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Sex-specific activity and function of hypothalamic nonapeptide neurons during nest-building in zebra finches

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ABSTRACT

Vertebrate species from fish to humans engage in a complex set of preparatory behaviors referred to as nesting; yet despite its phylogenetic ubiquity, the physiological and neural mechanisms that underlie nesting are not well known. We here test the hypothesis that nesting behavior is influenced by the vasopressin–oxytocin (VP–OT) peptides, based upon the roles they play in parental behavior in mammals. We quantified nesting behavior in male and female zebra finches following both peripheral and central administrations of OT and V_{1a} receptor (OTR and V1aR, respectively) antagonists. Peripheral injections of the OTR antagonist profoundly reduce nesting behavior in females, but not males, whereas comparable injections of V1aR antagonist produce relatively modest effects in both sexes. However, central antagonist infusions produce no effects on nesting, and OTR antagonist injections into the breast produce significantly weaker effects than those into the inguinal area, suggesting that antagonist effects are mediated peripherally, likely via the oviduct. Finally, immunocytochemistry was used to quantify nesting-induced Fos activation of nonapeptide neurons in the paraventricular and supraoptic nuclei of the hypothalamus and the medial bed nucleus of the stria terminalis. Nest-building induced Fos expression within paraventricular VP neurons of females but not males. Because the avian forms of OT (Ile^8-OT; mesotocin) and VP (Ile^3-VP; vasotocin) exhibit high affinity for the avian OTR, and because both peptide forms modulate uterine contractility, we hypothesize that nesting-related stimuli induce peptide release from paraventricular vasotocin neurons, which then promote female nesting via peripheral feedback from OTR binding in the oviduct uterus.
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Introduction

Despite the importance of nesting for offspring survival in many species, remarkably little is known about the relevant physiological and neural mechanisms that underlie nesting behaviors. Studies of the physiological mechanisms associated with nesting have primarily been performed in female mammals in which nesting is typically initiated prior to parturition. The initiation of nesting often follows substantial changes in hormonal milieu; mainly, changes in circulating levels of progesterone, estradiol and prolactin (González-Mariscal et al., 1996; Lisk et al., 1969; Negatu and McNitt, 2002; Richards, 1969). Estradiol, progesterone and prolactin all play important roles in mammalian pregnancy, parturition, and maternal care (Bridges et al., 1997; Chaim and Mazor, 1998; González-Mariscal et al., 2007), and it is therefore not surprising that they are also involved in female nesting behavior. Additional work shows similar hormonal mechanisms influence nesting behavior in birds (Martinez-Vargas and Erickson, 1973; Murton et al., 1969; Steel and Hinde, 1972). However, nesting and parental behavior in male mammals (which is rare) are obviously not associated with parturition and lactation, and thus, it remain to be determined whether similar hormonal mechanisms regulate nesting behavior in males.

Given that nesting is present in such a wide range of species, relevant neural mechanisms that promote nesting may be somewhat conserved, even if the specifics of timing (relative to offspring arrival) and hormonal modulation are not. The nonapeptides oxytocin (OT) and vasopressin (VP) are good candidates as mechanisms of vertebrate nesting, given their importance for mammalian parental behavior (Bosch and Neumann, 2008) and the strong conservation of nonapeptide systems across the vertebrate classes. The ancestral peptide vasotocin (VT; Ile^3-VP) underwent a gene duplication approximately 450 MYA, giving rise to two groups of peptides (Acher and Chauvet, 1988), the first including VT (present in all non-mammalian taxa) and various other forms of VP in mammals, and a second lineage that includes various OT forms such as mesotocin (MT; Ile^8-OT), which is found in amphibians, reptiles, birds, and some marsupials; Leu^8-OT, which is found in most eutherian mammals and various cartilaginous fish (Donaldson and Young, 2008; Goodson, 2008); and Pro^8-OT, which is found in New World monkeys (Lee et al., 2011). The peptides themselves are highly conserved (e.g. only one amino acid residue separates VT from Leu^8-OT) and it is important to note that VP-OT peptides are relatively promiscuous, such that some effects of OT are mediated via the V_{1a} receptor (V1aR) and some effects of VP are mediated via the OT receptor (OTR). For example, VP infusions into the lateral septum induce pair bonding in male prairie voles, and this effect can be blocked with administration of an OTR antagonist (Liu et al., 2001). Similarly, in zebra

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finches, competitive binding assays show that VT and MT displace an iodinated OTR antagonist with comparable efficacy (Leung et al., 2009).

