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Minireview

Sculpting reproductive circuits: Relationships among hormones, morphology and behavior in anole lizards

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ABSTRACT

Morphology parallels function on a variety of levels in reproductive circuits in anole lizards, as in many vertebrate groups. For example, across species within the anole genus the muscle fibers regulating extension of a throat fan used in courtship are larger in males than females. Endocrine factors controlling behavior and morphology have been studied in detail in one species, the green anole (*Anolis carolinensis*). This review briefly describes the results that have been obtained and highlights key areas for future investigation that will provide insights on mechanisms from a comparative perspective.

1. Introduction

Relationships between structure and function have long been investigated across diverse areas of biology. Some of the most intriguing examples exist in the field of reproduction. Specific regions of the brain and spinal cord, as well as particular muscles associated with sexual behaviors, are often enlarged in animals that display sexual behaviors more frequently. These types of parallels between morphology and behavior exist at multiple levels, including sex differences that develop permanently during ontogeny and plasticity that occurs across breeding seasons in adulthood.

Structures regulating male courtship behaviors are often larger in males than females. For example, species of frogs, fish and songbirds all produce vocalizations to attract females, and in each case the muscles and motoneurons are larger in males compared to females (reviewed in [45]). Areas of the forebrain involved in the learning and production of birdsong are also enhanced in males [47]; the neurons in these areas are increased in size and number.

These types of sex differences in both structure and function are commonly regulated by steroid hormones. During a critical period in development, testosterone (T) can permanently masculinize components of the nervous system and muscles, as well as the capacity to display adult sexual behaviors. This process is referred to as "organization". In adulthood, the same hormone typically acts on these structures to permit or facilitate the production of specific masculine behaviors, which is known as "activation" [2]. In many cases, it is not just the behaviors that are affected, but also morphology. Muscle fibers and motoneurons associated with courtship and copulation grow with seasonal increases in T (see [48] and references therein). In parallel, forebrain areas regulating the production of song can grow in some species via the incorporation of new neurons on a seasonal basis; the survival of these cells is modulated by T as well as singing itself [28,41].

These diverse models have provided a wealth of information regarding relationships between anatomy and behavior, as well as the endocrine and in some cases molecular mechanisms regulating both structure and function within species. However, it has been challenging to draw conclusions about mechanisms on a broad scale. It has also been difficult to evaluate their evolution. At least two main factors contribute to these issues. First, courtship and copulatory systems have largely been investigated in different vertebrate groups – the former in fish, frogs and birds, and the latter primarily in mammals. Second, even within courtship systems, the structures are diverse. Many involve the generation and perception of acoustic cues, but the motor systems and end-organs differ dramatically. For example, frogs generate sounds via the larynx, birds through the syrinx, and some of the fish most thoroughly investigated (plainfin midshipman; *Porichthys notatus*) use their swim bladders for these signals.

2. Anole lizards

Anoles offer some advantages over these other model systems. A long history of research into the hormones, brain and behavior exists for one species, the green anole (*Anolis carolinensis*), and a substantial amount of data is also available for the brown anole (*A. sagrei*). These studies indicate that the hormonal regulation of behavior appears quite similar in these two species of anoles

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(reviewed in [46]). The genome of the green anole has recently been sequenced, which greatly facilitates investigations at the molecular level [1]. Two features, however, provide unique power for the investigation of mechanisms regulating structure and function. First, three sexually dimorphic systems exist within the same individuals – portions of the limbic forebrain, which control higher level or more motivational aspects of sexual behavior, and both courtship and copulatory neuromuscular systems, all of which lend themselves to investigations in the field and laboratory. Second, more than 350 species of anole lizards span the Southeastern US, Caribbean islands and Central and South America [29]. Information on the behavioral ecology and phylogenetic history of many of these is accessible. And, while limited data on the neural and muscular structures regulating courtship and copulation are currently available, it is clear that species across the genus exhibit beautiful variation in the degree of sexual dimorphism in morphology on a gross level. Anole lizards therefore represent a terrific opportunity for more detailed investigations from an evolutionary perspective.

These animals exhibit stereotypical sequences of behaviors, which have been studied in the most detail in *A. carolinensis*. The displays are remarkably similar in the field and laboratory, making this species particularly useful for the investigation of relatively natural functions in a controlled setting [46]. During the breeding season (which extends from approximately April through July for green anoles), males are quite aggressive with each other and defend territories. Females hold smaller, satellite territories, surrounding those of males. In both aggressive (with another male) and courtship (with a female) contexts, male green anoles extend a red throat fan (dewlap) in conjunction with a series of head bobs (Fig. 1). The animal's posture is different in these two situations, but dewlap extension is a feature common to both aspects of the reproductive process – establishment and defense of a territory and attracting females. Females green anoles do extend their dewlaps in aggressive encounters, but do so far less frequently than males. Relative size and degree of use of the dewlap varies tremendously across anole species (see below), and the coloration differs in stunning ways across species. However, the origins and evolution of these visual patterns are not clear [36].

