19 Social Regulation of Reproduction: What Changes and Why?

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Chapter Outline

Glossary

immediate early gene Genes activated rapidly and transiently in response to a wide variety of stimuli.

umwelt The unique perceptual world of each species.

19.1 Introduction

Different animal species experience life somewhat differently because their sensory systems are responsive to unique perceptual worlds and, correspondingly, their motor abilities determine how they can act in that private world. Von Uexküll (1921) first described the perceptual world as the umwelt of a species and since then, scientists have discovered new dimensions of the umwelts for many species. Bats, for example, flying at night, use the echoes from ultrasounds they emit to probe the darkness, forming images from sound reflected off their surroundings. This allows them to function in total darkness via a sensory channel unavailable to most other animals. Bats can also use ultraviolet vision, possibly for nectar foraging (Winter et al., 2003) giving some bat species two unusual windows onto the world. While Von Uexküll intended his umwelt idea in relation to physical stimuli, Lorenz (1932) extended this concept by recognizing that animals also have a social umwelt because signals from other individuals can have important influences on behavior. Lorenz' influential article, 'Companions as factors in the bird's environment', showed that behavioral scientists should include other individuals in the umwelt and, importantly, the overall social context of the behavior. Given that behavior is the ultimate arbiter of animal survival, it is the response of animals during their interactions with others and with their environment that shapes the phenotype. Behavior, in turn, depends on intricate physiological, cellular, and molecular adaptations forged during evolution and modified during development. Ultimate questions about the evolution and control of behavior and especially interactions that sculpt behavior require understanding the causal mechanisms responsible as animals interact with one another, preferably in a natural setting. Yet, the vast majority of experiments are performed on isolated individuals, typically in domesticated species. Clearly, little can be learned about how evolution has shaped social behavior by analyzing individual animals.

## 19.2   Fish Models for the Study of Social Behavior

Fish species have emerged as important models for studies of social behavior and its neural underpinnings due to the many examples of sophisticated behavioral interactions. For example, it has been shown that fish can exploit Machiavellian strategies (e.g., Bshary and Wurth, 2001), cooperate (e.g., Pitcher et al., 1986), learn in a social context (Laland et al., 2003), eavesdrop on interactions among conspecifics to gain social insights (McGregor, 1993), show transitive inference (Grosenick et al., 2007), and generally display a wide range of social activities comparable in some instances with those of primates (e.g., Bshary et al., 2002). Fish have also proven useful for mechanistic studies of the determinants of social behavior. With several fish genomes now sequenced, it has become much easier to trace genetic and neurobiological mechanisms responsible for sophisticated social interactions in fish.

Why might fish social behavior provide general insights about brain mechanisms of social interactions? Stable social systems in any animal species require that individuals behave predictably. What an individual does at any moment in time, however, depends on its status relative to other individuals, its reproductive state, and its recent behavioral interactions. In addition, environmental factors (e.g., predators, prey, or resource competitors) also need to be incorporated into any plan for behavioral action. So, to be successful in a social group, individuals must be aware of the immediate behavior of others and use that information to regulate their own activity. But what exactly does an individual need to know and how do they acquire the knowledge that lets them act appropriately? It is possible that the apparently subtle social interactions can be explained and understood in terms of contingencies. That is, a set of if–then rules with associated probabilities might suffice in many situations for explaining the behavior of animals in social groups. Because it has been argued that species in the fish taxon have demonstrated many, but not all, social skills that arguably led to the evolution of complex brain structures in primates (Bshary, 2002), it is tempting to exploit fish social skills for understanding the neural mechanisms that underlie social behavior and its impact on the brain. This chapter describes results from experiments using the relationship between social dominance and reproduction to understand how social signals regulate the hypothalamic–pituitary–gonadal (HPG) axis

in *Astatotilapia burtoni*. This chapter also explores the range of social requirements for *A. burtoni* to be successful and describes evidence about how social behavior sculpts the brain in ways that depend on the developmental stage, social circumstance, and environmental context.

19.2.1   *A. burtoni* – Natural History

There is a direct relationship between social dominance and reproductive physiology that has been well studied *in Astatotilapia* (formerly *Haplochromis*) *burtoni*. In *A. burtoni*, there are two types of adult males: those with and those without territories (Fernald, 1977). Territorial (T) males are brightly colored, with basic blue or yellow body coloration, a dark black stripe through the eye, a black spot on the tip of the gill cover, and a large red humeral patch just behind it. In contrast, nonterritorial (NT) males are cryptically colored, making them difficult to distinguish from the background and from females that are similarly camouflaged (**Figure 1**). In their natural habitat, the shallow shorepools, and river estuaries of the Lake Tanganyika (Fernald and Hirata, 1977a; Coulter, 1991), *A. burtoni* live in a lek-like social system in which T males vigorously defend contiguous territories (Fernald and Hirata, 1977a,b). Social communication among these fish appears to depend primarily on visual signals (Fernald, 1984; see below).
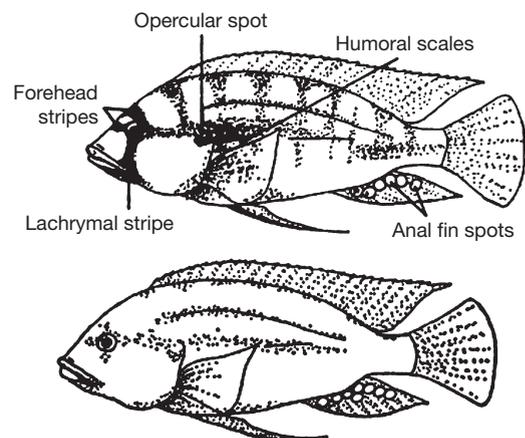
Figure 1 Illustration of the body patterns for typical territorial (top) and nonterritorial (bottom) males. Territorial males have distinct anal fin spots, dark forehead, and lachrymal (eye-bar) stripes and are brightly colored, including orange humeral scales. Nonterritorial males lack the robust markings of their territorial counterparts and are colored to maximize camouflage. The overall body color may be either yellow or blue.

