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Fish sex: why so diverse?

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Introduction

In most animal species, males and females behave differently, especially when it comes to sex and related social behaviors. These behaviors evolved to ensure successful reproduction and typically include some genetically pre-programmed displays. There are ~25,000 known species of fishes, by far the largest group of vertebrates, and they express a remarkable variety of adaptive responses to aquatic habitats with associated ecological constraints [1]. Moreover, teleosts have evolved in a relatively short time (~200 My) [2] producing virtually every reproductive option open to vertebrates: they bear live young, brood offspring in their mouths or body cavities, lay eggs (sometimes even out of water) or simply release their gametes into the plankton. In addition, mating/brood-care systems range from monogamous bi-parental to polygamous non-parental. In some species, females can reproduce parthenogenetically, males may become pregnant, and fish of both genders can change sex [3,4]. This brief summary of the range of fish reproductive behaviors highlights why they offer so much as reproductive systems for analysis.

Here we address the following questions: 1) What is known about the physiological mechanisms underlying sex determination and sex-specific behaviors in teleost fish species? 2) How do different sensory inputs and mating systems interact to influence reproductive function? 3) How do the special cases of alternative reproductive tactics, sex-role reversal, and sex change in fish give insight into the vertebrate sexual brain? 4) How can genomic information and epigenetic change influence brain areas controlling reproduction?

Sex determination

Some sex-determining mechanisms have been conserved over vast stretches of evolutionary time. For example, in

birds and mammals, all extant species share a ZW system of female heterogamety (e.g., production of 2 kinds of gametes) and an XY system of male heterogamety. In both these cases, the different sexes are always represented by two different individuals (e.g., gonochorism, [1]). By contrast, fish show a wide variety of sex determination systems, some via sex-determining chromosomes, others via autosomal genes and still others via environmental or social signals [4–6]. Numerous studies have shown how morphological specialization and life-history differences between fish species translate directly into behavioral differentiation between the sexes. More subtle behavioral differences may arise as a consequence of the different reproductive roles taken by males and females. In gonochoristic fish species, all possible forms of genetic sex determination have been observed from male and female heterogamety with or without the influence of autosomal genes, to more complicated systems involving several loci but without sex chromosomes or with several pairs of sex chromosomes [7]. For example, in the striated spined loach (*Cobitis taenia*) sex is determined through multiple sex chromosomes where females have $X_1X_1X_2X_2$ while males have X_1X_2Y sex chromosomes [8].

In many fish species temperature and/or pH of the hatching water determines sex. In a mouthbrooding cichlid, *Oreochromis niloticus*, for example, Baroiller *et al.* [9] showed that housing mouthbrooding females in higher temperatures increased the male proportion in their brood from 33% to 81%. Phenotypic sex can also be fully reversed by hormone treatment in female Chinook salmon (*Oncorhynchus tshawytscha*) where a brief treatment with an aromatase (enzyme that converts T to E_2) inhibitor during sex differentiation causes chromosomally female animals to develop as normal males [10]. Nonetheless, the core of the vertebrate sex determination/differentiation cascade is conserved in fishes [11,12,1]. *Dmrt1*, named for a common DM domain is considered to be involved in sex determination and/or sex differentiation and its expression is central to the development of the male tetrapod phenotype. This gene has a similar role in sex determination in both hermaphroditic and gonochoristic fish [13–17]. In the medaka (*Oryzias latipes*) sex differentiation is chromosomal (male heterogamy XX-XY) and recently, functional and expression analyses have shown that *Dmrt1* is the master gene for male sex determination [18]. However, in many fish species, once sex has been determined, reproductive ability can be regulated through social cues (e.g., [19]).

How do social and environmental signals regulate reproduction? Little is known about the actual pathways

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through which social signals act, but the final common output pathway requires hypothalamic gonadotropin-releasing hormone (GnRH1) signaling. The GnRH1-containing neurons are known to have a variety of inputs that are sexually dimorphic, change with reproductive status, and include many well-known neurotransmitters as well as other signaling molecules [20]. Ultimately GnRH1 expression depends on the integration of this wide variety of input signals and regulates reproduction.

