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Historical perspective: Hormonal regulation of behaviors in amphibians

Frank L. Moore[a,*], Sunny K. Boyd[b], Darcy B. Kelley[c]

[a]Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, USA
[b]Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556-0369, USA
[c]Department of Biological Sciences, Columbia University, 911 Fairchild Center, M.C. 2432, New York, NY 10027, USA

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Abstract

This review focuses on research into the hormonal control of behaviors in amphibians that was conducted prior to the 21st century. Most advances in this field come from studies of a limited number of species and investigations into the hormonal mechanisms that regulate reproductive behaviors in male frogs and salamanders. From this earlier research, we highlight five main generalizations or conclusions. (1) Based on studies of vocalization behaviors in anurans, testicular androgens induce developmental changes in cartilage and muscles fibers in the larynx and thereby masculinize peripheral structures that influence the properties of advertisement calls by males. (2) Gonadal steroid hormones act to enhance reproductive behaviors in adult amphibians, but causal relationships are not as well established in amphibians as in birds and mammals. Research into the relationships between testicular androgens and male behaviors, mainly using castration/steroid treatment studies, generally supports the conclusion that androgens are necessary but not sufficient to enhance male behaviors. (3) Prolactin acts synergistically with androgens and induces reproductive development, sexual behaviors, and pheromone production. This interaction between prolactin and gonadal steroids helps to explain why androgens alone sometimes fail to stimulate amphibian behaviors. (4) Vasotocin also plays an important role and enhances specific types of behaviors in amphibians (frog calling, receptivity in female frogs, amplectic clasping in newts, and non-clasping courtship behaviors). Gonadal steroids typically act to maintain behavioral responses to vasotocin. Vasotocin modulates behavioral responses, at least in part, by acting within the brain on sensory pathways that detect sexual stimuli and on motor pathways that control behavioral responses. (5) Corticosterone acts as a potent and rapid suppressor of reproductive behaviors during periods of acute stress. These rapid stress-induced changes in behaviors use non-genomic mechanisms and membrane-associated corticosterone receptors.

Keywords: Hormonal regulation; Amphibians; Behavior

Introduction

In his “unauthorized” autobiography (published recently by his son), the endocrinologist Lancelot Hogben provides an early defense of the use of experimental model systems in biological sciences (Hogben and Hogben, 1998). Hogben asserts: “In many fields of experimental biology, advance in the understanding of a function takes place on a wider front and at a greater tempo if one can find the animal uniquely fitted for study. For example, the expansion of genetics was spectacular when the Columbia School was able to exploit the many advantages of the fruit fly, *Drosophila*. . .For my purpose, the South African clawed toad, *Xenopus laevis*, proved to be a godsend. . .” (p. 101). Hogben discovered melanocyte stimulating hormone using *Xenopus* as a source and a bioassay. The profound conservation of the hormones themselves—and the variety of uses to which they are put by different organisms—insured that his discoveries were of both general and particular interest. These advantages hold as well for the behavioral neuroendocrinologist. The use of anurans in behavioral endocrinology has a long and distinguished history; publications appeared as early as the late 1800s (Steinach, 1894) and continued at steady rate through the 1990s (the period covered by this review: e.g., Berk, 1939; Russell, 1954; Dodd, 1960; Palka and Gorb-

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* Corresponding author. Fax: +1 541 737 0501.
E-mail address: Frank.Moore@oregonstate.edu (F.L. Moore).

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man, 1973; Lofts, 1974; see also papers cited here). For urodeles (salamanders and newts), research on the neuroendocrine control of behaviors has been greatly helped by early neuroanatomists, such as J.B. Johnston and C. Judson Herrick, and the development of several species (*Cynops pyrrhogaster*, *Taricha granulosa*, and *Triturus carnifex*) as research models. This review describes some contributions gleaned from study of amphibians, focusing on the hormonal control of vocal behaviors and of clasping in anurans (frogs and toads) and the hormonal control of clasping and non-clasping behaviors in urodeles (primarily newts).

Hormonal control of vocal behaviors

Frogs and toads typically use a few stereotyped vocalizations to communicate with conspecifics. The most studied vocal behaviors are the "advertisement calls" produced by males to attract females and, in some species, maintain territories, and the "release calls" emitted by males and sexually unreceptive females when clasped by other individuals. Hormones regulate many aspects of vocal behaviors in anurans, ranging from the development of calling structures and neural circuitry to the modulation of call characteristics.

