

# How do social dominance and social information influence reproduction and the brain?

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**Synopsis** How does living in a social environment influence the brain? In particular, we ask the following questions: How do animals perceive and use social information? How does the perception of social information influence the reproductive system? Where is this represented in the brain? We present a model system in which these questions can be addressed, focusing on the brain's role in integrating information. In the social fish, *Astatotilapia burtoni* (*Haplochromis*), the relationship between social status and gonadotropin-releasing hormone (GnRH1) has been well established. Change in status results in numerous changes in the physiology of *A. burtoni* at every level of organization. Social status can regulate reproduction via the hypothalamic–pituitary–gonadal (HPG) axis. GnRH1 is used by the brain to signal the pituitary about reproductive state so reproductive control depends on regulation of this signaling peptide. In this fish, social dominance is tightly coupled to fertility. Here, we have exploited this link to understand the regulatory systems from circulating hormones, brain volume to gene expression.

## Dominance influences reproductive physiology in many vertebrate species

All animal species experience life somewhat differently because their sensory systems capture unique perceptual worlds and their motor abilities determine how they can act in that world. Von Uexküll (1921) first described the perceptual world as the “*umwelt*” of a species and scientists have continued to discover new dimensions of the *umwelt*. While Von Uexküll intended his idea of the *umwelt* to apply principally to physical stimuli, Lorenz (1935) extended this concept by recognizing that animals also have a social *umwelt* since signals from other individuals can have important influences on their behavior. Lorenz's (1935) influential article, “Companions as Factors in the Bird's Environment” showed that behavioral scientists needed to expand their notion of an animal's perceptual world to include other individuals and, importantly, the overall social context. Since behavior is the ultimate arbiter of animals' survival, response of animals during their interactions with others and with their environment 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 require understanding

mechanisms responsible for the control of behavior as animals interact with one another in a natural setting. Yet, the vast majority of experiments are performed on two interacting individuals rather than on groups of individuals, typically using domesticated species. Much more can be learned about how evolution has shaped complex social behavior by analyzing groups of interacting animals.

Fish species have emerged as important models for studies of social behavior and its underpinnings. For example, it has been shown that fish might adopt “Machiavellian” social strategies (e.g., Bshary and Würth 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) and generally display a wide range of social activities comparable in some instances with those of primates (e.g., Bshary et al. 2002). In addition to their social sophistication, fish have proven useful for investigating the underlying mechanisms of behavior. In particular, several fish genomes have been sequenced, making it easier to trace and identify mechanisms responsible for sophisticated social interactions.

The cichlid fish *Astatotilapia burtoni* is a unique model system for studying the influence of the social environment on the brain. In *A. burtoni*, there are two types of adult males: those with (T) and those without (NT) territories (Fig. 1; Fernald 1977).

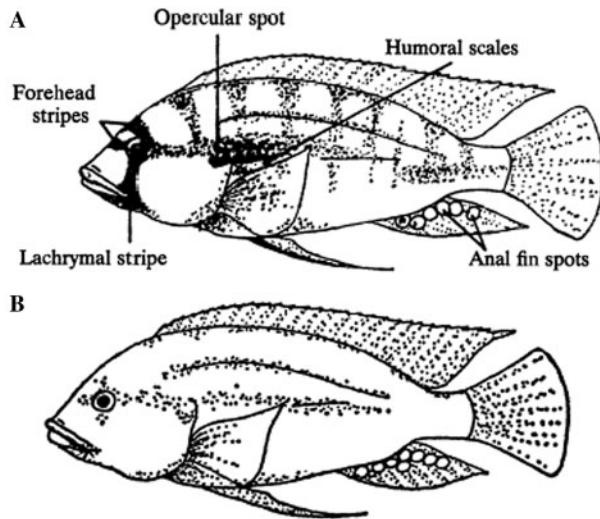
From the symposium, “Advances in Neurobiology” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 2–6, 2008, at San Antonio, Texas.

