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Review

Neural and hormonal mechanisms of reproductive-related arousal in fishes

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ABSTRACT

The major classes of chemicals and brain pathways involved in sexual arousal in mammals are well studied and are thought to be of an ancient, evolutionarily conserved origin. Here we discuss what is known of these neurochemicals and brain circuits in fishes, the oldest and most species-rich group of vertebrates from which tetrapods arose over 350 million years ago. Highlighted are case studies in vocal species where well-delineated sensory and motor pathways underlying reproductive-related behaviors illustrate the diversity and evolution of brain mechanisms driving sexual motivation between (and within) sexes. Also discussed are evolutionary insights from the neurobiology and reproductive behavior of elasmobranch fishes, the most ancient lineage of jawed vertebrates, which are remarkably similar in their reproductive biology to terrestrial mammals.

Contents

Introduction: Evolutionarily conserved neurochemicals and pathways of sexual arousal . . . 616
What is known of the neural circuitry of “sexual arousal” in fishes? . . . 617
  Connectivity, neurochemistry and function of the POA/anterior hypothalamus . . . 617
  GnRH in the terminal nerve ganglion . . . 618
  Olfactory pathways and sexual behavior . . . 619
  Neurochemical arousal pathways in the “paracore” . . . 620
  Steroid hormone receptors in circuits involved in reproductive behavior . . . 621
Brain arousal and reproductive behavior in vocal fishes . . . 623
Neural substrates for sexual arousal and reproductive behavior in elasmobranch fishes . . . 623
Concluding comments . . . 625
Acknowledgments . . . 625
References . . . 625

Introduction: Evolutionarily conserved neurochemicals and pathways of sexual arousal

Mong et al. (2003) comment that “high arousal is reflected by high sensory responsiveness, high motor activity, and high emotional reactivity.” Ultimately, changes in levels of arousal of any one sensory or motor system depend on some form of modulatory input originating from what Nieuwenhuys et al. (1988) define as the neurochemically rich “core” and “paracore” that together form a neuroendocrine “axis” in the brain. Core regions, like the preoptic area (POA), lie adjacent to the brain's ventricular spaces and contain neuronal populations that synthesize a wide range of neuropeptides, concentrate androgens and estrogens, and are broadly implicated in the control of homeostatic and social behaviors. A laterally positioned “paracore” region at brainstem levels is especially rich in monoamines (serotonin and catecholamines) and interconnected with the core region. These peptidergic-containing nuclei and their fiber tracts can be designated as a caudally extended limbic system that includes the

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midbrain periaqueductal gray, the nucleus of the solitary tract and area postrema in the caudal medulla, and the central gray of the spinal cord (Nieuwenhuys et al., 1988). The core–paracore regions also include the essential nodes of a proposed "social behavior network" for vertebrates (Goodson, 2005; Newman, 1999). In sum, this highly conserved area of the vertebrate brain suggests its key role in survival by modulating brain arousal to affect behavior in an adaptive fashion, including daily and seasonal extremes in activity.

The motivation to reproduce, i.e., sexual arousal, activates physiological processes that can eventually lead to sexual behavior, inclusive of hormonal, genetic and neural-dependent mechanisms (Schober and Pfaff, 2007). The major premise of this article is not to re-review activational effects of steroid hormones or peptides on reproductive behavior in fishes (e.g., Bass and Forlano, 2008; Godwin, 2010; Oliveira and Gonçalves, 2008), but rather to highlight examples where the neurochemically-rich core of the central nervous system interacts with specific sensory and motor systems underlying reproductively motivated behaviors. We focus our discussion on two groups of fishes, teleosts and elasmobranchs. Jawed vertebrates include bony and cartilaginous fishes (Fig. 1) (Nelson, 2006). Bony fishes are divided into two major clades, Actinopterygii and Sarcopterygii. The majority of actinopterygians are teleosts, the largest group of living vertebrates with at least 30,000 species, and the principal focus of this review. Sarcopterygians include lungfish (Dipnoi), coelacanths (Coelacanthimorpha, *Latimeria*), and tetrapods (we are all fishes!) (Fig. 1). The more basal cartilaginous fishes (Chondrichthyes) include holocephalans (chimaeras/ ratfish) and elasmobranchs (sharks, skates and rays).

What is known of the neural circuitry of "sexual arousal" in fishes?

Connectivity, neurochemistry and function of the POA/anterior hypothalamus

The POA and anterior hypothalamus, neurochemical "core" areas essential for the control of reproductive physiology and hence behavior in all vertebrates, show a highly conserved pattern of anatomical organization (Butler and Hodos, 2005; Meek and Nieuwenhuys, 1998). The POA and anterior hypothalamus can be viewed as one functional unit, the POA, because of their shared developmental origin (Puelles, 2001) and obvious homologies between neuropeptide-containing cell groups in the POA of teleosts (e.g., see Goodson et al., 2003) and the anterior hypothalamus of tetrapods (e.g., the paraventricular and supraoptic nuclei) (see Bass and Forlano, 2008 for further discussion).