The various forms of OT and VP modulate aspects of reproduction and affiliation across all vertebrate taxa. For instance, nonapeptides modulate partner affiliation in fish (Oldfield and Hofmann, 2011), pair bonding in birds (Klatt and Goodson, 2013; Pedersen and Tomaszycki, 2012), and partner preference, affiliation, and pair bonding in mammals (Cho et al., 1999; Smith et al., 2010; Snowdon et al., 2010; Williams et al., 1994; Winslow et al., 1993). Interestingly, although OT has long been known to mediate many aspects of maternal physiology and behavior (Pedersen et al., 1982), recent data suggests that maternal behavior may actually be more strongly dependent upon VP (Bosch and Neumann, 2008), which is also important for paternal behavior in voles (Wang et al., 1994).

A limited amount of data suggests that VP–OT peptides modulate nesting behavior, as well. For instance, in a male house mouse (*Mus domesticus*) line artificially selected for low levels of thermoregulatory nest building, the number of VP-immunoreactive (−ir) cells in the suprachiasmatic nucleus is 1.5 fold higher than a line selected for high levels of nest building (Bult et al., 1992). However, it is not clear whether VP neuron number correlates similarly with nesting in a reproductive context. Another study demonstrates that central OT administrations in virgin female rats induce maternal behavior towards foster pups, including nesting, however maternal care was assigned an overall score and thus specific data regarding nesting cannot be parsed out from other maternal behaviors measured in this study (Fahrbach et al., 1984).

We here test the hypothesis that VP–OT peptides promote nesting behavior in male and female zebra finches. Zebra finches are ideal subjects for the study of nesting given that they are obligate nest builders in which both males and females participate in nest construction, and a great deal is known about zebra finch reproductive physiology and the role of nonapeptides in various sociosexual behaviors. For instance, nonapeptide receptors promote pair bonding (Klatt and Goodson, 2013; Pedersen and Tomaszycki, 2012) and gregariousness (Goodson et al., 2009b; Kelly et al., 2011) as well as modulating anxiety-like behavior (Kelly et al., 2011). VP–OT peptides influence numerous other aspects of avian reproduction and behavior, as well. Peripherally, nonapeptide receptors in the hen oviduct facilitate smooth muscle contractions of the uterus during oviposition (Takahashi and Kawashima, 2003, 2008), and centrally, avian nonapeptides modulate copulation (Castagna et al., 1998), territorial song (Goodson, 1998b), and reproductive aggression (Goodson and Adkins-Regan, 1999; Goodson et al., 2004b; Kabelik et al., 2009).

Methods

Subjects

Zebra finches were housed in male–female pairs in cages measuring 91 cm W × 43 cm H × 36 cm D and provided ad libitum access to food and water on a 14L:10D photoperiod with lights on at 0700 h. Subjects were prescreened for nesting behavior over a period of 4 days, during which unlimited access to nesting material (shredded burlap) and a nest cup was provided. At the end of prescreening, all nesting material and nests were removed and subjects failing to construct a nest were removed from the study. Subjects were given 4–5 days between prescreening and testing with no access to nesting material in an effort to promote nesting behavior during trials. Experiments were conducted in a humane manner and in compliance with all federal and institutional regulations.