19.2.1.1 Behaviors of territorial males

A. burtoni T males perform 19 distinct behavioral patterns during social interactions (Fernald, 1977). T males dig a pit in their territory, exchange threat displays with neighboring territorial males, chase NT animals from their territories, and solicit and court females. T males display bright coloration patterns, particularly during courtship. A T male will lead a female toward his territory, typically using large movements of his tail; he will court by quivering his opened, brightly colored anal fin in front of the female. When a T male manages to lure a female into his territory, she will normally eat by sifting the substrate in the territory. NT males will mimic female behavior sufficiently well so that the T male allows NTs to enter the territories and feed before their deception is discovered. This NT male behavior occurs because only sites defended as territories contain food, so that NT males need to enter to eat. Normally, however, the NT female impersonator is quickly chased off. If a female responds to male courtship, the T male will lead her to his pit and continue courtship movements. T males swim vigorously in front of the female, quivering their entire body with spread anal fins. If appropriately stimulated, the female will lay her eggs in the pit and collect them in her mouth immediately. After she has deposited several eggs, the male will swim in front of her displaying the egglike spots on his anal fin (ocelli). T males display this fin because the spots may seem to the female like eggs not yet collected (Wickler, 1962). Thus, while attempting to collect the egg-spots, the female ingests milt ejected near them by the male and ensures fertilization. The spawning male may repeatedly interrupt his courtship and mating to chase off intruders into his territory. After several bouts of egg laying and fertilization, the female departs with fertilized eggs that she broods in her mouth for approximately 2 weeks (Fernald, 1984).

Even this abbreviated description of the natural behavior of *A. burtoni* shows the important role visual signals play in mediating social behavior. As is typical for this kind of rapid social interactions, each behavioral act influences the next, both in the individual and in other animals involved in the encounter. What do animals attend to during aggressive social interactions? Using ethological methods, early workers identified several fixed action patterns and key stimuli that mediate social signaling in *A. burtoni*. Specifically, Leong (1969) analyzed the role of the black eyebar by testing how T males responded to *A. burtoni* dummies painted with various configurations of the distinctive body patterns. When the eyebar was presented alone, T males increased their readiness to attack targets while presentation of the orange-red patch of humeral scales alone decreased attack readiness. Subsequent experiments tested the importance of the orientation of the eyebar relative to the body and other visual stimuli (Heiligenberg and Kramer, 1972; Heiligenberg et al., 1972). All the work supported the hypothesis that the black eyebar and the red humeral patch influence the aggressiveness of T males in opposite directions.

19.2.1.2 The social environment of A. burtoni

Following release of the young by the mother, the growth, behavioral, and gonadal development of the fry depends critically on the social environment (Fraley and Fernald, 1982). Rearing animals either physically isolated with visual contact or in groups of broodmates produced no difference in growth based on standard length and weight for the first 10 weeks (Figure 2). Group-reared males that become NT gain less weight than those that become T though this difference is no longer evident at 20 weeks. Gonads also develop more rapidly in T males than NT males though more slowly than isolated males at 14 weeks. Physically isolated males effectively become T males and display all the behaviors associated with that status. Possibly they develop larger size and gonads because they face no actual physical competition. When comparing the onset of behavioral attributes, group-reared T males exhibit characteristic agonistic behaviors (chase, tail-beat, and fin spread) and coloration (eyebar and opercular spot) more than 2 weeks prior to animals reared in physical isolation (Figure 3). Note that these aggressive behaviors are fully suppressed in NT males reared in groups. In the *A. burtoni* social system where territorial space is a limiting factor, this robust regulation of maturation in early development seems to be an adaptive solution to a limited resource.