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*Integrative and Comparative Biology*, volume 48, number 5, pp. 596–603  
doi:10.1093/icb/icn089

Advance Access publication October 4, 2008

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**Fig. 1** Illustration of the body patterns for typical T (A) and NT (B) males. T males have distinct anal-fin spots, dark forehead, and lachrymal (eye-bar) stripes and are brightly colored, including orange humoral scales. NT males lack the robust markings of their T counterparts and are colored in ways that maximize camouflage. The overall body color may be either yellow or blue.

This fish, endemic to Lake Tanganyika in east Africa, lives in a complex social environment where T males vigorously defend a breeding territory and frequently exchange threat displays and overt aggression with neighboring males. In addition, they often chase NT males from their territory and solicit and court females (Fernald 1984). These phenotypic states (T and NT) are fully reversible: when NT males are moved to communities with small conspecifics they become T. In addition, when T males are moved to communities with larger T males, they become NT. As is typical of cichlids using rapid social interactions, each behavioral act influences the next and results in changes in behavior of both the individuals involved and the other animals witnessing the encounters (Fernald and Hirata 1977a). Living in a social environment influences growth, behavior, and gonadal development in *A. burtoni*. Gonads develop more rapidly in group-housed T males than in group-housed NT males. However, the group-housed males had much slower gonadal development at 14 weeks than did the isolated males (Fraley and Fernald 1982).

Why might fish social behavior yield general insights about brain mechanisms underlying social interactions? Stable social systems in any animal species require that individuals behave predictably. However, what an individual does at any moment in time may depend on its status relative to others, its reproductive state, and its recent behavioral interactions. In addition, environmental factors

(e.g., predators, prey, or competitors) also need to be incorporated into any plan for action. 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. 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 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 to explain the behavior of animals in social groups (Hsu et al. 2006). Since it has been argued that fishes have demonstrated many, but not all, the social skills that arguably accompany the evolution of complex brain structures in primates (Bshary 2002), how could we exploit the social skills of fish to discover underlying neural mechanisms? Given the complex social environment in which *A. burtoni* lives, we present it as a model system for understanding the underlying neural and endocrine mechanisms governing social behavior. We also explore the range of social requirements for *A. burtoni* (among a range of other vertebrates) to achieve social dominance through use of social information. Finally, we suggest possible avenues for continued research to discover which brain areas are involved in the control of behavior in a social environment. Importantly, the *A. burtoni* system provides evidence for how social behavior shapes the brain in ways that depend on developmental stage, social circumstance, and environmental context.

## Use of social information

Social living requires significant cognitive abilities in many vertebrates because the social environment offers individuals an opportunity to gather and use information about the behavior of others (Brown and Laland 2003; Danchin et al. 2004; Laland 2004). How do animals use the social information they gather (for reviews see McGregor 2005; Brown et al. 2006)? Social eavesdropping behavior, best documented in conflict situations, suggests that individuals use a signaling interaction (such as territorial singing among males of many bird species, or agonistic displays between fish) to adjust future interactions with heard or seen individuals (McGregor and Peake 2000, 2001; Johnstone 2001; Johnstone and Bshary 2004; McGregor 2005). Social eavesdropping in agonistic contexts has been documented across a wide range of vertebrate species (McGregor 2005; Bshary and Grutter 2006; Bonnie and Earley 2007). First, we review how social information, including social

eavesdropping, is used in assessing the fighting ability of the opponent, the quality of potential mates, the propensity to cooperate, and dominance. We use specific examples from teleost fish and provide evidence that *A. burtoni* is an ideal model system for better understanding the communication and use of social information.

### Social eavesdropping on agonistic encounters

Studies of teleost fish have demonstrated that male bystanders can estimate the quality and fighting ability of other individuals by using social information (for review see Valone 2007). Males that watched others fight modulated their agonistic decisions based on information obtained from watching aggressive signaling between males (for review see Bonnie and Earley 2007). In *A. burtoni*, we know that males pay close attention to, and watch contests between, other males and that this information influences subsequent preference for affiliative partners (Grosenick et al. 2007). What has not been shown in *A. burtoni* is whether males base subsequent agonistic encounters on such social information. In green swordtails, Earley and Dugatkin (2002) and Earley et al. (2005) showed that individuals allowed to observe contests between opponents modify their behavior when engaged in aggression with those opponents. Males were less prone to engage in escalated fights either with winners or with losers that had escalated while losing their fight. In addition, swordtails only modified their behavior when engaged in fights with individuals they actually observed in contests; watching a fight did not modify behavior towards an unknown opponent (Earley et al. 2005). This means that swordtails can discriminate amongst individual opponents and that they learn something about the fighting ability of opponents by watching the opponents' contests with others.

