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Arginine Vasotocin Interacts with the Social Environment to Regulate Advertisement Calling in the Gray Treefrog *(Hyla versicolor)*

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Amphibian · Advertisement call · Gray treefrog · *Hyla versicolor* · Social environment · Vasotocin

Abstract
Arginine vasotocin (AVT) has different effects on social behaviors across species with different social systems. However, less attention has been directed towards the way environmental stimuli interact with AVT to affect social behaviors. Previous work found that AVT affects the production of advertisement calls and the outcome of competitive interactions between male gray treefrogs *(Hyla versicolor)*. We conducted a field study to investigate how the presence of other males in a chorus influenced the production of advertisement calls in males treated with AVT or saline. After hormone treatment we placed individuals in call sites either within 50 cm of another calling male (proximate), or more than 2 m away from any calling male (distant). Males treated with AVT produced significantly longer calls with more pulses when placed at proximate call sites, but not distant call sites. Nonsignificant trends indicated that these increases in call length coincided with a decrease in call rate. There was no effect of call site distance on advertisement calls when males were treated with saline. These results indicate that the social environment can modulate the action of AVT on an important reproductive behavior, and that AVT does not influence call duration and pulse number unless another male is nearby. Understanding how social stimuli regulate the action of AVT on behavior could provide insight on the diversity of AVT function across species.

Introduction

The peptide arginine vasotocin (AVT) and its homologue arginine vasopressin (AVP) are well known for their effects on social behaviors in a wide variety of vertebrates [for reviews see Goodson and Bass, 2001; Marler et al., 2003]. The AVT/AVP system has generated interest because of its remarkable plasticity. A growing number of studies have found that the effects of AVT/AVP on behaviors can vary considerably across species, and variation in social systems could play an important role in determining how the AVT/AVP system functions. For example, AVT was found to promote aggressive behaviors in colonial zebra finches, *Taeniopygia guttata* [Goodson and Adkins-Regan, 1999], but inhibit aggressive behaviors in territorial field sparrows, *Spizella pusilla* [Goodson, 1998a], territorial violet wax-bills, *Uraeginthus granatina* [Goodson, 1998b], and Japanese quail, *Coturnix japonica* [Riters and Panksepp, 1997]. Similarly, AVP injections increased aggression in socially monogamous prairie voles, *Microtus ochrogaster,* but had no effect on aggression in polygamous montane voles,

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M. montanus [Young et al., 1997]. Currently it is not clear why AVT/AVP has such different effects on behavior in species that vary in behavioral ecology.

In addition to variation among species, there are several cases in which AVT/AVP has different effects on behavior within species. For example, in bluehead wrasse *(Thalassoma bifasciatum)* AVT injections given to dominants increased courtship behaviors but decreased aggressive behaviors [Semsar et al., 2001]. However, AVT injections given to subordinates increased both courtship and aggressive behaviors [Semsar et al., 2001], even though subordinates rarely exhibit these behaviors. Central AVT infusions reduced electrical activity associated with aggressive vocalizations in territorial morphs, but not non-territorial morphs of the plainfin midshipman, *Porichthys notatus* [Goodson and Bass, 2000]. The mammalian homologue AVP also exhibits plasticity, as central injections of AVP increased dominance behaviors in subordinate, but not dominant male golden hamsters, *Mesocricetus auratus* [Ferris et al., 1986]. In contrast, treatment with an AVP antagonist decreased dominance in dominant hamsters, but not in subordinate males [Ferris et al., 1986; Potegal and Ferris, 1990]. Examining how social interactions within a species affect AVT function might help to construct a framework for understanding interspecific variation in AVT/AVP function. Anurans are an attractive model to study interactions between AVT and the social environment as advertisement calls can be readily observed in the field and several studies have documented the effects of AVT on advertisement calling.