Effects of peripheral antagonist injections on nesting

In the first two experiments, we quantified nesting following peripheral administration of 5 μg (first experiment; $n = 11$ males, 11 females) or 500 ng (second experiment; $n = 10$ males, 10 females) of a highly selective OTR antagonist (desGly-NH_2,d$(CH_2)_5$[Tyr(Me)^2,Thr^4] ornithine VT) in 0.05 ml of 0.9% saline (Goodson et al., 2009c). Injections were administered subcutaneously into the inguinal leg fold between 0800 and 0900 in a within-subjects design, counterbalanced for the order of vehicle and antagonist administrations. The peripheral and central doses (described below) of OTR antagonist have been used previously and were chosen to provide maximum blockade of receptors (Goodson et al., 2009c; Klatt and Goodson, 2013; Pedersen and Tomaszycki, 2012). These doses provide robust effects on sociality and pair bonding without affecting other behaviors including aggression, feeding, or grooming. Importantly, the peripheral dose of 5 μg, based on work in voles (Cushing and Carter, 2000), alters gregariousness in a manner that is virtually identical to the 250 ng dose administered centrally (Goodson et al., 2009c), suggesting that these doses are well-suited for comparisons of peripheral and central effects on nesting behavior.

Behavioral observations began 30 min after injection. At the beginning of each behavioral observation, a large quantity of shredded burlap nesting material was placed in the cage. Observations were conducted from behind a curtain blind by an observer blind to the treatment. The number of burlap pieces picked up, the number taken to the nest site, and the amount of time spent in the nest site were recorded. Tests were 30 min. Subjects were tested with both antagonist and vehicle in a counterbalanced order with 48 h between tests. Partners in the same cage were tested on alternating days and sex testing order was likewise counterbalanced across cages.

A third experiment tested the effects of a peripheral V1aR antagonist on male and female nesting behavior. Prior to testing, subjects ($n = 16$ males, 15 females) were prescreened as described above. Subjects were administered a selective V1aR antagonist JNJ-17308616 that is known to cross the blood–brain barrier (Johnson & Johnson; Raritan, NJ, USA) at a dose of 60 mg/kg (Goodson et al., 2009a) in 0.05 ml of 0.9% saline or vehicle into the inguinal leg fold between 0800 and 0900. This antagonist is effective at modulating behavior at 60 mg/kg in rats without non-selective peripheral effects (manufacturer's data), and this dose administered peripherally in birds produces effects on aggressive behavior (Goodson et al., 2009b) that are the reverse of central VT infusions (Goodson, 1998a), and comparable to effects obtained with central infusions of VT and 250 ng of a different V1aR antagonist (Goodson et al., 2004b), as described in the next section, suggesting that the doses used here are well-suited for comparisons of peripheral and central effects. Thirty minutes following administration, subjects were provided nesting material and behavior was quantified as described above.

Effects of central antagonist infusions on nesting

Following prescreening, subjects were stereotaxically implanted with a guide cannula directed at the caudal aspect of the right lateral ventricle. Birds were anesthetized using isoflurane delivered at 1.5 to 3.5% of a compressed air flow. A single 26-gage guide cannula (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 from the anterior pole of the cerebellum at a 21° angle towards medial. The cannula was adhered to the skull using dental cement (Stoelting Co., Wood Dale, IL) and veterinary grade cyanoacrylate glue (3 M, Saint Paul, MN). Injection cannulae projected 1 mm beyond the tip of the guide cannula. Following surgery, subjects were returned to their home cage and given a minimum of 5 days recovery.

Subjects were infused 30 min prior to testing with 0.5 μl of 0.9% saline vehicle, vehicle containing 250 ng OTR antagonist, or vehicle containing 250 ng of a selective V1aR antagonist ([β-Mercapto-β,β-cyclopentamethylenepropionyl^1,O-Me-Tyr^2,Arg^8]-Vasopressin; V2255, Sigma-Aldrich, St. Louis, MO) in a within-subjects design and tested every other day over the course of six days. All tests were counterbalanced for the order of treatments and subject sex in each pair.

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