Effects of hormones on development of vocalization structures

The development of central nervous system and laryngeal structures involved in production of anuran vocalizations has been investigated only in *Xenopus laevis*. Androgens play a pivotal role in masculinization of this species. Synthesis of testosterone and dihydrotestosterone in *X. laevis* begins around stage 47 in tadpole development, before substantial gonad differentiation can be observed (Kang et al., 1995), but sex differences in circulating androgen concentrations are not obvious until early adulthood (about 1 year post-metamorphosis). Within this period, the male larynx develops more muscle fibers (Sassoon and Kelley, 1986; Marin et al., 1990) and a preponderance of fast-twitch fibers (Sassoon et al., 1987; Tobias et al., 1991a; Catz et al., 1995). Sex differences in numbers of vocal motor neuron numbers begin before metamorphosis and are due to less ontogenetic cell death in males (Kelley and Dennison, 1990; Kay et al., 1999). Castration of males or treatment with the anti-androgens flutamide and hydroxyflutamide prevents these dimorphisms and androgen treatment enhances the masculinization of the female *X. laevis* larynx (Sassoon and Kelley, 1986; Tobias et al., 1991b; Kay et al., 1999). Although serum androgen levels are not sexually dimorphic during the period of most rapid masculinization, androgen receptor levels in the larynx are greater in males; regulation of receptor levels participates in sexual differentiation of the vocal organ (Kelley et al., 1989; Fischer and Kelley, 1991; Kang et al., 1995). The masculinization of the *X. laevis* larynx requires androgen, but other hormones, namely thyroid hormones and prolactin, have critical roles as well (Cohen and Kelley, 1996; Robertson and Kelley, 1996; for a review, see Kelley, 1996). In *X. laevis*, the laryngeal neuromuscular synapse is feminized by estrogens during early adulthood (Tobias and Kelley, 1995; Tobias et al., 1998a). The changes produced by estrogen are reversible while those due to androgen are usually irreversible.

Hormonal control of advertisement calling

While castration will often result in the cessation of advertisement calling (see below), cause and effect relationships between the display of advertisement calls and plasma androgen levels in natural populations have not been resolved. Several studies found a positive correlation between calling and plasma testosterone levels (Townsend and Moger, 1987; Marler and Ryan, 1996; Harvey et al., 1997; Solis and Penna, 1997), and at least one study found the opposite, namely that calling males have lower androgen levels (*Rana catesbeiana*; Mendonca et al., 1985). Other studies revealed positive correlations between androgen levels and vocalization effort (Emerson and Hess, 1996) and evidence that exposure of male frogs to vocalizations of chorusing males results in significantly higher plasma androgens in those males, compared to males that heard only tones or no sound (Brzoska and Obert, 1980). Whether these correlations reflect androgen control of calling, calling influence on androgens, or both remains to be resolved and may reflect species-specific mechanisms.

Advertisement calling can be abolished by castration of adults (*X. laevis*; *Rana pipiens*, *Hyla cinerea*, *Hyla versicolor*) (Palka and Gorbman, 1973; Kelley and Pfaff, 1976; Wetzel and Kelley, 1983; Penna et al., 1992). Only in *X. laevis*, however, has androgen replacement therapy been shown to restore calling in castrated males (Wetzel and Kelley, 1983). In intact females, androgen treatment can induce advertisement call-like vocalizations (Penna et al., 1992). Sites in the central nervous system pathway controlling vocalization in anurans and the larynx are major androgen target tissues, suggesting that androgens might modulate calling by acting centrally (Kelley and Tobias, 1999). Strong evidence for this relationship is lacking, however, for all anurans except *X. laevis*.

The neuropeptide arginine vasotocin has been implicated in the control of advertisement calling in several amphibian species. Vasotocin administration facilitates the display of advertisement calling in *R. catesbeiana*, *H. cinerea*, *H. versicolor*, *Acris crepitans*, and *Bufo cognatus* (Penna et al., 1992; Boyd, 1994a; Marler et al., 1995; Propper and Dixon, 1997; Chu et al., 1998; Tito et al., 1999).