Arginine vasotocin promotes advertisement calling behavior in several anuran species. In bullfrogs, *Rana catesbeiana* [Boyd, 1994], cricket frogs, *Acris crepitans* [Marler et al., 1995], and green treefrogs, *Hyla cinera* [Burmeister et al., 2001], AVT injections increased the probability of calling in a chorus. Subsequent studies on cricket frogs found that AVT increased the persistence of calling behavior in response to a simulated acoustic agonistic encounter, but did not change other call parameters altered during aggressive interactions [Chu et al., 1998]. This study suggested that AVT increases the motivation to call in cricket frogs, but does not necessarily alter the calling behavior per se. Recent studies on gray treefrogs, *H. versicolor*, suggest that the effects of AVT on advertisement calls can be more complex. Injections of AVT increased call duration and pulse number in a dose-dependent fashion, but had no effect on call effort or dominant frequency [Klomberg and Marler, 2000]. Injections of AVT also promoted advertisement calls in individuals placed on other males' territories [Semsar et al., 1998], even though intruders usually do not call when placed on an established territory [Fellers, 1979]. These AVT-treated intruders proved effective at displacing resident males, as almost half of the residents vacated their calling site. Very little overt aggression was observed, so it is likely that the advertisement calls produced by the AVT treated intruders influenced residents' decisions to abandon calling sites. These data suggest that AVT might modulate not only the decision to call, but also what kinds of calls are produced. These data do not, however, demonstrate that the effect of AVT on call characteristics are dependent on the social environment.

Advertisement calls are used by male *H. versicolor* to attract females, and are also modulated during interactions with other males. Females prefer longer advertisement calls that have more pulses and longer call durations [Gerhardt, 1991; Schwartz et al., 2001]. Gray treefrogs use shorter, non-pulsatile, aggressive calls during intense aggressive interactions [Fellers, 1979; Tito et al., 1999]. These lower amplitude calls are used infrequently compared to advertisement calls [Fellers, 1979; B.C.T., K.L.R., C.A.M., personal observation]. In less intense interactions, males probably use advertisement calls instead of aggressive calls, as male residents produce calls with longer duration in high density choruses [Klump and Gerhardt, 1987]. Advertisement calls can inhibit calling behavior of non-resident males. Relocated males only call if the sound pressure levels of their nearest neighbor's calls are 95 decibels (dB) or lower [Fellers, 1979]. We hypothesized that because 1) AVT modulates advertisement calling in gray treefrogs and 2) advertisement call production is modulated by social stimuli, the effects of AVT on advertisement calling might depend on the social environment.

To determine how social interactions influence the effects of AVT on advertisement calling, we conducted a field study in which we manipulated both AVT and the proximity of other calling males. We injected field caught males with AVT or a saline solution and placed these individuals either in close auditory contact with another male in the chorus or at a more distant location from calling males, but within the chorus. If the social environment indeed regulates the action of AVT on advertisement calls, then the effects of AVT on advertisement calls should differ depending on an individual's distance from other calling males in the chorus. Understanding how social interactions affect the physiological action of AVT within a species might aid in understanding why AVT has such different actions across species with varying behavioral ecology.

Materials and Methods

Experimental Design

We used a two by two experimental design using hormone treatment and call site distance as our independent variables. We randomly assigned males to receive either a subcutaneous injection of AVT (25 µg in 25 µl saline) or saline. This dose is known to facilitate advertisement calling in *H. versicolor* [Semsar et al., 1998; Klomberg and Marler, 2000] and is similar to doses used in studies of other anurans [e.g., *H. cinera*, Penna et al., 1992; *R. catesbeiana*, Boyd, 1994; *A. crepitans*, Chu et al., 1998]. We manipulated call site distance by placing subjects within 50 cm of another unmanipulated calling male (proximate) or at a location within the chorus in which no males were calling within 2 m (distant). We used the 50 cm criteria for the proximate call site distance because past studies on *H. versicolor* indicated that resident males changed their advertisement calls when other males are within 75 cm [Fellers, 1979]. Locations of chorus males were visually confirmed. We used the 2 m criteria for the distant call site because previous research indicated that intruder males would call if placed >1 m away from a resident male. By manipulating hormone treatment and call site distance, we created a total of four treatment groups: AVT proximate, AVT distant, saline proximate, saline distant.

