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Endogenous vasotocin exerts context-dependent behavioral effects in a semi-naturalistic colony environment

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ABSTRACT

Arginine vasotocin (VT), and its mammalian homologue arginine vasopressin (VP), are neuropeptides involved in the regulation of social behaviors and stress responsiveness. Previous research has demonstrated opposing effects of VT/VP on aggression in different species. However, these divergent effects were obtained in different social contexts, leading to the hypothesis that different populations of VT/VP neurons regulate behaviors in a context-dependent manner. We here use VP antagonists to block endogenous VT function in male zebra finches (*Taeniopygia guttata*) within a semi-natural, mixed-sex colony setting. We examine the role of VT in the regulation of aggression and courtship, and in pair bond formation and maintenance, over the course of three days. Although our results confirm previous findings, in that antagonist treatment reduces aggressive mate competition during an initial behavioral session during which males encounter novel females, we find that the treatment effects are completely reversed within hours of colony establishment, and the antagonist treatment instead facilitates aggression in later sessions. This reversal occurs as aggression shifts from mate competition to nest defense, but is not causally associated with pairing status per se. Instead, we hypothesize that these divergent effects reflect context-specific activation of hypothalamic and amygdalar VT neurons that exert opposing influences on aggression. Across contexts, effects were highly specific to aggression and the antagonist treatment clearly failed to alter latency to pair bond formation, pair bond stability, and courtship. However, VT may still potentially influence these behaviors via promiscuous oxytocin-like receptors, which are widely distributed in the zebra finch brain.

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Introduction

Arginine vasotocin (VT) and its mammalian homologue arginine vasopressin (VP) are neuropeptides known to modulate social behaviors and stress responsiveness in virtually all vertebrate groups (Caldwell et al., 2008; De Vries and Boyle, 1998; Goodson, 2008; Goodson and Bass, 2001). However, the relationships between VT/VP and social behaviors are often not consistent across species, contexts, and behavioral phenotypes (Caldwell et al., 2008; Goodson, 2008; Greenwood et al., 2008; Semsar and Godwin, 2004). For instance, VP release into the lateral septum (LS) decreases during resident–intruder tests in aggressive, low-anxiety rats, but increases in less aggressive, high-anxiety rats (Beiderbeck et al., 2007). In songbirds, VT infusions into the LS or lateral ventricle facilitate aggression in male zebra finches (*Taeniopygia guttata*) during mate competition (Goodson and Adkins-Regan, 1999; Goodson et al., 2004), but inhibit territorial (resident–intruder) aggression in field sparrows (*Spizella pusilla*) (Goodson, 1998a) and violet-eared waxbills (*Uraeginthus granatina*) (Goodson, 1998b).

Given these potential context-dependent effects, the precise involvement of VT/VP in the regulation of many social behaviors remains unclear. This is particularly the case for behaviors that are expressed in the context of large social groups, since few laboratory species are both highly gregarious and readily observed in a colony environment. Zebra finches are a notably tractable, colonial species, but to date, VT effects on zebra finch behavior have been examined only in the context of short-duration tests of courtship and aggression that involve only two or three animals. We know little about the regulation of behavior in many other social contexts that are unique to group-living animals. For instance, information is lacking about the involvement of VT/VP in long-term regulation of social behaviors within mixed-sex social groups in semi-natural settings. Another important question is whether endogenous VT is necessary for naturally occurring pair bond formation in birds (see Goodson et al., 2004), as is known for endogenous VP in microtine voles (Lim and Young, 2006; Wang and Aragona, 2004). Indeed, given that pair bonding is an evolutionarily labile behavior, it is particularly important to ask whether vole-like peptide functions have also evolved in support of monogamous bonding in non-microtine taxa. We attempt to address these questions in the present study.

To address these questions, it is important to keep in mind that VT/VP neurons project broadly throughout the basal forebrain and

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brainstem (Goodson and Bass, 2001), and also to the anterior pituitary, where VT/VP release synergizes with corticotropin-releasing factor to regulate secretion of adrenocorticotropic hormone and thereby glucocorticoids (Aguilera and Rabadan-Diehl, 2000; Baeyens and Cornett, 2006; Lightman, 2008). Furthermore, when VT/VP is released centrally, it can include both axonal and dendritic release (Bergquist and Ludwig, 2008; Landgraf and Neumann, 2004). There are thus multiple avenues by which VT/VP may be involved in the regulation of social behaviors, including via feedback from the periphery.

Context-dependent effects of VT are likely associated with different patterns of neuromodulation arising from different populations of VT neurons (Goodson, 2008). Of particular interest in relation to social behavior are the VT/VP neurons in the medial bed nucleus of the strial terminalis (BSTm), a component of the medial extended amygdala (Goodson, 2008). In songbirds, these neurons exhibit increased Fos expression, a proxy marker of neuronal activity, in the presence of positive social stimuli, and depressed activity in relation to aversive social stimuli (Goodson and Wang, 2006). VT/VP projections from the BSTm target multiple areas of the basal forebrain, including the LS, where VT/VP release regulates social recognition, agonistic communication, anxiety, and stress responses (Caldwell et al., 2008; Goodson, 2008). Whereas the BSTm neurons appear to selectively process stimuli related to affiliation, VT neurons in the paraventricular nucleus of the hypothalamus (PVN) are strongly responsive to emotional stressors (Goodson and Evans, 2004; Wotjak et al., 1996), and these neurons also project centrally and likely to the LS (Goodson and Kabelik, in press).