Neurons that synthesize vasotocin and neurons that express vasotocin receptors are strategically located throughout vocal control neural circuitry. The distribution of vasotocin cells and fibers is well described for several anurans, primarily Ranid and Pipid frogs (Conway and

Gainer, 1987; Boyd, 1994b, 1997; Boyd et al., 1992; Gonzalez and Smeets, 1992; Gonzalez et al., 1995; Mathieson, 1996; Marler et al., 1999). For anuran amphibians, the brain distribution of vasotocin receptors has only been described for *R. catesbeiana* (Boyd, 1997). Concentrations of vasotocin are higher in the amygdala and pretrigeminal nucleus of male *R. catesbeiana* than in females (Boyd, 1994c; Boyd et al., 1992). Vasotocin concentrations are also sexually dimorphic in the nucleus accumbens of *A. crepitens* and vasotocin in this area is negatively correlated with calling behavior (Marler et al., 1999). Vasotocin receptor concentrations are sexually dimorphic and sensitive to steroid hormone manipulations in the *R. catesbeiana* vocalization pathway, notably the pretrigeminal nucleus and amygdala (Boyd, 1997). Therefore, one mechanism hypothesized to explain the actions of steroid hormones on vocalization in anurans is that androgens and estrogens regulate vasotocin peptide or receptor concentrations in critical brain areas.

Hormonal control of release calling

Sexually unreceptive male and female anurans of most species produce a “release call” (Bogert, 1960; Martin, 1972). Sex steroid hormones may influence release calls by exerting effects on laryngeal muscles and associated tissues. Sexual differences in laryngeal mass are found in many species (e.g., Sassoon and Kelley, 1986; McClelland and Wilczynski, 1989b; McClelland et al., 1996, 1997; Boyd et al., 1999). The dominant frequency of the release call differs significantly between sexes in many species (Walkowiak, 1988; McClelland and Wilczynski, 1989a), a character that may reflect sex differences in laryngeal structure (McClelland and Wilczynski, 1989b; McClelland et al., 1996). Males and females also produce release calls that differ in temporal characteristics (e.g., call rate, interpulse interval) associated with sexual and seasonal differences in plasma sex steroids (Walkowiak, 1988; McClelland and Wilczynski, 1989a; Boyd, 1992). Although ovariectomy can increase release calling in *X. laevis* (Kelley, 1982), neither ovariectomy nor ovarian steroid treatments altered release calling rates in *R. pipiens* (Diakow et al., 1978). Thus, there is scant direct evidence for involvement of gonadal steroid hormones in the control of release calling.

Vasotocin also alters release calling in some anurans but the pattern varies with the sex and species of the animal. In female *R. catesbeiana* and *R. pipiens*, vasotocin administration decreases release calling (Diakow, 1978; Boyd, 1992). In males, vasotocin administration has been show to increase, decrease, or not effect release call rates (Boyd, 1992; Raimondi and Diakow, 1981; Tito et al., 1999) depending on the frog species. In addition to vasotocin, prostaglandin E2 and prolactin also are linked to the suppression of releasing calling in sexually receptive females (Diakow and Nemiroff, 1981; Weintraub et al., 1985; Boyd, 1992).

Hormonal control of other call types

The hormonal control of aggression-specific vocalizations has been investigated in a few cases. In *H. versicolor*, which produce distinct aggressive calls during interactions between two males, vasotocin administration enhances aggressive calling (Tito et al., 1999) (Fig. 1). The peptide also influences other territorial behaviors in male *H. versicolor* and *Eleutherodactylus coqui* (Semsar et al., 1998; Klomberg and Marler, 2000). On the other hand, in *A. crepitans*, vasotocin increases overall levels of calling but alters call characteristics in a direction typical for a less aggressive male (Marler et al., 1995).

Hormonal control of phonotaxis

Females of many anuran species move toward the advertisement calls of conspecific males at the time of ovulation. Positive phonotaxis and ability to discriminate calls appear to co-vary with the narrow time period directly around ovulation. Phonotaxis has been enhanced by injections with various types of hormones including hCG (Schmidt, 1985; Picker, 1983), combined treatment with progesterone, prostaglandin $F_{2\alpha}$ and vasotocin treatment (Schmidt, 1985), or treatment with vasotocin (Boyd, 1994a). Careful studies of changes in steroids, peptides, and prostaglandins associated with changes in phonotaxis would provide new insight into normal mechanisms for hormonal control of phonotaxis in female anurans.

Amplectic clasping behavior in male anuran amphibians

Male frogs and toads typically clasp females for long periods. Despite the prolonged, obvious, and important nature of amplexus, we know very little about its hormonal control in most anurans. Display of clasping is positively