19.2.1.3 Social status and the HPG axis

Clearly, being reared with broodmates suppresses early social and physical development, but in *A. burtoni* an even more effective social regulation of development occurs when older animals are housed with younger animals. Davis and Fernald (1990) raised animals from hatching in the presence of adult males and showed that these fish have suppressed gonadal maturation relative to fish reared without the presence of adults. This experiment showed that the suppressed animals had not only hypogonadal testes but also smaller gonadotropin-releasing hormone
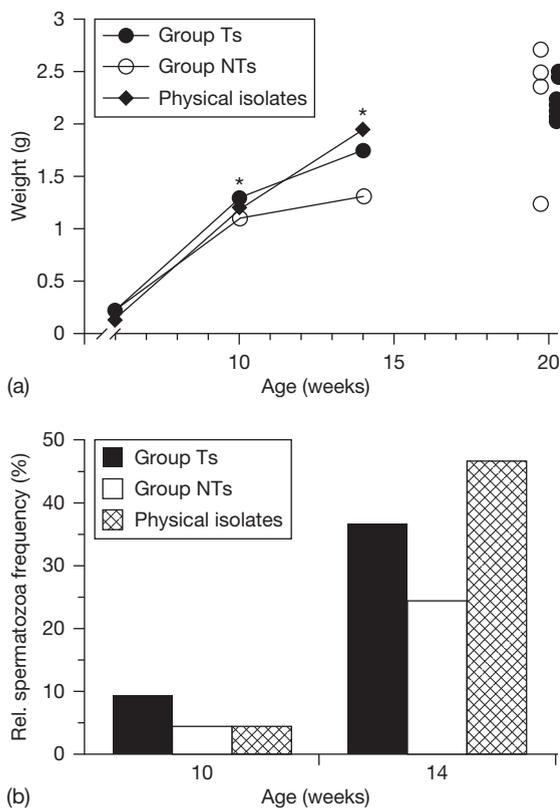
Figure 2 Development and maturation in group-reared (open and filled circles) and physically isolated (diamonds) juvenile *A. burtoni*. (a) Growth rates expressed as body weight for the different categories. Asterisks indicate that group-reared territorial fish (filled circles weigh significantly more after 10 and 14 weeks than their nonterritorial (open circles) tank mates. (b) Relative estimates of mature spermatozoa in cross-sections of the central testicular lobule. Note the rapid increase in physically isolated males between week 10 and week 14. From Fraley NB and Fernald RD (1982) Social control of developmental rate in the African cichlid, *Haplochromis burtoni*. *Zeitschrift Für Tierpsychologie* 60: 66–82; Davis MR and Fernald RD (1990) Social control of neuronal soma size. *Journal of Neurobiology* 21: 1180–1188.

(GnRH)-containing neurons in the preoptic area (POA). Because GnRH neurons are the controlling point in the HPG axis regulating reproduction in all vertebrates via a projection to the pituitary (Bushnik and Fernald, 1995) where they release GnRH, the signaling peptide sent from the brain to the pituitary to trigger release of gonadotropins and ultimately testes growth. Davis and Fernald (1990) showed that the GnRH-containing cells in the brain are eightfold larger in T than in NT males. Thus, the social control of maturation in *A. burtoni* is achieved by changing the GnRH-containing cells in the brain.
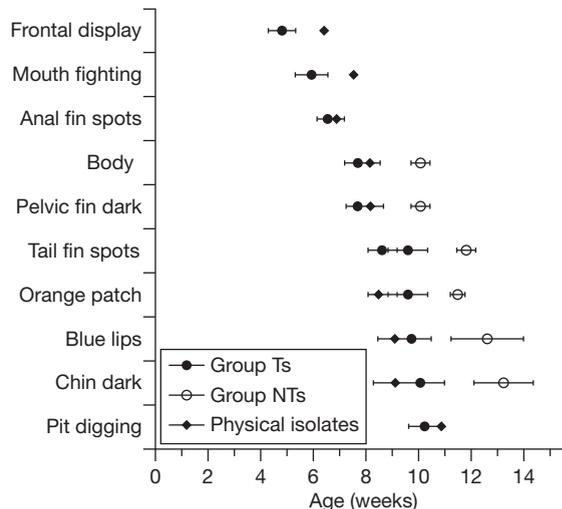

Figure 3 Ontogeny of color patterns and agonistic behavioral patterns in *A. burtoni* fry reared in groups or isolated. Symbols representing social conditions show means ± standard deviations in days when each patterns was first observed. The origin is when the fry were released from the mouth. Modified from Fraley NB and Fernald RD (1982) Social control of developmental rate in the African cichlid, *Haplochromis burtoni*. *Zeitschrift Für Tierpsychologie* 60: 66–82.

Social status can regulate the physiology of the reproductive state, even in adult *A. burtoni* as shown by converting males from T→NT or NT→T by moving them to new communities. Specifically, when T males were moved to communities containing larger T males, they rapidly became NT (e.g., T → NT) and similarly when NT males were moved to communities with smaller conspecifics, they became T (e.g., NT → T). Following 4 weeks in the altered social setting, GnRH cell size was measured (**Figure 4**). The results indicated that changing the social status alone was sufficient to change GnRH neuron size in the brain. As expected, the gonadosomatic index (GSI) changed correspondingly (Francis et al., 1993). Thus, reproduction is socially controlled in adults, as well as juveniles, via changes induced in the GnRH neurons in the brain.