Field Site and Observations

We conducted field experiments both in the Dunlap Creek drainage area (off Highway 19) in Dane County, Wisconsin and at Steinke Basin (off Highway DL) at Devil's Lake State Park in Sauk County, Wisconsin. Observations were conducted from 12 June 2001 to 9 July 2001 and from 1 June 2002 to 3 June 2002. All observations were conducted from 21.30 to 00.30 h, when tree frog choruses begin to subside.

We used headlamps to locate male frogs and captured individuals by hand. Immediately after capture, males (study subjects) were randomly assigned to one of four treatment combinations and given the appropriate injection. Males were then transferred to acoustically transparent wire mesh containers (45 × 30 × 30 cm) containing a small clump of vegetation to serve as a calling substrate. All males were moved at least 1 m from their original calling site.

After a 30-min post-injection acclimation period, we recorded advertisement calls for 5 min with a Sennheiser directional microphone (ME67 with K6 power unit) and a Marantz portable recorder (PMD430). Males assigned to all treatment groups readily called from the containers. However, a subset of males did not call: AVT proximate (0/10) AVT distant (1/11), saline proximate (2/11), saline distant (5/15). Only males that produced advertisement calls were included for call analyses so that our final sample sizes were: AVT proximate (n = 10), AVT distant (n = 10), saline proximate (n = 9), saline distant (n = 10).

To determine whether our study subjects affected the advertisement calling of neighboring males (chorus males), we analyzed calls from unmanipulated neighboring males that could be detected on recordings of our study subjects. The orientation of the microphone and the number of chorus males in the area limited how many recordings could be used (AVT proximate, n = 6; AVT distant, n = 5; saline proximate, n = 7; saline distant, n = 8). After the recording period, we measured air temperature, snout-vent length (SVL), and leg length of study subjects.

We analyzed call parameters on a computer using Cool Edit by Syntrillium Software as described by Klomberg and Marler [2000]. Recordings were digitized at 32 kHz with 16-bit resolution and were analyzed without knowledge of treatment groups. We analyzed all calls from the 5-min recording periods and recorded the number of pulses per call (pulse number), the length of each call (call duration), the number of calls per minute (call rate), the number of pulses per minute (call effort), and the time between calls (intercall interval). The quality of oscillograms from chorus males was generally lower compared to those of study subjects. Thus we recorded only pulse number and call duration to obtain a rough estimate of how our treatments of study subjects affected chorus males.

We used Q-Q plots to check each variable for normality assumptions and checked cell means for homogeneity of variance. Transformations were not necessary for pulse number, call duration, chorus pulse number, or chorus call duration. However, square root transformations were applied to intercall interval, call rate, and call effort scores. We used two-way analyses of variance to analyze all call variables to test for main effects and the interaction between hormone treatment and call site distance. For analyses of pulse number, call duration, intercall interval, and call rate we used Julian date as a covariate because it was significantly correlated with these variables (table 1). We also included temperature as a covariate in analyses of intercall interval, call rate, call effort, chorus pulse number, and chorus call duration (table 1). There were no significant differences in any of the call parameters between the two field sites, therefore we combined the data from both sites for analyses.

Table 1. Pearson correlations between call characteristics and Julian date. Correlations between call characters and temperature are partial correlations controlling for Julian date used as covariates

Call parameters	Julian date	Temperature
Pulse number	–0.53**	0.02
Call duration	–0.67**	0.15
Intercall intervall	–0.34*	0.32*
Call rate	0.32*	–0.20⁺
Call effort	–0.17	–0.32*
Chorus pulse number	–0.66**	–0.39*
Chorus call duration	–0.67**	–0.55**

* $p < 0.05$; ** $p < 0.01$; ⁺ $p = 0.22$.