### Mate-choice copying

Social factors also play a role in mate choice in a number of fishes, including mollies, guppies, gobies, and others (Westneat et al. 2000; Brown and Laland 2003). In studies of mate choice by females, there is increased probability of mating with a male if a female sees that male mate with another female (for review see Valone 2007); this is called "mate-choice copying." In *A. burtoni*, it has been shown that gravid females prefer T males while nongravid females prefer NT males, thereby minimizing aggression from T males (Fig. 2; Clement et al. 2005).

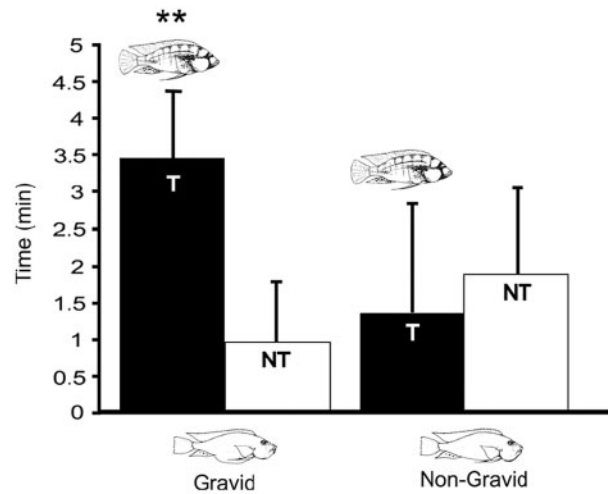


Fig. 2 Gravid and nongravid female affiliation with T and NT male phenotypes. The graphs show average time that females affiliated with T and NT males, who were confined to opposite ends of a tank. Affiliation time is corrected by baseline measurements of time spent at either end while males were obscured.

Given this preference was shown by isolated females, it is likely that *A. burtoni* females in social groups would benefit from being able to copy the choice of other females. While mate-choice copying has been documented in the laboratory, very few supporting data have been found in wild populations of fish. In the sailfin mollies (*Poecilia latipinna*), in which experiments on males' and females' mate-choice copying were conducted in the wild, Witte and Ryan (2002) found that both males and females showed signs of mate-choice copying. Males preferred to associate with a female adjacent to a male rather than with a lone female, suggesting that these males are more likely to choose a female who has already mated. In addition, females preferred to associate with a male adjacent to a female rather than with a lone male. These preferential associations could not be explained by shoaling behavior (Witte and Ryan 2002).

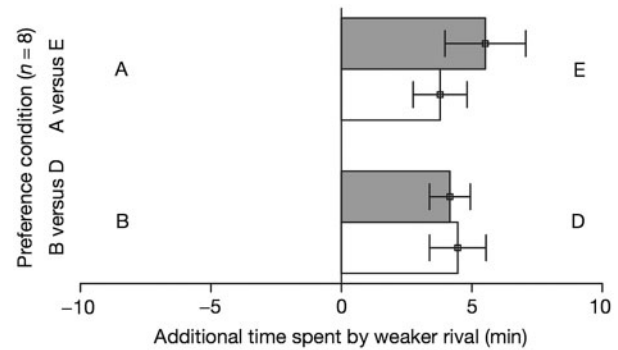
### Transitive inference

Transitive inference (TI) is the ability to infer relationships among items that have not been seen together. In a TI task, a subject is given information about a specific relationship among items based on a property of each item. An animal capable of TI can deduce the relationship among a series of the items and thus the relationships among all items. The value of an object in the natural world is a function of its relationship to other simultaneously available alternatives and the ability to rank objects (such as

