate Group, Department of Neurobiology, Physiology and Behavior, University of California Davis, Davis, CA, USA

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ABSTRACT

Social information is used by many vertebrate taxa to inform decision-making, including resource-mediated movements, yet the mechanisms whereby social information is integrated physiologically to affect such decisions remain unknown. Social information is known to influence the physiological response to food reduction in captive songbirds. Red crossbills (*Loxia curvirostra*) that were food reduced for several days showed significant elevations in circulating corticosterone (a “stress” hormone often responsive to food limitation) only if their neighbors were similarly food restricted. Physiological responses to glucocorticoid hormones are enacted through two receptors that may be expressed differentially in target tissues. Therefore, we investigated the influence of social information on the expression of the mineralocorticoid receptor (MR) and glucocorticoid receptor (GR) mRNA in captive red crossbill brains. Although the role of MR and GR in the response to social information may be highly complex, we specifically predicted social information from food-restricted individuals would reduce MR and GR expression in two brain regions known to regulate hypothalamic-pituitary-adrenal (HPA) activity - given that reduced receptor expression may lessen the efficacy of negative feedback and release inhibitory tone on the HPA. Our results support these predictions - offering one potential mechanism whereby social cues could increase or sustain HPA-activity during stress. The data further suggest different mechanisms by which metabolic stress versus social information influence HPA activity and behavioral outcomes.

1. Introduction

Individuals must make behavioral and physiological adjustments as environmental conditions change if they are to survive and reproduce successfully. Animals use a wide variety of information sources to assess environmental conditions – the most obvious being through direct experience, such as assessment of food availability as an individual animal attempts to assimilate energy from the environment (i.e., optimal foraging) (Charnov, 1976; Pyke et al., 1977). However, animals also use indirect assessments to inform decision-making. Social information, or information obtained through observation of and/or communication with other individuals is an important indirect information source used by animals to assess conditions and make decisions (Valone, 1989; Valone and Templeton, 2002). For example, social information can change the duration individuals forage on a patch if other individuals are present to provide information (Smith et al., 1999; Templeton and Giraldeau, 1995) and can influence large-scale, facultative migratory

responses to resources as well (Chan, 1994). The physiological mechanisms for how such social information might influence behavioral outcomes, however, remain poorly understood - though some evidence suggests that the endocrine system may be involved (Cornelius et al., 2010).

The endocrine system acts as a broad-scale messenger between neural processing centers and the body and, thus, provides a tool for measuring physiological responses to different environmental and endogenous conditions. Corticosterone, for example, is a steroid hormone implicated in metabolic processes and survival behaviors during food shortage (Astheimer et al., 1992; Cornelius et al., 2010; Fokidis et al., 2012, 2011; Kitaysky et al., 1999, 2010; Krause et al., 2017; Lynn et al., 2003, 2010). The amount of corticosterone that is released in response to a physical or metabolic stressor is regulated by the hypothalamic-pituitary-adrenal (HPA) axis, which is itself under neural control from multiple processing centers of the brain (de Kloet, 2014; Joels et al., 2008; Sapolsky et al., 2000). The elevation in corticosterone levels

* Corresponding author at: Department of Biology, Eastern Michigan University, Ypsilanti, MI 48198, USA.

E-mail addresses: jcornel7@emich.edu (J.M. Cornelius), valerie.bishop@rosin.ed.ac.uk (V.R. Bishop), jskrause@ucdavis.edu (J.S. Krause), raesmith@ucdavis.edu (R. Smith), tpahn@ucdavis.edu (T.P. Hahn), simone.meddle@rosin.ed.ac.uk (S.L. Meddle).

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during food restriction is likely due to detection of metabolic imbalance (e.g., plasma fatty acids in birds) and subsequent stimulation of the HPA via adrenergic or cholinergic inputs (Calogero, 1995; Landys et al., 2004a, 2004b; Tsagarakis et al., 1988). Plasma corticosterone then coordinates broad scale cellular responses that influence metabolism and behavior. For example, increased plasma corticosterone has been linked to fatty acid metabolism in birds (Landys et al., 2004a, 2004b) and has been correlated with enhanced activity in captive birds when food is absent or unpredictable (Astheimer et al., 1992; Cornelius et al., 2010; Krause et al., 2017), altitudinal migration in wild birds to escape bad weather when food becomes unavailable (e.g., covered in snow) (Breuner and Hahn, 2003) or when conditions are extreme (Krause et al., 2016). For corticosterone to achieve these effects it must bind with receptors at the target tissues.

Hormone receptors detect the presence of the hormone message and instruct the receiving cell to respond in a target-specific manner. Increasing the system's complexity, these receptors are expressed in brain regions influencing HPA activity such that the binding of corticosterone can inhibit HPA-activity (i.e., negative feedback) regardless of the continued presence of a stressor or stimulus (de Kloet, 2014; Joels et al., 2008; Sapolsky et al., 2000). Ultimately the amount of corticosterone circulating in the blood stream is controlled by the neural networks that stimulate corticosterone release and those that regulate negative feedback – both of which can be influenced by the two corticosterone receptors: the high affinity mineralocorticoid receptor (MR) and the low affinity glucocorticoid receptor (GR) (Breuner and Orchinik, 2009; Lattin et al., 2012).