Results

Interactions between AVT and Social Environment

Although there was no significant difference in the probability of calling across all four treatment groups ($\chi^2 = 5.618$, p = 0.14), there was a nonsignificant trend for a greater probability that AVT males would call compared to saline treated males (Fisher Exact Test, p = 0.06). Treatment with AVT influenced pulse number and call duration, although main effects were mostly superceded by the interaction term. Males treated with AVT produced calls with longer duration (fig. 1a; $F_{1,35} = 9.10$, $p < 0.01$) and more pulses (fig. 1b; $F_{1,35} = 7.528$, $p = 0.01$) than saline-treated males. However, these effects of AVT were driven largely by significant hormone treatment by call site distance interactions for both pulse number ($F_{1,35} = 6.77$, $p = 0.014$) and call duration ($F_{1,35} = 7.01$, $p = 0.012$). Post-hoc Tukey tests indicated that males treated with AVT produced longer calls ($p < 0.001$; fig. 1b) with more pulses ($p < 0.001$; fig. 1a) in the proximate call sites compared to the distant call sites. In contrast, males treated with saline did not differ significantly in pulse number or call duration between proximate and distant call sites and neither differed from AVT-treated males in distant call sites. There was no main effect of call site distance on either pulse number ($F_{1,35} = 0.63$, $p = 0.43$) or call duration ($F_{1,35} = 0.64$, $p = 0.43$). Thus, males gave longer calls with more pulses in response to AVT only when other calling males were in close proximity.

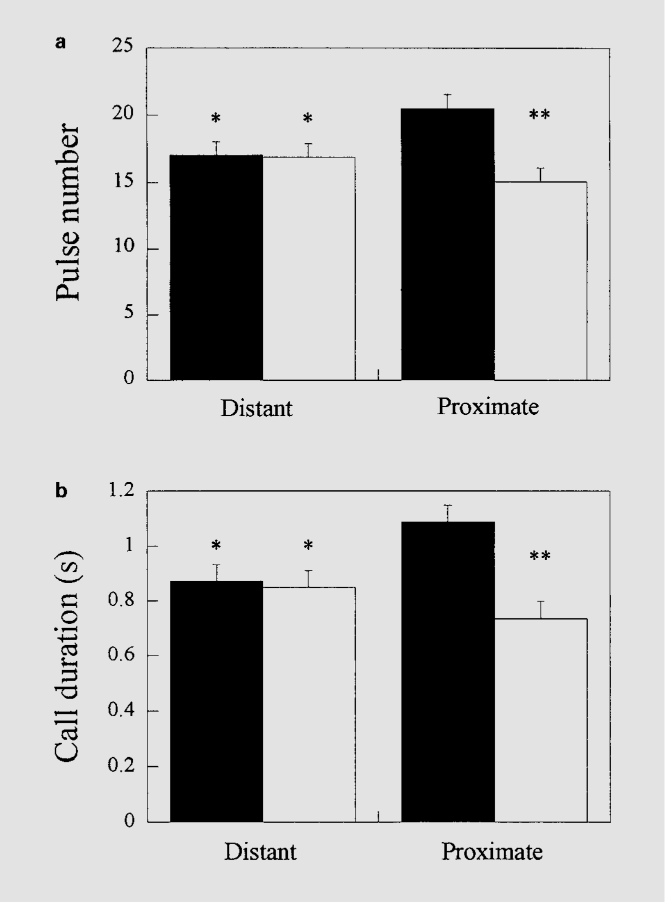

Fig. 1. Pulse number (**a**) and call duration (**b**) for male gray tree frogs in different treatment groups: black bars, AVT; open bars, saline. *$p < 0.05$ Tukey comparison to AVT proximate; **$p < 0.001$ Tukey comparison to AVT proximate. Data are presented as corrected (for Julian date) means ± standard errors.