19.2.1.4   Rapid changes in brain structure induced by social stimuli

Although causing a large change in brain structure by changing social status is quite remarkable, the timescale of this initial experiment did not reflect how rapidly behavioral and neural changes could occur. Indeed, the 4-week interval tested was substantially
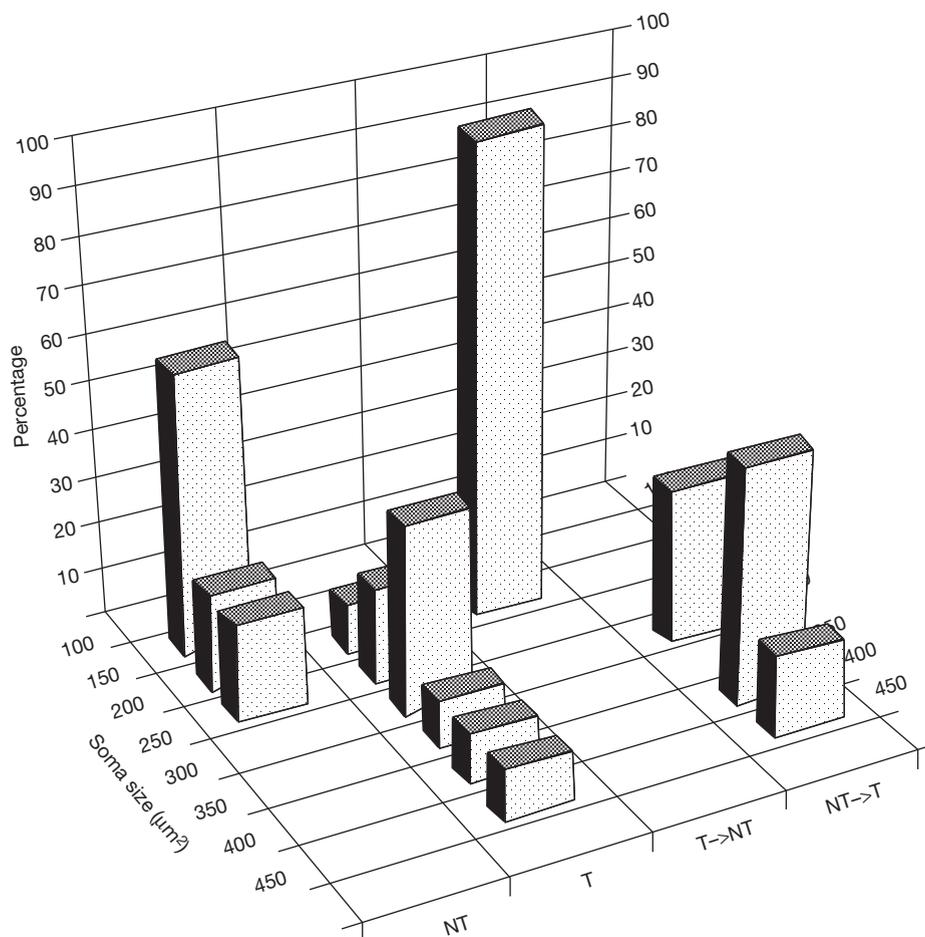
Figure 4 Three-dimensional plot of mean soma sizes of POA GnRH-ir neurons, showing significant differences between T and T→NT males and between NT→T males. Percentage of individuals with mean soma size in a given size bin is plotted for each treatment condition. Reproduced from Francis RC, Soma K, and Fernald RD (1993) Social regulation of the brain–pituitary–gonadal axis. *Proceedings of the National Academy of Sciences of the United States of America* 90: 7794–7798, with permission of PNAS.

longer than any observed changes in behavior following status switches, which can occur in minutes. Analyzing socially induced changes in neural structures on a significantly shorter timescale revealed another surprise.

Using a paradigm of changing social status by moving animals similar to that described above, White et al. (2002) discovered several important novel features about the social control of the reproductive axis. First, upon social ascent from NT to T status, the change in GnRH neuron size was quite rapid, with substantial growth in a single day. The typical T male GnRH cell size was reached in less than 1 week. The GnRH neurons actually continued to grow still larger so that at 2 weeks they were significantly larger than normal T male size before returning to the size appropriate for a T male (**Figure 5**). This substantial