MR is predominately expressed in the hippocampus in birds and mammals (Baugh et al., 2017; de Kloet, 2014; Dickens et al., 2009; Hodgson et al., 2007; Joels et al., 2008; J. Krause et al., 2015; Senft et al., 2016; Zimmer and Spencer, 2014). In the rodent brain MR are activated by basal concentrations of corticosterone and are thought to regulate basal levels of corticosterone with an overall inhibitory tone (Reddy et al., 2009; Zilliacus et al., 1995). Studies in rodents further indicate that MR can be targeted for insertion in the cellular membrane and this form is thought to act similarly to the low affinity GR receptor to help facilitate the stress response by promoting rapid behavioral responses to elevated plasma corticosterone (Joels et al., 2008). The low-affinity GR is a nuclear receptor with transcriptional activity that is predominately expressed in the paraventricular nucleus, amygdala, cerebral cortex and the hippocampus in rodents (de Kloet, 2014; Joels et al., 2008; Sapolsky et al., 2000). Similar patterns of GR exist in birds except for expression in the hippocampus, which seems more variable across species (Baugh et al., 2017; Hodgson et al., 2007; J. Krause et al., 2015; Senft et al., 2016; Zimmer and Spencer, 2014). GR becomes activated in mammals when corticosterone levels rise during the circadian peak, during a stress response or when metabolic demands rise (Reddy et al., 2009; Reul and de Kloet, 1985; Zilliacus et al., 1995). Changes in MR and GR expression in the avian brain have been correlated with seasonal changes in hormone profiles, selection for high stress responsiveness, and under chronic stress (Dickens et al., 2009; Hodgson et al., 2007; J. Krause et al., 2015). More importantly, food restriction in rodents has been shown to reduce receptor expression in the brain leading to reduced negative feedback and elevated levels of corticosterone (Lee et al., 2000). The interaction between circulating levels of corticosterone, MR and GR expression in the brain and social information to regulate physiology and decision-making processes, however, remain completely unexplored in any taxa.

Cornelius et al. (2010) previously demonstrated that social information can alter corticosterone secretion in a bird that is highly adapted to coping with unpredictable food resources. Red crossbills (*Loxia curvirostra*) that were provided with 75% of their average daily food intake had larger increases in plasma corticosterone if their neighbors were similarly food reduced, compared to those whose neighbors were given food ad libitum. Here we investigate a potential role for corticosteroid receptors in the response to social information

and food cues. We call special attention to brain regions that regulate the sensitivity of the HPA axis: the hippocampus and paraventricular nucleus (PVN). We predict that social information from food-deprived individuals reduces inhibition of the HPA-axis, thereby allowing the system to respond more aggressively to food stress. Further, if alterations in these receptor populations are involved in processing of the food and social cues in this context, we predict that social information will enable enhanced HPA-activity during food limitation by reducing expression of MR and GR in these regions.

2. Methods

2.1. Birds and experimental outline

This experiment replicates the methods described in Cornelius et al. (2010), with a few exceptions as described below. Red crossbills occur as a suite of eco-types that differ in vocal call structure and body/bill size. Type 3 is the smallest eco-type specializing on small, soft-coned conifers and is known to exhibit mass migratory movements related to food availability. Briefly, 32 adult male type 3 red crossbills were captured on the Olympic Peninsula in Washington State (47° 27' 25.92" N, – 123° 43' 54.48" W), USA, in July 2008 and transported to facilities at University of California-Davis. Males were used exclusively to avoid potentially confounding effects of mixed sex pairs and to preserve sample sizes within treatment groups. Based on prior results (Cornelius et al., 2010) we do not predict males to have a qualitatively distinct corticosterone response relative to females in this experimental design, though females would need to be tested to determine if there are sex-specific differences in receptor mRNA expression. The experiment was performed in February and March 2008 and birds were housed on naturally changing photoperiod. This is a time of year that natural declines in conifer seed supplies may require these birds to move (Cornelius and Hahn, 2012; Hahn, 1998). All birds were kept in individual cages for two months prior to any manipulations on an ad libitum diet of Roudybush pellet food and a daily allotment of 2 pine nuts per bird. Morphological and hormone data were collected from each individual in a repeated measures design with pre-treatment (Day 0) and treatment (Day 14) sampling points (Fig. 1). All experiments were approved by University of California Davis Institutional Animal Care and Use Committee under protocol 05-12095.

2.2. Experimental treatments

Individuals were housed on shelves in acoustic isolation chambers (IAC 250 “Mini” Sound Shelters, 61 cm wide by 86 cm deep by 168 cm high inside dimensions; Industrial Acoustics Company, Bronx, New York) with visual and acoustic access to a single neighboring bird. Four social and food treatment groups were created by randomly assigning individuals to the following housing configurations: ad libitum subject with an ad libitum neighbor A(a), ad libitum subject with a food reduced neighbor A(f), food reduced subject with an ad libitum neighbor F(a), and food reduced subject with a food reduced neighbor F(f).

“Food Reduced” individuals had their food restricted to 75% of their average daily intake of food pellets and they received no pine nuts during the treatment period (Days 10–14; Fig. 1). Food reduction



Fig. 1. Experimental timeline. Daily food intake (dashed line) was measured for one week prior to the start of the experiment. Body condition and CORT (stars) were collected on days 0 and 14. Activity (camera beam) was filmed daily from days 8 to 14. Food was reduced (hashed box) in the food treatment group beginning on day 10, which marks the change from the pre-treatment to treatment phase of the experiment. Brains were collected on day 14 (open arrow).

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