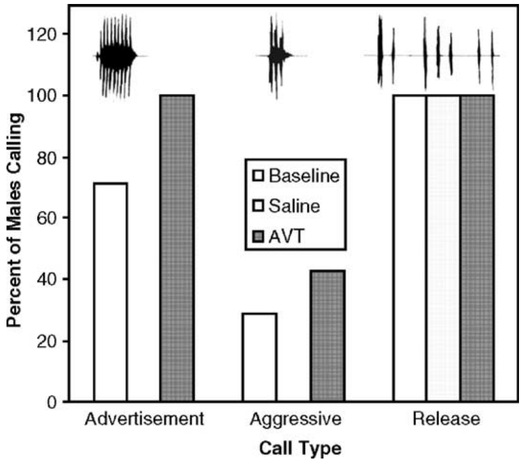

Fig. 1. Effects of AVT or saline on the percent of male gray tree frogs (*Hyla versicolor*) that give advertisement, aggressive or release calls 90 min after treatment. Baseline values taken before intraperitoneal injections. No saline-injected males gave advertisement or aggressive calls. Representative oscillograms of the three call types are located above the bars (adapted from Tito et al., 1999).

correlated with plasma androgen at a general seasonal level (Siboulet, 1981; Licht et al., 1983; Rastogi et al., 1986; Delgado et al., 1989; Itoh and Ishii, 1990; Itoh et al., 1990; Kao et al., 1993; Huang et al., 1997). Clasping and circulating androgens are sometimes correlated in an individual and sometimes not. Male *Rana esculenta*, *Bufo marinus*, *Bufo mauritanicus*, *E. coqui*, and *Scaphiopus couchii* sacrificed in amplexus had significantly higher plasma testosterone than males not in amplexus (Siboulet, 1981; Townsend and Moger, 1987; Orchinik et al., 1988; Harvey et al., 1997; Gobbetti and Zerani, 1999). This relation was not, however, observed in *Bufo japonicus*, *R. catesbeiana*, or *R. pipiens* (Wada et al., 1976; Licht et al., 1983; Mendonca et al., 1985; Itoh and Ishii, 1990). Because the performance of amplexus behavior can cause significant increases in plasma gonadotropins, differences in plasma androgens between claspers and non-claspers may be the result—rather than the cause—of the behavior (Ishii and Itoh, 1992).

A direct relation between circulating androgens and clasping behavior has been demonstrated only in *X. laevis* (Kelley and Pfaff, 1976). Castrated males stop clasping, and clasping can be reinstated with either testosterone or DHT (but not estradiol) implants. Ovariectomized female *X. laevis* could be induced to clasp with testosterone treatment. Clasping also disappears upon castration in *R. pipiens* but androgen treatment was not effective in restoring clasping in that species (Palka and Gorbman, 1973). Androgens are probably required for display of robust clasping behavior, but may not be sufficient in all species.

Clasping behavior of anurans is also influenced by chemical messengers other than gonadal steroids. Two peptide hormones have been found to enhance amplectic clasping behavior in anurans-GnRH (Propper and Dixon, 1997) and thyrotropin-releasing hormone (Taylor and Boyd, 1991). Injections of hCG also can enhance amplectic clasping in male *X. laevis*, but its site and mechanism of action are unknown (Kelley and Pfaff, 1976).

Amplectic clasping behavior in caudate amphibians

Of the 500+ species of caudate amphibians (i.e., urodeles, salamanders) in the world, research into the hormonal control of behaviors has been mainly restricted to three species of newts in the family Salamandridae—North American rough-skinned newt (*T. granulosa*), Japanese fire-bellied newt (*C. pyrrhogaster*), and Italian crested newt (*T. carnifex*).

Activation of amplectic clasping behaviors by hormones

Amplectic clasping behaviors are used during the courtship and mating sequences by species of *Taricha*, but not by newts in *Cynops* or *Triturus* genera. In *T. granulosa*, amplexus involves a male initiating courtship by embracing a female in amplexus and gripping her firmly with his fore and hind legs.

Evidence that testicular steroids regulate amplectic clasping behaviors in *T. granulosa* comes from the positive correlation between plasma testosterone levels and seasonal changes in male sexual activity. But the seasonal steroid profiles are complex. In *T. granulosa*, testes secrete both testosterone and DHT (Moore et al., 1979b), but only testosterone shows marked increases in concentration prior to and into the breeding season (Moore et al., 2000; Specker and Moore, 1980). Males have higher plasma concentrations of testosterone than females, and in males the plasma testosterone concentrations reach peak levels prior to the onset of the breeding season and then decline rapidly to near undetectable levels before the breeding season ends (Deviche et al., 1990). Female *Taricha* have higher plasma 17β-estradiol than males, whereas males and females have similar amounts of plasma DHT (Moore et al., 2000).