upregulation of GnRH production very likely allows the socially ascending animal to achieve reproductive competence rapidly and was obviously not observed in the 4-week experiment described above. The behavioral switch from NT to T, while immediately evident as a change from nonaggressive to aggressive behavior, does not fully match that of a stable T male for approximately 1.5 weeks. The second discovery in this experiment was that the change between T and NT is remarkably asymmetric. Fish of descending social status (T → NT) stop displaying aggressive behaviors immediately but the GnRH-containing neurons in the POA do not reduce to NT size until approximately 3 weeks after defeat, whereas the NT → T ascent takes less than a week. The significance of this lies in the idea that neural and behavioral changes between T and NT males may be explained as a consequence of a life in an
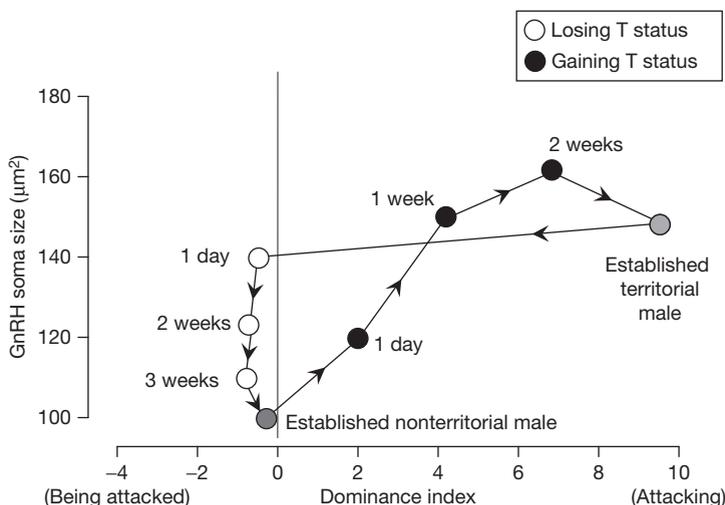
Figure 5 Mean two-dimensional GnRH-ir neuronal soma size plotted against the frequency of aggressive and submissive behaviors expressed as a dominance index (sum of aggressive acts minus sum of escape events/3-min observation interval). Note the hysteresis-like function as social status changes are asymmetric in regard to behavior and soma size. Although the behavioral change in T→NT males is significantly faster (*c*. 1 day) than in NT→T males (*c*. 2 weeks), the latter achieve soma sizes equivalent to those of T's in 1 week, while T→NTs require 3 weeks for their neurons to shrink to NT sizes. Empty circles indicate cases where soma size is hypothetical. Variances not shown for clarity. Data from Hofmann HA and Fernald RD (2001) What cichlids tell us about the social regulation of brain and behavior. *Journal of Aquariculture and Aquatic Sciences* 9: 17–31.

unstable world where reproductive opportunities may arise quickly (see below). After a defeat, switching to subordinate behaviors rapidly likely reduces the chances of injuries to the loser. However, given that the chance to establish a territory could arise soon, maintaining an active reproductive system for a bit longer may be adaptive.

Clearly, social status sets both soma size of POA GnRH-containing neurons and, through this pathway, GSI, and these effects are reversible. The relatively large testes and GnRH neurons characteristic of T males are a consequence of their social dominance, and when this dominance advantage is lost, both neurons and testes shrink, although as seen here (White et al., 2002), there is striking asymmetry in the physiological responses. Social information about status causes the changes in the brain but how this is achieved is not known.

White et al. (2002) also showed that the socially induced changes in status resulted in significant changes in gene expression in the brain. Measuring changes in mRNA from all three forms of GnRH found in *A. burtoni*, they found that only the POA GnRH1 mRNA was regulated corresponding to a change in social status. The change in mRNA in the POA form of GnRH1 was evident at 3 days after a change in social status. Such social regulation demonstrates clearly that key social information is

used to control specific cellular and molecular processes in the brain.

### 19.2.2 Three Distinct Populations of GnRH-Containing Neurons

It is important to emphasize that the effect of social status on GnRH cell size and GnRH mRNA expression is limited to the GnRH-containing neurons of the POA. As we have shown, *A. burtoni* has three distinct genes that code for three distinct GnRH-like molecules (White et al., 1994; White and Fernald, 1998) expressed at three distinct sites in the brain (White et al., 1995). The GnRH forms not found in the POA are expressed in two other distinct cell groups, one located in the terminal nerve region (GnRH3), the other in the mesencephalon (GnRH2; see White et al. (1995) for details). Neither of these other GnRH-containing cells showed any changes in size or mRNA production as a function of social status (Davis and Fernald, 1990; White et al., 2002). Males and females share the brain–pituitary–gonadal axis used to control reproduction but female *A. burtoni* have a strikingly different system that regulates reproduction. GnRH1-containing cells in the POA of females also change size, but size change depends on reproductive status alone (White and Fernald, 1993).

Given the rapid macroscopic change in GnRH neurons following a change in status, we devised a novel behavioral paradigm to test the speed of this process. We placed a T male in an aquarium with one NT male and three females, with associated fish colonies on each side. The target T male was removed before dawn so when the lights came on, the NT male was the sole male in the tank with three females. We videotaped the response and kept track of when the NT male first exhibited an eyebar and related T behavior. Twenty minutes after the first expression of T behavior, we sacrificed the animal and subsequently mapped the expression of an activity-dependent immediate early gene (*egr-1*; Burmeister et al., 2005). We found a rapid genomic response in the GnRH neurons of the POA in response to the perception of social opportunity 20 min after the NT male adopted dominant coloration and behaviors. This suggests that these animals are fully primed to ascend and, based on their recognition of the new circumstances, they respond extremely rapidly at both the behavioral and molecular levels.

19.2.3 Role of Androgen in Regulation of GnRH-Containing Cell Size

As one might expect, social control of the reproductive axis via GnRH also influences important endocrine factors, including androgen released from the gonads. Castrated *A. burtoni* T males have hypertrophied GnRH neurons (Francis et al., 1992a; Soma et al., 1996) showing that androgen has a feedback effect on GnRH cell size (**Figure 6**). The important discovery is that the set point for this feedback loop is the social status, as T males have larger GnRH neurons despite having higher androgen levels (Soma et al., 1996). T males that are castrated are able to maintain their rank despite having lowered androgen levels (Francis et al., 1992b). Prior dominance experience on the part of the T male and the size difference among animals possibly both contribute to this result.