There was no significant interaction between hormone treatment and call site distance for intercall interval (table 2; $F_{1,34} = 3.29$, $p = 0.08$). There was no significant interaction between hormone treatment and call site distance interaction for call rate (table 2; $F_{1,34} = 2.85$, $p = 0.10$). There were no main effects of hormone treatment or call site distance on intercall interval or call rate. There was no effect of hormone treatment, call site distance, or the interaction on call effort.

Effects on Unmanipulated Chorus Males

There was a nonsignificant trend for a main effect of call site distance on chorus pulse number ($F_{1,34} = 3.28$, $p = 0.058$). Chorus males tended to use more pulses when study subjects were at proximate call sites (mean ± SE; distant 14.94 ± 0.52; proximate 16.42 ± 0.51). There was no significant effect of hormone treatment or the interaction on chorus pulse number. There was no significant effect of hormone treatment, call site distance, or the interaction on chorus call duration.

Discussion

We found that the effects of AVT on vocalizations depended on an individual's proximity to other calling males in *H. versicolor*. When treated with AVT, frogs pro-

Table 2. Call characteristics for male *H. versicolor*; data are presented as means ± SE

Call variable	Proximate		Distant	
	saline	AVT	saline	AVT
Intercall interval, s	2.45±0.16	2.72±0.15	2.65±0.15	2.45±0.14
Call rate, sqrt calls/min	3.61±0.18	3.09±0.18	3.37±0.18	3.35±0.17
Call effort, sqrt pulses/s	1.93±0.08	1.96±0.07	2.01±0.08	2.02±0.07

duced calls of longer duration and with more pulses only if they were in close proximity to other calling males. Although we did not find significant effects of the treatments on intercall interval or call rate, analyses of these data suggest AVT treated males might produce fewer calls than saline treated males in proximate call sites, even though AVT treated males were more likely to call after handling. Future studies should investigate this hypothesis, as it is also consistent with our lack of evidence for changes in call effort, despite the large increases in pulse number and call duration between AVT and saline treated frogs in proximate call sites. Although many studies have examined the effects of AVT on vocalization behaviors, few have examined the importance of social context that might mediate these effects.

Interpretation of the behavioral effects of AVT in *H. versicolor* is complicated by the observations that males give longer advertisement calls when in higher density choruses [Klump and Gerhardt, 1987], and that females prefer long duration advertisement calls [Gerhardt, 1991; Schwartz et al., 2001]. It is therefore difficult to distinguish whether an increase in call duration is directed at males, females, or both. One way to evaluate this question is to consider the production of aggressive calls used in the most intense encounters [Pierce and Ralin, 1972; Fellers, 1979]. We periodically heard aggressive calls in the choruses but never in any of our observations, despite the relatively large effects of AVT on pulse number and call duration observed at proximate call sites. Chorus males exposed to our study subjects also did not use aggressive calls, although there was a nonsignificant trend for chorus males to have a higher pulse number in proximate call sites across both saline and AVT treatments. In addition, no increase in aggressive calls was found in response to AVT in a study by Tito et al. [1999]. It is possible that closer contact (<10 cm) among males is necessary to elicit aggressive calls, or that aggressive calls were used during the acclimation period and males habituated afterwards. However, Semsar et al. [1998] observed that the production of aggressive calls by AVT-treated intruder males was not necessary for displacing resident males from calling sites. Currently it is unclear how the effect of AVT on advertisement calling influences male-male competitive interactions.