Sensory inputs regulating reproduction

Sensing potential mates in water offers special challenges. Underwater optics and lighting are limiting, chemical signals can diffuse quickly, and other modalities such as weak electrical signaling and sound have distance limitations. Nonetheless, teleost fish have adapted to nearly every kind of water habitat imaginable, including very cold (-17°C) and very hot (38°C) water, low pressure at the water's surface and enormous pressures at 9000 m in depth, and in currents as different as a stagnant swamp to raging torrents. This diversity of habitats has result in a spectacular range of adaptations in teleost vision, particular in those species where seeing is the most important sense.

Vision

Among teleosts, cichlid fish species have been well studied and, in particular, for *Astatotilapia burtoni*, a cichlid fish endemic to Lake Tanganyika in the African Rift Valley, the visual system is well understood. *A. burtoni* has both rods (500 nm) and cone vision with cells tuned to λ_{max} values of 454 nm, 523 nm, and 562 nm [(for review see 21)]. In this species, visual cues play a role in female mate choice [22] and in male assessment of dominance and fighting ability [23,24]. When a non-dominant male sees a larger more dominant competitor, he stops displaying and courting females, turns off his body coloration, and acts submissively towards the more dominant individual [24]. Visual information is processed by the standard vertebrate pathway: From the eye to the nuclei of the accessory optic tract, the dorsal thalamus, the ventral thalamus, the pretectal region, and the optic tectum [25]. But exactly how and where reproductive information is collected and processed is not known. No sensory system operates in isolation, so olfactory, mechanosensory, and auditory pathways collaborate to provide information about reproduction.

Olfaction, mechanosensation, electroreception, and audition

The most ancient of the sensory systems (>500 My) are chemosensation, olfaction, and gustation, which are the major sensory pathways for detection and identification of chemical stimuli in the environment [26]. In teleost fish, paired olfactory organs are unlike terrestrial vertebrates since there is no direct contact between the olfactory and respiratory systems [26]. In crucian carp (*Carassius car-*

assius) the olfactory system detects preovulatory pheromones reflected in key amino acids in the water [27,28]. Treatment with preovulatory pheromones stimulates testicular hormone production in goldfish that in turn evokes increased milt production and courtship behaviors towards females [29]. Similar findings have been shown in the Rose bitterling (*Rhodeus ocellatus ocellatus*) [30], common carp (*Cyprinu carpio*) [29], and crucian carp (*C. carassius*) [31].

The fish mechanosensory system or lateral line organ, present in all fishes and aquatic amphibians [32–34], detects near field water movements relative to the skin surface [35]. Some fish even use self-induced water motions to detect stationary objects with the aid of the lateral line. This ability is well developed in the blind Mexican cavefish (*Astyanax mexicanus*), which when confronted with a new object, accelerates and then glides past it in close proximity. Environmental information is collected by analyzing distortions of the self-induced flow field using the lateral line [36,37]. In the hime salmon (*Oncorhynchus nerka*), sexual behavior depends on the use of body vibration and electromyographic activity of the trunk muscles of both males and females. These vibrations act as timing cues not only to synchronize the chain reaction of sexual behaviors but also to synchronize gamete release [38]. When using the lateral line, displacement of hair cells by viscous drag due to water movements causes modulation of the spontaneous primary afferent discharges sent to the mechanosensory processing centers in the hindbrain [39,40].

Electric fish generate weak electric organ discharges from a muscle-derived electric organ and use these fields for electrolocation and communication. Use of weak electrical signals has evolved twice, in the mormyriiforms and the gymnotiforms [41]. In both of these groups of fishes, electric fields are used for sophisticated communication between individuals and the detection and identification of nearby objects [42]. The electrical organs are distributed over the entire body surface of fish and can be classified into two major classes: tuberous organs, specialized to high-frequency self-generated electrical fields and ampullary organs, specialized for the detection from external sources, like those generated from other animals [43]. The information gathered by these specialized organs is processed in the posterior lateral line lobe that projects to multiple brain areas [44].

Some teleost fish species generate acoustic signals for vocal communication. Carp (*Cyprinus carpio*), cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*) use sound and can readily discriminate its amplitude and direction. The Hawaiian sergeant fish (*Abudefduf abdominalis*) produces sounds at close distances to the intended receiver with different pulse characteristics that are associated with aggression, nest preparation, and courtship

behaviors [45]. The plainfin midshipman (*Porichthys notatus*), a territorial fish uses vocalizations to court females and defend a territory against conspecific intruders. There is a direct relationship between rhythmic, patterned output of a brainstem pacemaker circuit and the physical attributes of species- and sex-specific vocalizations [46].