Clearly social status regulates the production and release of GnRH into the pituitary. Another potential site for regulation is the GnRH receptor in the pituitary. Recent work in our laboratory has shown that *A. burtoni* has genes that encode two distinct GnRH receptors (Robison et al., 2001; Flanagan et al., 2007). Using real-time polymerase chain reaction (PCR), we have been able to show that the mRNA of one of these receptor types is upregulated rapidly and dramatically in the pituitary of T males compared with NT males (Au et al., 2006). It remains to be discovered whether this receptor regulation results
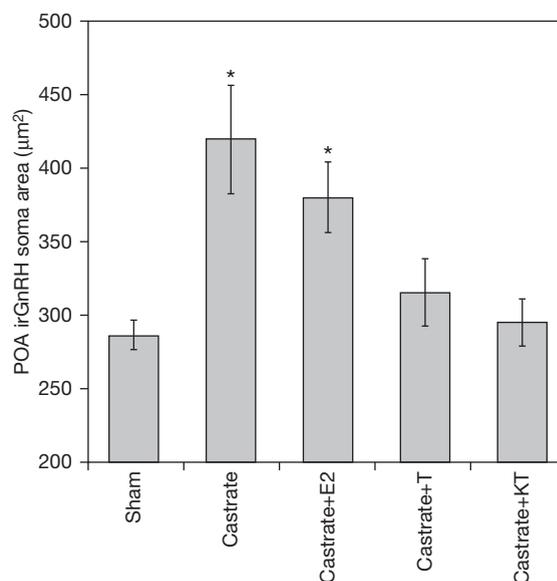

Figure 6 Soma area of POA irGnRH neurons plotted as a function of experimental treatment. Values shown are mean ± SE. Castrated animals (CASTRATE, $n = 4$) had significantly larger mean soma areas than intact sham-operated controls (SHAM, $n = 5$), and hormonal treatments in castrates had different effects on POA irGnRH cell size. In castrates treated with testosterone (CASTRATE + T, $n = 4$), androgen replacement significantly reduced neuronal hypertrophy. In contrast, castrates treated with estradiol (CASTRATE + E2, $n = 4$) had significantly large mean somas than the SHAM group. Groups that are significantly different from the SHAM group are indicated with an asterisk. Reproduced from Soma KK, Francis RC, Wingfield JC, and Fernald RD (1996) Androgen regulation of hypothalamic neurons containing gonadotropin-releasing hormone in a cichlid fish: Intergration with social cues. *Hormones and Behavior* 30: 216–226, with permission of Elsevier Ltd.

solely from a change in social status or if other factors are also involved. In addition to its primary role, analysis of the distribution of GnRH receptors (Chen and Fernald, 2006) revealed that this peptide must play a modulatory role in the animal as well as regulating reproduction.

The next steps are to understand how the preoptic area GnRH1 neurons function together, using imaging to record from many cells simultaneously which will allow us to understand the dynamics of the GnRH1 circuit.

19.3 What Social Information Influences Changes in Status?

Social living requires more sophisticated cognitive abilities in many vertebrates because the social
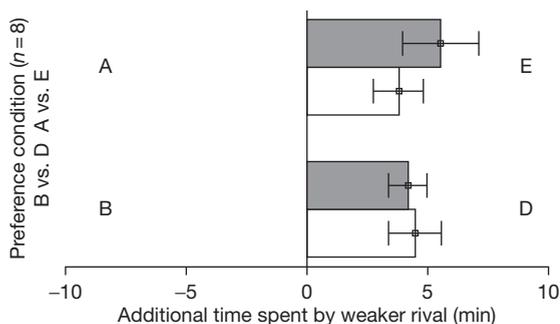
Figure 7 Time spent near rival males during preference testing. Bar plots of the difference in time spent near the higher-ranking vs. the lower-ranking rival (T_s) in the AE (top) and BD (bottom) preference tasks by context. Filled bars, familiar context; open bars, novel context. Error bars indicate SE. Reproduced from Grosenick L, Clement TS, and Fernald RD (2007) Are fish logical? Bystanders infer social rank by observation alone. *Nature* 445: 429–432, with permission of Nature Publishing Group.

environment offers individuals an opportunity to gather and use information about the behavior of others (Brown and Laland, 2003). But how do animals collect and use social information (McGregor, 2005; Brown et al., 2006)? Eavesdropping, the collection of information via observation can provide benefits to the bystander (McGregor, 2005). Eavesdropping behavior, best documented in conflict situations, suggests that individuals adjust their fighting behavior according to knowledge gained by observing their opponent (Johnstone, 2001; Johnstone and Bshary, 2004).