An alternative hypothesis is that AVT alters advertisement calls so that they are more attractive to females. This and a previous study [Klomberg and Marler, 2000] found that AVT increases call duration. Females often prefer exaggerated signals [Ryan and Keddy-Hector, 1992], including longer call duration in *H. versicolor* [Gerhardt, 1991; Schwartz et al., 2001]. Many studies on amphibians and fish have found that AVT exerts positive effects on courtship and mating behaviors. Arginine vasotocin promoted electrical chirps used only in male-female interactions in the weakly electric fish, *Apteronotus leptorhynchus* [Bastian et al., 2001] and increased courtship displays in *T. bifasciatum* [Semsar et al., 2001]. Arginine vasotocin increased amplectic clasping during courtship in the rough-skinned newt, *T. granulosa* [Thompson and Moore, 2000], as well as in the Japanese newt, *Cynops pyrrhogaster* [Iwata et al., 2000]. The effects of AVT on mating behavior have been studied primarily in newts [see Rose and Moore, 2002 for review], although a recent study suggests that the act of mating could affect advertisement calling in frogs. Male *Hyperolius marmoratus* that successfully mated were more likely to mate again on future nights independent of body mass or condition [Dyson et al., 1998]. This raises the possibility that mating could influence advertisement calling in much the same way that winning aggressive encounters affects aggression [Chase et al., 1994; Beaugrand and Goulet, 2000; Oyegbile and Marler, 2001]. Vasotocin could modulate such a relationship, as it can regulate both mating and advertisement displays in amphibians. For example, AVT injections facilitated advertisement calling but not amplexus in male Great Plains toads, *Bufo cognatus* [Propper and Dixon, 1997]. Thus, if mating triggered the release or production of AVT, advertisement calling could become more frequent. Interestingly, plasma AVP levels increase during sexual arousal in human males [Murphy et al., 1987].

Klomberg and Marler [2000] reported effects of AVT on *H. versicolor* call parameters that were similar to what we observed: significant increase of call duration and pulse number, nonsignificant trend for a decrease in call rate, and no effect on call effort. Our findings might explain why Tito et al. [1999] did not observe changes in call duration or pulse number of advertisement calls in response to AVT treatment in a different population of *H. versicolor*. Tito et al. [1999] observed AVT-treated males in enclosures outside of a chorus, whereas Klomberg and Marler [2000] observed AVT-treated males at their calling sites. Our study indicates that enclosures alone do not block the action of AVT, but that enclosures must be placed in close contact with other calling males to observe effects of AVT on pulse number and call duration.

Previous studies of treefrogs have found negative effects of saline injection and handling procedures on vocalization production, although the magnitude of these effects has been variable [Tito et al., 1999; Klomberg and

Marler, 2000; Burmeister et al., 2001]. In our study, the injection and handling procedure inhibited calling more frequently in saline groups compared to AVT groups. However, call parameters for saline-treated males are very close to mean values reported for undisturbed calling males [Klomberg and Marler, 2000]. Thus it appears that handling reduces the motivation to call, but does not affect calling parameters per se. In contrast, AVT appears to increase the motivation to call and increases the length of advertisement calls. Interestingly, unmanipulated chorus males tended to use more pulses in their calls when study subjects were within 50 cm regardless of hormone treatment. This finding is in agreement with previous observations that males give longer calls in high-density choruses [Klump and Gerhardt, 1987]. Our study subjects, however, did not respond to social stimuli in the same way as residents, suggesting that relocation inhibits this response.

Previous studies have hypothesized that AVT might activate anuran motivational systems associated with communication [Burmeister et al., 2001; Goodson and Bass, 2001] or increase selective attention to social stimuli [Chu et al., 1998; Goodson and Bass, 2001]. Our data suggest that both hypotheses might be valid for *H. versicolor*. A role for AVT in promoting motivation to call is supported by the observation that AVT treated males were more likely to call than saline-treated males, as in other anurans [Boyd, 1994; Marler et al., 1995; Semsar et al., 1998; Burmeister et al., 2001]. A role for AVT in promoting selective attention is supported by the observation that AVT-treated males change their call characteristics only when stimulated by nearby calling males. Our results suggest that systemic manipulations of AVT combined with manipulations of social stimuli could lead to interesting observations in other species. These data show that as researchers examine the variation in AVT/AVP function across species, it will be critical to consider manipulations of social context to accurately characterize the effects of AVT/AVP on behavior.

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