How did these sensory systems contribute to the evolution of mating?

Mating systems

Understanding the evolution of neural control of reproduction requires comparing model organisms with a variety of reproductive systems. Since teleost fish have the widest range of reproductive behaviors and mating systems among vertebrates [(c.f., 47)], these species offer unique opportunities to study both the evolution and the function of the variation in neural pathways involved in mating systems. In addition to primary reproductive strategies, alternative reproductive tactics abound, typically in species where males compete for access to mating territories to gain access to females. Smaller males with a reduced competitive ability may use one of multiple alternative tactics to achieve fertilization of part of the clutch [48]. In one cichlid, *Telmatochromis vittatus*, 4 alternative reproductive tactics exist [49]. Adult males can be: 1) territorial and defend a nest; 2) 'pirates' that displace territorial males; 3) satellite males, submissive to territorial and pirate males; and 4) sneaker males, who parasitize spawnings by releasing sperm when the territorial or pirate is absent [50]. In some species, younger males adopt a sneaker strategy until they grow big enough to become territorial (e.g., *Pomatochistus microps*) [51]. Interestingly, though, sneaker and territorial tactics may produce equivalent fitness (*Lepomis*, *Oncorhynchus*) [52]. Despite having mature gonads, males using alternative reproductive tactics do not show secondary sex characters typical of the dominant males of the species and the effects of high levels of circulating androgens are somehow differentially suppressed [53]. It is not known in these morphs how different aspects of male reproductive physiology including control of gonadal maturation, expression of secondary sexual characteristics, and activation of male sexual behavior are suppressed. For example, androgen profiles vary according to male mating tactics and courting males consistently have higher levels of 11KT (a fish-specific androgen) but not of T than non-courting males [(c.f., 54)].

Sex-role reversal occurs when females compete more intensely than males for access to mates, and hence such females have higher potential reproductive rates than males [55]. Male pregnancy in pipefishes and seahorses (*Syngnathidae*) suggests that females compete most intensely for access to males, because males limit female reproduction. Mayer *et al.* [56] measured plasma levels of androgens in three species of pipefish to discover

whether sex-role reversal and male pregnancy was correlated with circulating hormone levels. In pipefish, males had higher levels of 11KT, typical for normal teleosts, while levels of 17 β -estradiol were higher in males than in females, markedly different from that of the typical teleost pattern. Although few studies have looked at the hormonal correlates of sex-role reversal, reversal of sex roles is not typically associated with dramatic endocrinological differences [55].

In addition to the gonochoristic varieties described above, some fish species are sequential hermaphrodites, in which individuals at a stage of their life cycle or social status change sex [57]. There are simultaneous hermaphroditic species as well as parthenogenic species where all individuals reproduce asexually (e.g., Amazon mollie: *Poecilia Formosa*) [48,58,59]. The change of sex in sequential hermaphrodites may be genetically controlled or triggered by external events, such as the loss of a dominant male from a harem or it may be affected by the combination of these two mechanisms [60]. However, most sex changing fish rely on social cues to initiate and orchestrate the development of the dominant phenotype [61], which requires correlated changes in a suite of characters including brain, behavior, hormones, gonads, genitalia, and other secondary sexual characters [62]. In the dramatic case of some wrasse species, removal of a dominant male from his harem produced sex change of the largest female, who assumed male coloration in four days and full gonadal maturation including the production of mature sperm in eight days [63]. The mechanisms of sex change are not understood and typical hormonal interventions (e.g., gonad removal) have no effect [64].