To investigate where testicular steroids might act to regulate male behaviors, the anatomical distributions of intracellular androgen (AR) and estrogen receptors (ER) were studied in *T. granulosa* using immunocytochemistry with anti-AR or anti-ER serum (Davis and Moore, 1996). AR-ir-labeled cells were found in the olfactory bulbs, habenula, pineal body, preoptic area, hypothalamus, cerebellum, and motor nuclei in the medulla. In addition, ER-ir-labeled cells were seen in the lateral septum, amygdala dorsolateralis, pallium, preoptic area, hypothalamus, and dorsal tegmentum. The only brain areas found to have both AR and ER immunoreactivity are the dorsal hypothalamus and ventral infundibulum. This distribution of AR and ER indicates that sex steroid receptors are located in brain areas that control sensory processing, neuroendocrine functions, and motor output—all possible substrates in the brain where sex steroid hormones might act to control reproductive behaviors, as reported earlier in *Xenopus* (Kelley, 1980).

As in most other vertebrates, castration of male *Taricha* eliminates amplectic clasping behavior, and implants of androgens (testosterone or testosterone plus DHT) to castrated newts maintain this behavior (Deviche and Moore, 1988; Moore, 1978). Outside the breeding season, however, androgen administration to intact or castrated males fails to stimulate amplectic-clasping behaviors (Deviche and Moore, 1988; Moore et al., 1978b). Thus, testicular androgens are necessary, but not sufficient, for activating reproductive behaviors in male *Taricha*. It is this observation that supports the notion that non-testicular hormones become elevated during the breeding season and function in combination with testicular steroids to enhance male reproductive behaviors in amphibians.

One non-testicular hormone that controls amplectic clasping behavior in *Taricha* is vasotocin. In *T. granulosa*, vasotocin injections into males increases the incidence of amplectic clasping behaviors, when tested just prior to or towards the end of the breeding season when sexual activity is below maximum (Moore and Miller, 1983; Moore and Zoeller, 1979). Conversely, injections of vasotocin antagonists or anti-vasotocin serum reduce the incidence of amplectic clasping (Moore and Miller, 1983).

Studies using immunocytochemistry and in situ hybridization histochemistry show that in *T. granulosa* there are about 20 populations of vasotocin-containing neurons in the forebrain and midbrain (Lowry et al., 1997), many of which are conserved across diverse vertebrate taxa (Goodson and Bass, 2001; Moore and Lowry, 1998; Smeets and Gonzalez, 2001). Vasotocin-containing neurons of greatest interest to discussions of reproductive behaviors are in the medial pallium, amygdala dorsolateralis, bed nucleus of the stria terminalis, anterior preoptic areas, ventral medial hypothalamus, and optic tectum.

Other studies using microdissection and radioimmunoassay procedures reveal that vasotocin content in specific sites in the brain correlates with the males' reproductive and behavioral status. In male *T. granulosa*, vasotocin concentrations in the optic tectum change seasonally and are highest during the breeding season (Zoeller and Moore, 1986). Vasotocin concentrations are higher in sexually responsive than in unresponsive males in the dorsal preoptic area, optic tectum, ventral infundibulum, and cerebrospinal fluid (Zoeller and Moore, 1988). Thus, there is evidence that vasotocin administration can activate amplectic clasping and that males showing amplectic clasping behaviors have higher vasotocin concentrations in specific brain areas.

Castration/steroid replacement studies in *Taricha* show that the induction of courtship behavior by vasotocin is androgen dependent, and that there is a slow post-castration decline in vasotocin responses unless the castrates are treated with androgens (testosterone or DHT) (Zoeller and Moore, 1982; Moore et al., 1992). This effect of androgens on courtship can be explained, at least in part, if androgens control the activity of vasotocin receptors in behaviorally important brain areas. Castration decreases the density of ^{3}H-vasopressin binding in the amygdala, but not in other brain areas (Boyd and Moore, 1990a). Sexual dimorphism in vasotocin neurons also suggests androgens modulate the activity of this system. Male *Taricha* have greater numbers of vasotocin neurons than females in the bed nucleus stria terminalis, amygdala, and anterior preoptic area (Moore et al., 2000), three brain areas associated with male behaviors (Fig. 2). These observations are consistent with the hypothesis that testicular steroids influence amplectic clasping by site- and sex-specific control of the vasotocinergic system in *Taricha*.