The role of the POA in brain and behavioral arousal is exemplified by its role as a sensorimotor integration center. Its motor outputs include connections with both the somatic and visceral motor systems (Fig. 2). The POA's effect on homeostatic function is enhanced by way of central visceromotor innervation of autonomic ganglia that project to either glands (including the adrenal medulla, a modified autonomic ganglion) or the visceral smooth muscle of multiple organ systems. The POA's pervasive influence on neuroendocrine function is achieved, in part, via its control over the release of several peptides from the anterior pituitary and of arginine vasotocin and isotocin (AVT/IT; arginine vasopression/oxytocin in mammals) from the posterior pituitary. Unlike the majority of vertebrates that have a blood portal system linking POA gonadotropin-releasing hormone (GnRH) neurons and the anterior pituitary, the GnRH POA neurons in teleosts directly innervate the pituitary (Peter and Fryer, 1983). This direct pathway may be a neuro-hormonal adaptation among teleosts allowing for rapid shifts in reproductive function (see Bass and Forlano, 2008 for more discussion). For instance, in the cichlid fish *Astatotilapia burtoni*, socially dominant territorial males are the only ones that reproduce. When given the opportunity to become dominant, a subordinate male will rapidly (within minutes) change its behavior. Within 30 minutes, neurons show an upregulation of the immediate early gene *egr*-1 in POA areas of high GnRH-1 expression (Burmeister et al., 2005). The physiological properties of GnRH neurons are also significantly different between territorial males and non-territorial males, which likely translates into less gonadotropin release in non-territorial males (Greenwood and Fernald, 2004). The reader is referred to Bass and Grober (2009) for a recent discussion of the diversity in organization of the POA in relation to the remarkable range of reproductive plasticity exhibited by teleost fishes.

The presence of the nonapeptide AVT/AVP in magnocellular and parvocellular neurons of the POA in all vertebrates exemplifies the conserved evolution of the neurochemical core of the brain over the last 500 million years or more. Furthermore, in all jawed vertebrates, neuropeptide-containing neurons in the POA project to similar extrahypothalamic brain regions including the ventral telencephalon, midbrain tegmentum, periaqueductal gray, and viscerosensory areas of the medulla (Goodson and Bass, 2001; Saito et al., 2004). AVT/AVP is well documented in its role in mediating vertebrate social behavior (Goodson and Bass, 2001), including AVT manipulations affecting male reproductive displays in teleosts (Carneiro et al., 2003; Salek et al., 2002; Santangelo and Bass, 2010; Semsar and Godwin, 2003; Semsar et al., 2001). In mammals, male penile erection is regulated by androgenic stimulation of oxytocin neurons in the paraventricular hypothalamus (PVN) (Argiolas and Melis, 2005). The magnocellular nucleus of the POA in teleosts is thought to be the PVN homologue, in part due to its abundance of AVT/IT neurons (Gilchriest et al., 2000; Kapsimali et al., 2001; see Forlano and Cone, 2007 for further discussion). Like mammals, these large neuroendocrine neurons also project to the spinal cord in teleosts (Demski and Sloan, 1985;

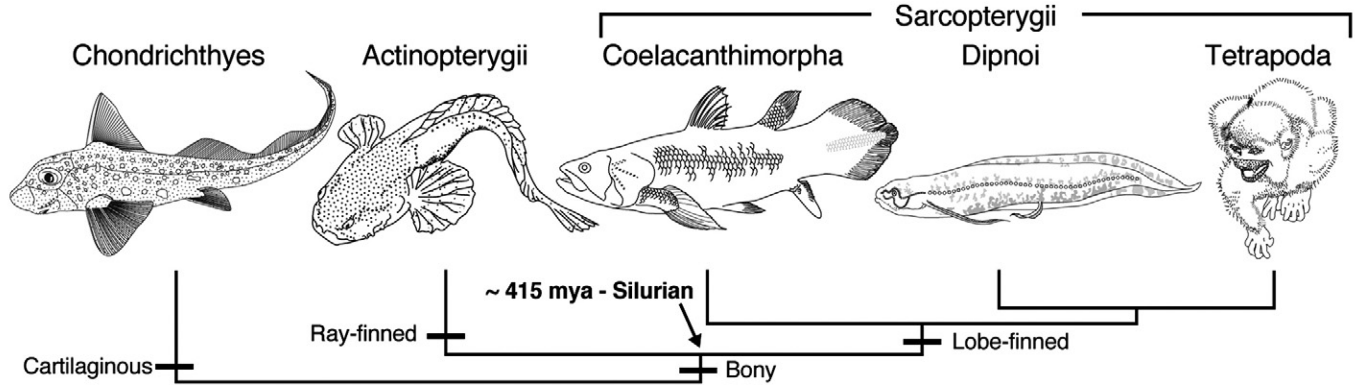

Fig. 1. Cladogram of living jawed vertebrates. Adapted from Ma et al. (2010).