We have recently shown in *A. burtoni* that males can infer who will win fights solely from observing pairs of individuals fighting. This ability, called transitive inference, is tested when a subject is given information about a specific relationship among items based on a property of each item. In social animals, the ability to make inferences about other individuals' relative place in a dominance hierarchy and, therefore, predict the outcome of competition should be a useful skill (Emery, 2006). Transitive inference has been demonstrated in a number of avian species, including pigeons, jays, and corvids (for summary and review, see Emery (2006)). However, we recently showed that *A. burtoni* males show transitive inference about dominance among other animals (Grosenick et al., 2007). Two groups of dominant bystander fish saw staged, pairwise fights between five pairs of conspecifics. One group of five had a dominance hierarchy of A > B > C > D > E, while the other had no dominance hierarchy (e.g., A = B = C = D = E). Bystanders were then tested

in a forced choice paradigm to demonstrate their preference for either A and E, or B and D. Both of these pairings were novel to the bystanders and differed only in their position in the inferred dominance hierarchy. In both tests (A vs. E and B vs. D), bystander fish spent more time near rival males that were lower in the dominance ranking (Figure 7). These results show that fish learned the implied hierarchy as bystanders and, importantly, that *A. burtoni* can use transitive inference to understand the likely outcome of fights between dominant males.

19.4 Conclusion

In this chapter, we have discussed how social information can influence reproduction, cognition, and the brain. In *A. burtoni*, social information via multiple sensory systems impacts complex behavioral patterns and the entire HPG axis from the expression and secretion of GnRH in the brain to the development of sperm in the gonads. While many of these effects are generally well understood, what remains a mystery are many of the details of how GnRH-containing neurons are connected to produce the requisite pulsatile secretion and how the effects of GnRH are coordinated with other body systems.

While we now have a better understanding of the relationship between social behavior, use of social information, and brain activation, we do not know how animals process and store social information and then retrieve it in the service of complex cognitive tasks. Because of its complex social organization and the wealth of background information into brain activation, the cichlid fish, *A. burtoni*, is likely to be integral in the study of dominance, social information, and their impacts on the brain.

References

Au TM, Greenwood AK, and Fernald RD (2006) Differential social regulation of two pituitary gonadotropin-releasing hormone receptors. *Behavioral and Brain Sciences* 170: 342–346.

Brown C, Laland K, and Krause J (2006) *Fish Cognition and Behavior*. Oxford: Blackwell.

Brown C and Laland KN (2003) Social leaning in fishes: A review. *Fish and Fisheries* 4: 280–288.

Bshary R (2002) Biting cleaner fish use altruism to deceive image scoring clients. *Proceedings of the Royal Society, B* 269: 2087–2093.

Bshary R, Wickler W, and Fricke H (2002) Fish cognition: A primate's eye view. *Animal Cognition* 5: 1–13.

Bshary R and Wurth M (2001) Cleaner fish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation. *Proceedings of the Royal Society, B* 268: 1495–1501.

Burmeister SS, Jarvis ED, and Fernald RD (2005) Rapid behavioral and genomic responses to social opportunity. *PLoS Biology* 3: e363.

Bushnik TL and Fernald RD (1995) The population of GnRH-containing neurons showing socially mediated size changes project to the pituitary in a teleost, *Haplochromis burtoni*. *Brain, Behavior and Evolution* 46: 371–377.

Chen CC and Fernald RD (2006) Distributions of two gonadotropin-releasing hormone receptor types in a cichlid fish suggest functional specialization. *Journal of Comparative Neurology* 495: 314–323.

Coulter GW (1991) *Lake Tanganyika and Its Life.* Oxford: Oxford University Press.

Davis MR and Fernald RD (1990) Social control of neuronal soma size. *Journal of Neurobiology* 21: 1180–1188.

Emery NJ (2006) Cognitive ornithology: The evolution of avian intelligence. *Philosophical Transactions of the Royal Society, B* 361: 23–43.

Fernald RD (1977) Quantitative observations of *Haplochromis burtoni* under semi-natural conditions. *Animal Behaviour* 25: 643–653.

Fernald RD (1984) Vision and behavior in an African cichlid fish. *American Scientist* 72: 58–65.

Fernald RD and Hirata NR (1977a) Field study of *Haplochromis burtoni* – habitats and cohabitant. *Environmental Biology of Fishes* 2: 299–308.

Fernald RD and Hirata NR (1977b) Field study of *Haplochromis burtoni* – quantitative behavioral observations. *Animal Behaviour* 25: 964–975.

Flanagan CA, Chen CC, Coetsee M, et al. (2007) Expression, structure, function, and evolution of gonadotropin-releasing hormone (GnRH) receptors GnRH-R1SHS and GnRH-R2PEY in the teleost, *Astatotilapia burtoni*. *Endocrinology* 148: 5060–5071.

Fraley NB and Fernald RD (1982) Social control of developmental rate in the African cichlid, *Haplochromis burtoni*. *Zeitschrift Für Tierpsychologie* 60: 66–82.

Francis RC, Jacobson B, Wingfield JC, and Fernald RD (1992a) Hypertrophy of gonadotropin releasing hormone-containing neurons after castration in the teleost, *Haplochromis burtoni*. *Journal of Neurobiology* 23: 1084–1093.

Francis RC, Jacobson B, Wingfield JC, and Fernald RD (1992b) Castration lowers aggression but not social dominance in male *Haplochromis burtoni* (Cichlidae). *Ethology* 90: 247–255.

Francis RC, Soma K, and Fernald RD (1993) Social regulation of the brain–pituitary–gonadal axis. *Proceedings of the National Academy of Sciences of the United States of America* 90: 7794–7798.