It is not known whether vasotocin exerts its effects by modulating the animals' central state of sexual motivation or by modulating sensorimotor processing of sexually relevant stimuli (for a review, see Rose and Moore, 2002). This latter explanation is supported by experiments in *Taricha* showing that vasotocin administration can increase responses to specific olfactory, visual, and tactile sexual stimuli (Rose et al., 1995; Thompson and Moore, 2000). In experiments with olfactory stimuli, vasotocin-injected males show increases in appetitive responses to sex-related olfactory information (female sex pheromones), but not to food-related olfactory information (earth worm odors). In tests with visual sexual stimuli, vasotocin administration increases male newts' behavioral responses to sex-related visual information (sexually mature female newts viewed through clear glass) (Thompson and Moore, 2000). Lastly, vasotocin administration enhances neuronal responses to clasp-triggering tactile stimulation of the cloacal region in male newts (Rose et al., 1995) (Fig. 3A). These studies suggest that vasotocin enhances responses to sexual stimuli by three different sensory modalities (olfactory, visual, and tactile) and that, at least in part, vasotocin functions by modulating sensorimotor processing of specific sexual stimuli.

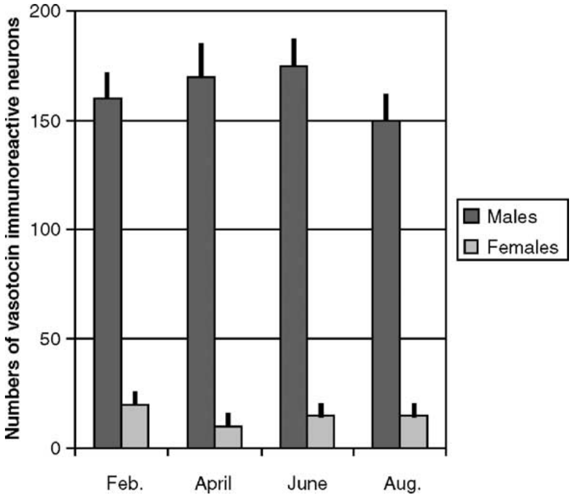

Fig. 2. Sexual dimorphism in the numbers of vasotocin neurons in the anterior preoptic area of *T. granulosa* (redrawn from Moore et al., 2000).

Suppression of amplectic clasping behaviors by hormones

Although frequently overlooked, the suppression of behaviors by hormones is important because an animal's behavioral state depends on the balance between stimulatory and inhibitory chemical messengers. Inhibitory chemical messengers have important biological consequences when animals must suppress courtship and mating displays to avoid life-threatening conditions. For example, when wild animals perceive potential predators, survival might depend on switching from conspicuous courtship displays to seeking shelter or fleeing predators. This type of rapid shift in behavioral state requires neuroendocrine mechanisms that can rapidly and selectively suppress specific behaviors. In *T. granulosa*, three types of chemical messengers have been shown to inhibit amplectic-clasping behaviors—corticosterone (Moore and Miller, 1984), GABA (Boyd and Moore, 1990b), and kappa opioid receptor agonists (Deviche and Moore, 1987).

In male *T. granulosa*, amplectic-clasping behaviors can be suppressed rapidly by corticosterone or by exposing males to conditions (stressors) that stimulate corticosterone secretion (Moore and Miller, 1984; Moore and Zoeller, 1985). The inhibitory effect of corticosterone on amplexus

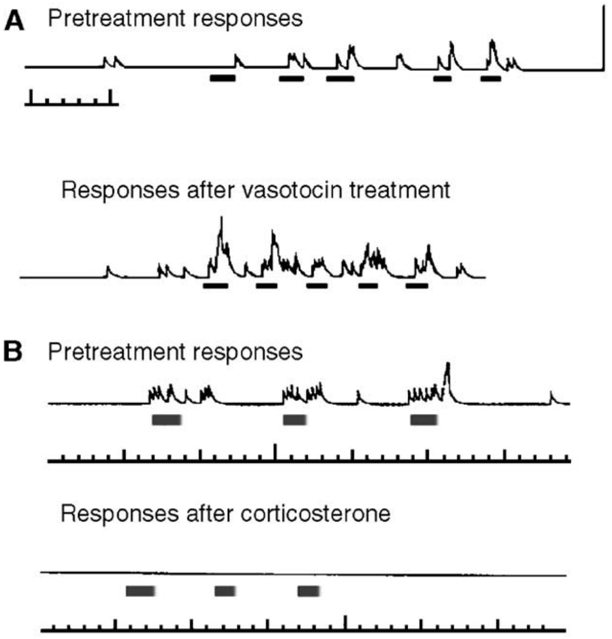

Fig. 3. Responses by medullary neurons (integrated unit firing) to clasp-triggering tactile stimulation (solid bars) before and after hormone treatment to male *T. granulosa*. Panel A shows that vasotocin treatment can enhance neuronal responses to somatosensory stimulation (redrawn from Rose et al., 1995). Panel B shows that corticosterone treatment can suppress neuronal responses to somatosensory stimulation (redrawn from Rose et al., 1998).