Once a male anole has successfully attracted a female, he will mount her back, grip the skin of her neck with his teeth, and maneuver his tail under hers to appose their cloacas. The male will then insert one of two bilateral, independently controlled hemipenises (Fig. 2). Females do not have an obvious receptive posture, other than a slight neck bend which facilitates the male's grip. However, they will not allow the male to engage in these behaviors under non-receptive conditions.

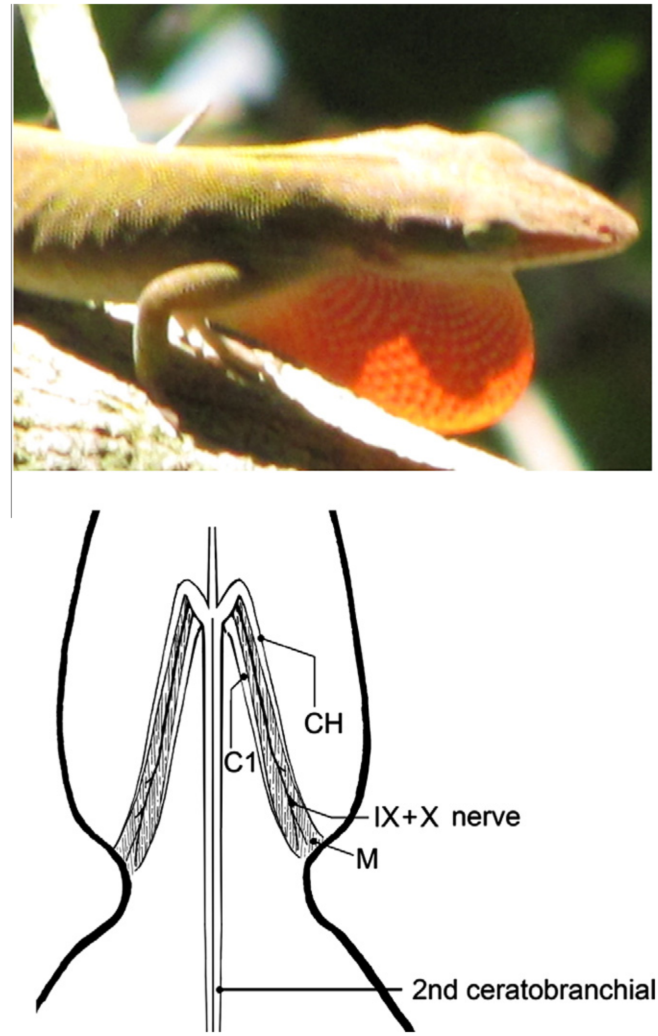

Fig. 1. Anole courtship behavior. The top panel shows a male extending his dewlap on a bright sunny day near St. Augustine, FL (photographed by a former graduate student in my lab, Rachel Cohen). The bottom panel diagrams the cartilage components (C1 = first ceratobranchial; CH = ceratohyal) and ceratohyoid muscle (M) required for the display. The combined IX + X cranial nerve carries axons from the motoneurons innervating this muscle. The drawing is reprinted with permission from a portion of a figure in [45].

2.1. Relationships between structure and function

2.1.1. Green anoles: Forebrain

At least three regions of the forebrain are involved in the display of reproductive behavior in lizards. Lesion and hormone implant studies have documented the importance of the preoptic area (POA) and ventromedial portion of the amygdala (AMY) in the display of sexual behaviors by male green anoles [15,17,33]. In females of this species, damage to the basal hypothalamus inhibits receptivity [16]. In other lizards, lesions of the ventromedial hypothalamus (VMH) specifically prevent the display of these female sexual behaviors [25]. Our research has focused on each of these three areas – the POA, AMY and VMH.

The basic morphology of these regions (defined with a Nissl stain) is enhanced in a variety of ways in unmanipulated animals that are more likely to display sexual behaviors. For example, the POA is larger in volume in males compared to females, and the POA and VMH are larger in the breeding than non-breeding season across the two sexes [4]. Cell bodies in the POA and AMY are larger in the breeding season as well [39]. One of the most direct parallels between morphology and function comes from the AMY in which the average size of cell bodies correlates positively with the rate at which individual males extend their dewlaps [34].

2.1.2. Green anoles: Dewlap neuromuscular system

Dewlap extension is controlled by a pair of muscles in the throat, the ceratohyoids. These run between bilateral cartilages attached to a long paired set of cartilage at the midline (2nd ceratobranchial) that lies under the skin of the throat and chest. The muscles are innervated by motoneurons in the caudal brainstem, in nucleus ambiguus X (AmbX) and the region containing nucleus ambiguus IX and the ventral motor nucleus of the facial nerve (AmbIX/VIImv). When these neurons provide a signal for the muscles to contract, the system of cartilages acts like a lever, causing the midline 2nd ceratobranchials to bow out and reveal the colored skin of the dewlap (reviewed in [45,46]; Fig. 1).

Male biased sex differences exist at a variety of levels in this system. Extended dewlap size is substantially larger in males,