Grosenick L, Clement TS, and Fernald RD (2007) Are fish logical? Bystanders infer social rank by observation alone. *Nature* 445: 429–432.

Heiligenberg W and Kramer U (1972) Aggressiveness as a function of external stimulation. *Journal of Comparative and Physiological Psychology* 77: 332–340.

Heiligenberg W, Kramer U, and Schulz V (1972) The angular orientation of the black eye-bar in *Haplochromis burtoni* (Cichlidae, Pisces) and its relevance to aggressivity. *Zeitschrift Für Tierpsychologie* 76: 168–176.

Johnstone RA (2001) Eavesdropping and animal conflict. *Proceedings of the National Academy of Sciences of the United States of America* 98: 9177–9180.

Johnstone RA and Bshary R (2004) The evolution of spiteful behaviour. *Proceedings of the Royal Society, B* 271: 1917–1922.

Laland KN, Brown C, and Krause J (2003) Learning in fishes: From three-second memory to culture. *Fish Fisheries* 4: 199–202.

Leong C-Y (1969) The quantitative effect of releasers on the attack readiness of the fish *Haplochromis burtoni*. *Zeitschrift Für Tierpsychologie* 65: 29–50.

Lorenz K (1932) Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie* 80, Heft 1.

McGregor PK (1993) Signaling in territorial systems: A context for individual identification, ranging and eavesdropping. *Philosophical Transactions* 340: 237–244.

McGregor PK (2005) *Animal Communication Networks.* Cambridge: Cambridge University Press.

Pitcher TJ, Green DA, and Magurran AE (1986) Dicing with death: Predator inspection behavior in minnow *Phoxinus phoxinus* shoals. *Journal of Fish Biology* 28: 439–448.

Robison RR, White RB, Illing N, Troskie BE, Morley M, Millar RP, and Fernald RD (2001) Gonadotropin-releasing hormone receptor in the teleost *Haplochromis burtoni*: Structure, location, and function. *Endocrinology* 142: 1737–1743.

Soma KK, Francis RC, Wingfield JC, and Fernald RD (1996) Androgen regulation of hypothalamic neurons containing gonadotropin-releasing hormone in a cichlid fish: Intergration with social cues. *Hormones and Behavior* 30: 216–226.

Von Uexküll J (1921) *Umwelt und Innenweld der Tiere.* Berlin: Springer.

White SA, Bond CT, Francis RC, Kasten TL, Fernald RD, and Adelman JP (1994) A second gene for gonadotropin-releasing hormone: cDNA and expression pattern in the brain. *Proceedings of the National Academy of Sciences of the United States of America* 91: 1423–1427.

White SA and Fernald RD (1993) Gonadotropin-releasing hormone-containing neurons change size with reproductive state in female *Haplochromis burtoni*. *Journal of Neuroscience* 13: 434–441.

White RB and Fernald RD (1998) Ontogeny of gonadotropin-releasing hormone (GnRH) gene expression reveals a distinct origin for GnRH-containing neurons in the midbrain. *General and Comparative Endocrinology* 112: 322–329.

White SA, Kasten TL, Bond CT, Adelman JP, and Fernald RD (1995) Three gonadotropin-releasing hormone genes in one organism suggest novel roles for an ancient peptide. *Proceedings of the National Academy of Sciences of the United States of America* 92: 8363–8367.

White SA, Nguyen T, and Fernald RD (2002) Social regulation of gonadotropin-releasing hormone. *Journal of Experimental Biology* 205: 2567–2581.

Wickler W (1962) Zur Stammesgeschichte funktionell korrelierter Organ-und Verhaltensmerkmale: Eiattrappen und Maubrüten bei afrikanischen Cichliden. *Zeitschrift Für Tierpsychologie* 19: 129–164.

Winter Y, Lopez J, and Von Helversen O (2003) Ultraviolet vision in a bat. *Nature* 425: 612–614.

Further Reading

Grutter AS and Bshary R (2003) Cleaner wrasse prefer client mucus: Support for partner control mechanisms in cleaning interactions. *Proceedings of the Royal Society, B* 340: 237–244.

Biographical Sketch

Russell D. Fernald is professor of biological sciences and neuroscience at Stanford University where he holds the Benjamin Scott Crocker Professorship. His research focuses on how social behavior influences the brain. Professor Fernald studied animal behavior with Konrad Lorenz and has combined field studies in Africa with laboratory research about the brain mechanisms related to behavior. Fernald was awarded a Jacob Javits Neuroscience Investigator Award by the National Institutes of Health. He became a fellow of the AAAS in 2003 and in 2004 he was awarded the Rank Prize in vision and optoelectronics for his research in to lens function. He serves on the editorial boards of several journals, including *Endocrinology*. He has been recognized for his contributions to undergraduate education at Stanford, including a Bing Fellowship (1996–99) for innovative contributions, the Allen V. Cox medal (1999) for fostering undergraduate students interest in research, and the Lloyd W. Dinkelspiel Award (2000) for distinctive contribution to undergraduate education. In 2003 he was named as the first Mimi and Peter Hass Fellow for his contributions to undergraduate education.