is very robust and occurs rapidly, within a time frame of a few minutes following corticosterone injection (Orchinik et al., 1991). Corticosterone administration also rapidly suppresses the activity of specific medullary neurons associated with clasp-triggering tactile stimulation (Rose et al., 1998; Rose and Moore, 1999; Rose et al., 1993a,b) (Fig. 3B). These responses to corticosterone are too rapid to be working through traditional genomic mechanisms and, instead, work through non-genomic mechanisms with a novel membrane corticosteroid receptor (Orchinik et al., 1991; Moore and Evans, 1999). Ligand-binding assays revealed that the membrane-associated corticosterone receptor (mCR) occurs in *T. granulosa* brain tissue and that it is pharmacologically distinguishable from intracellular glucocorticoid (iGR) and mineralocorticoid (iMR) receptors. Similarly, in *Ambystoma tigrinum* the mCR in the neuronal membranes is pharmacologically distinguishable from ^{3}H-CORT-binding sites in plasma (steroid-hormone-binding globulins) and cytosolic fractions (iGR) (Orchinik et al., 2000). Other studies show that this mCR fits the model for being in the G-protein-coupled receptor family (Orchinik et al., 1992; Evans et al., 2000a). Furthermore, because there is concordance between the potencies of corticosteroids to suppress amplectic clasping behavior and the potencies of the same corticosteroids to bind to compete for ^{3}H-CORT-binding sites, the mCR apparently is the receptor that inhibits amplectic-clasping behaviors (Orchinik et al., 1991). The exact molecular structure of this mCR has not yet been identified, although it contains characteristics reminiscent of kappa opioid-like receptors (Evans et al., 2000b).

Non-clasping behaviors in caudate amphibians

Control of non-clasping reproductive behaviors by hormones

Courtship behaviors in male *Cynops* and *Triturus* do not include amplectic clasping, and instead males attract sexually active females with pheromones and use blocking and tail-vibration behaviors during sexual interactions. In *Taricha* and other species, the seasonal onset of reproductive behaviors occurs when testicular steroids are elevated. This generalization holds for many urodeles, including species not in Salamandridae—*Ambystoma opacum*, *A. tigrinum*, and *Hynobius nigrescens* (Hasumi et al., 1993; Houck et al., 1996). In male *C. pyrrhogaster*, plasma T concentrations peak in February near the onset of the breeding season and then decline to minimum levels by April. Plasma DHT concentrations, in contrast, fluctuate seasonally with peaks occurring in May, February, and September (Imai et al., 1985; Tanaka and Takikawa, 1983). Male *Triturus* have measurable levels of testosterone, DHT, progesterone, and 17β-estradiol in plasma, and as the breeding season progresses plasma concentrations of testosterone decline and 17β-estradiol rise (Gobbetti et al., 1991). In *T. carnifex* and *C. pyrrhogaster*, surgical removal of testes reduces androgen levels and male courtship behaviors; whereas androgen implants (especially testosterone) in castrated males maintain male reproductive behaviors (Andreoletti et al., 1983; Malacarne and Giacoma, 1980; Toyoda et al., 1993).

When these males perform courtship behaviors, testosterone concentrations decrease and estradiol concentrations increase (Zerani et al., 1992). To explain the declining testosterone levels, Gobbetti et al. (1991) propose that as the breeding season progresses, plasma prostaglandin F2 alpha concentrations increase and induce changes in aromatase activity that favor the conversion of testosterone to 17β-estradiol. In *Plethodon jordani*, high levels of plasma testosterone concentrations coincide with the season when courtship and mating occur (Fall). In another Plethodon, *Desmognathus ochrophaeus*, both testosterone and DHT concentrations are elevated during the fall and spring breeding seasons (Woodley, 1994). These studies demonstrate that male urodeles have detectable levels of the major gonadal steroids (testosterone, DHT, 17β-estradiol, and progesterone). The consistent feature in the steroid profiles is the peak in plasma testosterone levels near the onset of the breeding season.

Prolactin is also important for the expression of androgen-dependent courtship behaviors in newts (Kikuyama et al., 2000). Blocking PRL secretion with ergocryptine injections (Giorgio et al., 1982) or blocking endogenous PRL activity with anti-PRL serum (Toyoda et al., 1996) can suppress courtship behaviors in sexually active newts. Conversely, courtship behaviors in sexually inactive males can be induced by PRL administration that is combined with gonadotropin injections in intact males or androgen implants in castrated males (Toyoda et al., 1993). Plasma PRL concentrations reach peak levels at the onset of the breeding season (Mosconi et al., 1994; Toyoda et al., 1996), adding further evidence that PRL plays an important role as an activator of male courtship behaviors in *Cynops* and *Triturus*. Comparable studies have not been reported for other urodeles, including *Taricha*.