The presence of multiple VT/VP populations that appear to regulate various aspects of social interactions leads us to ask the question of how endogenous VT/VP regulates initial and long-term social interactions and pair bond formation. Does a shift occur from the dominance of one neuronal population to another when mate competition decreases and nest defense increases? Given the diversity of VT/VP cell groups and their unique response profiles, it seems impossible to obtain a full and accurate view of VT/VP functions if we restrict our analyses to highly controlled and somewhat contrived behavioral tests (Ophir et al., 2008a,b). However, no experiments to date have examined the behavioral effects of chronic VT/VP manipulations in a semi-natural (e.g., colony) context. Therefore, we here examine aggression, courtship, and pair bond formation in a colony context over the course of three days in male zebra finches treated with either VP antagonists (VPant) or saline control. We show that while VPant manipulations primarily influence aggression, they do so in a highly dynamic manner.

Methods

Subjects

A total of 64 male and 80 female adult zebra finches were used for behavioral observations during prescreening and experimental sessions. Of these, cannulation surgeries were performed on 39 experimental male zebra finch subjects. All birds had *ad libitum* access to food and vitamin-enriched water, and were maintained on a 14:10 light cycle. All procedures were conducted in a humane manner and in compliance with federal and institutional guidelines.

Prescreening

Not all zebra finches are successful at pairing in a colony environment and we therefore prescreened subjects for pairing ability in order to obtain a subject population for cannulation surgeries. Zebra finches were transferred from same-sex housing into colony cages in groups of four males and five females each. Colony cages were 1.2 m long (120 cm W × 40 cm H × 36 cm deep) and were supplied with plastic nest cups in each of the four corners of the cage. Food, water dishes, and burlap nesting material were placed centrally on the cage floor. Observations were conducted twice daily for three days to assess pairing status (Fig. 1). Zebra finch pair bonds are easily detected based on selective affiliation, inclusive of "clumping" (perching for periods in physical contact), following, allopreening, and co-occupation of a nest cup. Male and female groups were then separated and housed without visual access to opposite-sex individuals for at least 10 days. This duration is completely sufficient to allow for the formation of new pair bonds, since wild zebra finches typically replace mates within several days following experimental mate removal (Zann, 1996).

Surgeries

Surgeries were conducted on 39 males (from 14 colony groups) that successfully pair-bonded during prescreens. Cannulation surgeries were conducted stereotaxically using isoflurane vapor anesthesia at 2–5% of a compressed air flow. Coordinates were referenced to the vascular convergence at the rostral tip of the cerebellum. A 26-gauge single guide cannula for small animals (Plastics One, Roanoke, VA) with a 4.6 mm extension beyond the pedestal was inserted 3.1 mm rostral, 1.7 mm right lateral, and 2.6 mm deep, at a 21° angle toward medial. These coordinates target the caudal portion of the lateral ventricle. The guide cannula was adhered to the skull using a combination of Nexaband S/C cyanoacrylate glue (Abbott Laboratories, North Chicago, IL) and Stoelting dental cement (Stoelting, Wood Dale, IL). A sterile cannula dummy with a wire obturator (Plastics One) was inserted into the guide cannula at all times other than during infusion procedures. Injection cannulae, but not cannula dummies, projected 1 mm beyond the length of the guide cannula. Subjects were allowed at least five days of recovery before subsequent testing.

Following all experimental procedures, birds were infused with 1 μl of ink, euthanized by isoflurane overdose, perfused with 0.1 M phosphate buffered saline followed by 4% paraformaldehyde, and their brains were sectioned on a cryostat at 40 μm. Six males showed no ink in the lateral ventricle and were therefore excluded from analyses. Of the 33 remaining males, 16 were in the VPant group and 17 were in the saline control group.

Antagonists and infusions

Infusions were either of vehicle (0.9% NaCl) or VPant. Treatments within colonies were counterbalanced as much as possible. Of the 14 colonies (mean cannulated subjects per colony = 2.36) that contained at least one cannulated male, 2 colonies had no VPant males (these colonies contained a total of 1 and 2 cannulated subjects), 8 had one VPant male, and 4 had two VPant males. Likewise, 2 colonies had no saline males (these colonies contained a total of 1 and 2 cannulated subjects), 7 had one saline male, and 5 had two saline males.

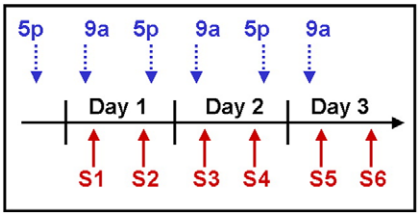

Fig. 1. A diagram depicting the timeline (horizontal arrow) of our experimental procedures. The dotted vertical arrows represent infusions of VPant or saline, either prior to daily observation sessions (approximately 9 am; 9a), or following daily observation sessions (approximately 5 pm; 5p). The vertical solid arrows represent observation sessions (S1–6). Two 10-min observations of each subject were conducted each day, one in the morning, and one in the afternoon, for a period of three days.

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