Genomic and epigenetic regulation

Teleost fish have experienced extremely rapid genomic evolution, with notably fast-paced genic and genomic duplication [65,66]. Genome-wide duplications increase the potential for evolutionary flexibility in sex-determining and other sexually dimorphic pathways [67] but the diversity of specific strategies through which this has happened is staggering. The genetic mechanisms underlying development or modification of reproductive systems are due to 1) changes in protein or mRNA concentration and targeting; 2) modification of protein trafficking and/or retention; or 3) post-translational modifications. As shown above, measurements of protein or mRNA level changes have been extensively studied in fish species in relation to sex, sex change, and changes in social system (e.g., AVT, GnRH, serotonin, dopamine, etc.) [20,68]. However, changes in protein processing and post-translational processes have not been analyzed in fish reproduction *in vivo*.

microRNAs (miRNAs) are another possible regulator of reproductive action. These small non-coding RNAs control the stability or translation of mRNA transcripts and

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are a recently discovered mechanism. In multicellular organisms, numerous miRNA genes can act post-transcriptionally to modulate the expression of more than a third of the coding mRNAs [69] and these miRNAs are expressed in adult neurons providing local translational control of plasticity [70,71]. For example, miRNAs are key regulators in the circadian-timing process: miR-219-1 is a clock controlled gene that plays a role in regulating the length of the circadian day, while miR-132 is light inducible and modulates the phase-shifting capacity of light [72].

Another potential avenue for regulation of sex and reproductive behavior is the methylation of coding DNA [73]. DNA methylation occurs in the genomes of a wide array of bacteria, plants, fungi, and animals [74] and the methylation of cytosine bases represents an important epigenetic mark that affects gene expression in diverse taxa [74,75]. DNA methylation in vertebrates typically occurs at cytosine-phosphate-guanine sites (CpG) and is catalyzed by DNA methyltransferase [76]. In honeybees (*Apis mellifera*)

different levels of methylation have been associated with different castes within the hive [77] and Kucharski *et al.* [78] showed that downregulation of a key DNA methyltransferase (Dnmt3) in developing bees resulted in profound changes in developmental trajectories, suggesting that DNA methylation is widespread and may play a crucial role in the unfolding of life-history strategies. In rats, maternal behavior towards pups resulted in stable alterations of DNA methylation and chromatin structure, providing a mechanism for the long-term effects of maternal care on gene expression in offspring [79].

Conclusion

Fish express extremely diverse sex determination systems, mating systems, sensory systems, and reproductive tactics that have evolved multiple times and account for their evolutionary success. The fine-tuning of each of these pathways is unlikely to be genetically determined but shaped by experience, ongoing behavior, the reproductive axis as well as neural and epigenetic changes (Figure 1).

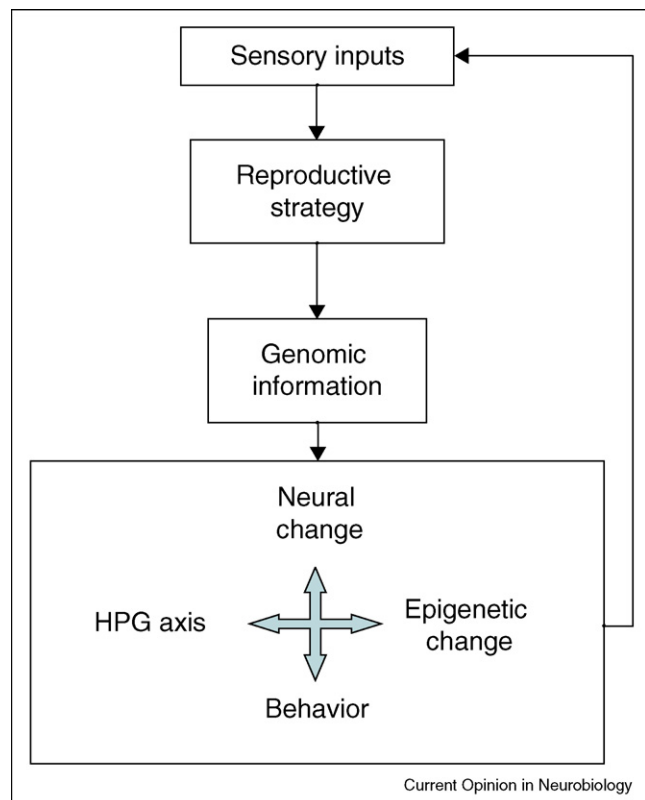
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Figure 1



Theoretical pathway of the interaction between sensory inputs, reproductive strategy, genomic information, the brain, and behavior. The signals received by the sensory system will generate behavioral outputs based on the reproductive strategy of the species as well as the encoded genomic information. Once this signal is passed on, neural change, epigenetic change, the HPG axis, and behavior will change depending on the state of each. The behavioral output will then in turn influence how sensory inputs are interpreted.

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