

A potential cardiovascular mechanism for the behavioral effects of central and peripheral arginine vasotocin

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Abstract

Few studies have attempted to separate the behavior modulating actions of central and peripheral arginine vasotocin/arginine vasopressin (AVT/AVP) from their roles in the endocrine and cardiovascular stress response. This series of experiments explored the relative contributions of AVT's central and peripheral mechanisms on altering behavior while simultaneously investigating AVT's effects on the behavioral, cardiovascular, and corticosteroid responses to acute stressors in European starlings (*Sturnus vulgaris*). Results illustrated peripheral AVT's ability to decrease feeding, drinking, preening, and overall activity. Effects on feeding, drinking, and preening were similar after AVT injection into the lateral ventricles, but the central effects were not blocked by dPTyr(Me)AVP, a selective AVT receptor blocker. This suggests that AVT's behavioral effects may not depend solely on a receptor mediated central mechanism. However, both central and peripheral AVT attenuated heart rate independent of increased plasma corticosterone. These data suggest that AVT's behavioral effects may be modulated by a corticosterone-independent cardiovascular mechanism.
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1. Introduction

The non-peptide arginine vasotocin (AVT) and its mammalian homologue arginine vasopressin (AVP) have been found to have diverse behavioral, cardiovascular, and endocrine effects in many species of vertebrates (Ames et al., 1971; Baerwolff and Bie, 1988; Goecke and Goldstein, 1997; Gray et al., 1990; Robinzon et al., 1993; Stallone and Braun, 1985). Physiologically, they are vital to maintaining fluid homeostasis and regulating heart rate (HR) and blood pressure (Robinzon et al., 1993; Wilson and West, 1986). Less is known about AVT's effects in birds, and identifying the regulatory mechanisms of AVT on cardiovascular effects has been somewhat inconclusive. Exogenous AVT has

been shown to increase (John and George, 1992), decrease (Robinzon et al., 1993) or have no effect (Hassinen et al., 1999) on HR in birds. There is a clear need for further study on AVT's role in cardiovascular regulation.

AVT/AVP have major roles in the stress response, where they both directly stimulate adrenocorticotropin (ACTH) release and have a synergistic effect with corticotropin releasing factor (CRF) on ACTH release at the anterior pituitary (Aguilera et al., 1996; Gillies et al., 1982; Wotjak et al., 1996). ACTH then stimulates the release of corticosterone (CORT), an important stress hormone in vertebrates. During chronic stress, AVP's resistance to corticosterone negative feedback provides a possible mechanism for the long-term maintenance of elevated CORT concentrations (Bartanusz et al., 1993; de Goeij et al., 1992; Scaccianoce et al., 1991).

In addition to these roles in cardiovascular and endocrine physiology, AVT/AVP also elicit a variety of behavioral effects, including the modulation of

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vocalization (Chu et al., 1998; de Kloet et al., 1993; Goodson, 1998; Maney et al., 1997), sexual behavior (Castagna et al., 1998), learning (Davis and Pico, 1984; Engelmann and Landgraf, 1994; Landgraf et al., 1995), aggression (Bester-Meredith et al., 1999; Delville et al., 1996; Ferris and Delville, 1994; Goodson, 1998), and general activity level (Boyd, 1991; Buwalda et al., 1993; Delanoy et al., 1978). The effects of AVT/AVP on behavior vary depending on species, gender, social organization, season, and nutritional state (Astheimer et al., 1992; Boyd, 1991; Chu et al., 1998). In rodents, AVP has been shown to stimulate grooming, foraging, and aggressive behaviors (Bester-Meredith et al., 1999; Delanoy et al., 1978). In bullfrogs (*Rana catesbeiana*), the effect of AVT on locomotion is dependent on the developmental stage and sex of the individual (Boyd, 1991). AVT can also increase or decrease mate calling in cricket frogs (*Acris crepitans*) depending on the season (Chu et al., 1998; Marler et al., 1999). In birds, patterns of AVT-modulated aggression have been hypothesized to be dependent on the social organization of the species being studied (Goodson, 1998), and AVT injections have been shown to decrease sexual activity in male Japanese quail (*Coturnix japonica*) (Castagna et al., 1998). While there is a wealth of data on AVT and AVP's physiologic roles, the connections between their physiological and behavioral functions during stressful events are poorly understood, especially in avian species. In addition, it is difficult to separate the direct behavioral effects of AVT with its indirect effects due to increased CORT release, as both hormones exert effects in similar time frames.

Numerous studies have found significant effects of CORT on numerous behaviors in birds, such as modulation of activity (Astheimer et al., 1992; Breuner et al., 1998), parental behavior (Silverin, 1986), and territorial behaviors (Romero et al., 1998; Wingfield and Silverin, 1986). These behavioral effects are similar to those elicited by AVT/AVP. It is not always clear, therefore, whether the behavioral effects of exogenous AVT/AVP (especially when injected peripherally) result from direct actions in the brain or indirectly through enhanced ACTH secretion leading to elevated CORT levels.

Unfortunately, few studies have attempted to separate the behavior-modifying actions of central and peripheral AVT from its roles in the endocrine and cardiovascular stress responses. In this series of experiments, we attempted to determine the relative contributions of central and peripheral mechanisms to AVT's effects on behavior while investigating AVT's effects on the behavioral, cardiovascular, and CORT responses to acute stressors in European starlings (*Sturnus vulgaris*). By subcutaneously and centrally injecting AVT and observing behavior, as well as measuring plasma CORT levels and HR, we examined both the direct and indirect effects of AVT administration.

2. Methods

2.1. Birds

Wild starlings (*S. vulgaris*) were captured during the fall in eastern Massachusetts while in non-breeding condition. The starlings were held in an indoor flight aviary on an 11L:13D light cycle until being moved into 45 × 37 × 33 cm individual cages at least 2 days prior to initiating an experiment. Subjects were given food and water ad libitum. All experimental protocols were performed according to AALAC guidelines and approved by the Tufts University Institutional Animal Care and Use Committee.

Behavioral experiments were performed in a room equipped with a two-way mirror. A digital video camera was set up outside the room for observation through the mirror, thus allowing behavioral monitoring without disturbing the birds. All starlings remained in visual and auditory contact with each other throughout the experiment.

2.2. Experiment 1: effects of subcutaneous AVT on behavior in starlings

Three doses of AVT (0.5, 4.0, and 8.0 µg) were dissolved in 10 µl lactated Ringers solution (LRS). Eight starlings were allowed at least 2 days to adjust to the individual cages after being transferred from the flight aviary and then injected subcutaneously in the back of the neck between the hours of 10:00 am and 4:30 pm. An earlier study indicated that at least the CORT response to stress remains constant throughout this time period (Romero et al., 2000). Control injections consisted of 10 µl LRS. Each bird received the three AVT doses and two control doses, two injections per day for two and a half days. Preliminary data (not presented) indicated that two injections a day with at least 5 h between injections did not significantly affect the results (no significant effects on behavioral or physiological variables). The first and last injections were controls, and the treatment injections were randomized. This design allowed us to assess the potential effects of the injection sequence.

Each bird was injected and video recorded for 55 min beginning 5 min after the injection. This delay controlled for differential behavioral reactions to the handling and injection. Preliminary observations indicated that it took approximately 5 min for the starlings to resume typical behavior after the injection procedure.

We scored four behavioral variables, consisting of feeding, drinking, preening, and hopping. One feeding count was defined as a single episode of feeding, irrespective of the length of time spent at the feed dish, and thus measured the number of trips to the feed dish where the subject consumed food. Drinking was defined in a similar manner. A preening bout consisted of continuous

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