Pheromones are used by certain salamanders as olfactory sensory cues for species recognition, identification and attraction of prospective mates, social interactions, and induction of female sexual receptivity (Cedrini and Fasolo, 1970; Malacarne and Vellano, 1982; Toyoda and Kikuyama, 2000; Toyoda et al., 1994; Park and Propper, 2001; Thompson et al., 1999; Rollmann et al., 1999). Research with caudate amphibians helps to explain how hormones control behaviors by controlling the production of specific pheromones. Female-attracting pheromones, named sodefrin and silefrin, have been identified and studied in *C. pyrrhogaster* and *Cynops ensicauda* (Kikuyama et al., 1995; Toyoda et al., 1994; Yamamoto et al., 2000). Vasotocin has been shown to enhance the secretion of sodefrin, the pheromone produced by male *C. pyrrhogaster* (Kikuyama et al., 2001). In addition, PRL and testosterone act synergistically to stimulate the synthesis of sodefrin (Toyoda et al., 1994; Yamamoto et al., 1996; Iwata et al., 2000b). Consistent with the above studies, plasma levels of both PRL and testosterone are elevated in sexually active male newts during the breeding season (Imai et al., 1985; Tanaka and Takikawa, 1983). Thus, there is strong evidence that the production of female-attracting pheromone by male newts is under the control of PRL and testicular androgens.

There is evidence that vasotocin is involved in enhancing male courtship behaviors in *C. pyrrhogaster* as well (Iwata et al., 2000b). Exogenous vasotocin administration into sexually active males increases the incidence of tail-vibration behaviors and the production of spermatophores. Furthermore, injections of vasotocin antagonists reduce the incidence of tail-vibration behaviors in *C. pyrrhogaster* (Iwata et al., 2000b). Interestingly, this means that vasotocin enhances courtship behaviors in two species with very different courtship behaviors—both amplectic clasping behaviors and tail-vibration behaviors. Perhaps, in *C. pyrrhogaster*, vasotocin increases the incidence of courtship by enhancing the responsiveness of males to female sexual pheromones, as is the case in *T. granulosa* (Thompson and Moore, 2000).

Suppression of non-clasping courtship behaviors

Our review of literature could find no experiments that investigated the effects of acute stress or corticosterone administration on courtship behaviors in any urodele other than *T. granulosa*. In *T. carnifex*, plasma corticosterone concentrations show a seasonal peak at the onset of breeding, and in sexually active males plasma corticosterone levels appear to increase during the performance of courtship behaviors (Zerani and Gobbetti, 1993). In *A. opacum*, plasma corticosterone concentrations are higher during the breeding season, but do not appear to increase in males performing courtship behaviors (Houck et al., 1996). An explanation for the apparent differences in behavioral responses to corticosterone among urodeles is that in *T. granulosa* corticosterone exerts its action specifically on amplectic behaviors and that, even in *T. granulosa*, corticosterone suppresses amplectic behaviors in a context-specific manner (Coddington and Moore, 2003).

Summary

The above review focuses exclusively on research into the hormonal control of behaviors in amphibians that was performed prior to the year 2000. Findings from this amphibian research reveal that frogs, toads, and salamanders use the same repertoire of hormones and endocrine mechanisms to modulate social behaviors as have been found in other vertebrate taxa. This concordance in control mechanisms among vertebrates shows that, at least for early-evolved behaviors (as in sex and stress behaviors), the underlying hormonal control mechanisms are highly conserved. Amphibian models revealed for the first time specific details about these control mechanisms and provided the original insights that stimulated research in other vertebrates. Examples of seminal contributions by amphibian research to the field of behavioral neuroendocrinology include the following: that vasotocin-like peptides can function as potent modulators of social behaviors (Diakow, 1978); that androgens and estrogens affect brain functions and behaviors by acting on neurons in sensory, central, and motor pathways (Kelley, 1980); that sex steroid hormones affect social behaviors, in part, by acting on vasotocin-like peptide systems (Moore and Zoeller, 1979); that during embryonic develop GnRH neurons migrate from the olfactory placode to anterior hypothalamic preoptic areas (Muske and Moore, 1988); and that corticosterone acts during acute stress to suppress reproductive behaviors (Moore and Miller, 1984) and does so by using non-genomic mechanisms and membrane-associated receptors (Orchinik et al., 1991).

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