food items) on an absolute scale would have significant adaptive value (von Fersen et al. 1991). A successful subject performs an operation equivalent to ranking the items, thus allowing direct derivations of relationships between any pair of items selected from the series (von Fersen et al. 1991). In social animals, the ability to make inferences about other individuals' relative place in a dominance hierarchy and, therefore, to predict the outcome of competition, should be a useful skill (Emery 2006). In the wild, TI may provide animals with the ability to judge whether the escalation of a fight is prudent when encountering novel competitors, thus avoiding costly fights. The ability to learn dominance hierarchies when given limited information via TI has been demonstrated in a number of avian species including pigeons, jays, and corvids (for summary and review see Emery 2006). The only existing evidence for TI in teleosts has been demonstrated in *A. burtoni*. Grosenick et al. (2007) trained dominant bystander fish by showing them staged, pair-wise fights involving five conspecifics, related in one of two ways. In one group of five, a dominance hierarchy existed such that  $A > B > C > D > E$  and one in which no dominance hierarchy existed, i.e.,  $A = B = C = D = E$ . Bystanders were then tested in a forced-choice paradigm to test their preference for either A and E, or B and D with B versus D being the critical test of TI given that both B and D had an equal number of wins and losses in the training phase. These pairings were novel to the bystanders and differed only in the position of the participants in the dominance hierarchy. In both tests (A versus E and B versus D), bystander fish spent more time near rival males that were lower in the dominance ranking (Fig. 3), when the dominance rank existed. These results show that fish learned the implied hierarchy as bystanders and that the fish can use transitive inference when trained on socially relevant stimuli.

### The social environment and the brain

Animals attend to social information and modulate their behavior accordingly. Not much is known, however, about how the brain changes when an animal processes complex social information. This requires experiments designed to discover brain activation as animals process socially relevant information or perform complex cognitive tasks to discover important features in their environment. In the next section, we will discuss current areas of research with teleost fish that explore at a gross level the relationship between social behaviors and brain volume (Krebs and Davies, 1997), as well as more



**Fig. 3** Time spent near rival males during preference testing. Bar plots of the difference in time spent near the higher ranking versus the lower ranking rival ( $T_s$ ) in the A and E (top) and B and D (bottom) preference tasks by context. Filled bars, familiar context; open bars, novel context. Error bars indicate SE.

subtle activation patterns in areas associated with a postulated “social behavior network” (Newman 1999; Goodson 2005), and finally specific areas of the brain including the lateral and medial divisions of the telencephalon (Vonderschen et al. 2002; Portavella et al. 2002, 2004; Salas et al. 2003; Northcutt 2006) and cerebellum (Paulin 1993; Rodríguez et al. 2005; Salas et al. 2006).

### Brain volume

In many avian species, the volumes of specific areas of the brain have been studied in relation to their importance for social behavior and cognitive function. The hippocampus, because of its role in spatial memory, has been shown to increase or decrease among species depending on the need for food storage and retrieval (Krebs et al. 1989). Hippocampal volume also increases within a species as the need for food storage increases during the feeding season (MacDougall-Shackleton et al. 2003). The volume of another brain area involved in song memory is positively correlated with the size of the song repertoire in passerine species (Devoogd et al. 1993). In addition, Burish et al. (2004) proposed that, among bird species, the fraction of the brain occupied by the telencephalon increases with the size of the social group, leading to the hypothesis that the volume and structure of the telencephalon may be related to social behavior and social complexity.

### The neural network of social behavior and the reception of social information

Newman (1999) originally proposed that social behavior was regulated by a network of six nodes in the brain: the extended medial amygdala, the lateral septum, the preoptic area, the anterior

hypothalamus, the ventromedial hypothalamus, and the periaqueductal gray. Since each of these areas has been implicated in the control of multiple forms of social behavior, Newman (1999) suggested that a large integrated neural network that controls not only males' mating behavior, but also females' sexual behavior, parental behavior, and various forms of aggression. His hypothesis also suggested that an individual animal's social responses can be more easily understood as a repertoire of closely inter-related, hormonally regulated behaviors, shaped by development and experience and modulated acutely by the proximate signals of the social environment (Newman 1999). In addition, it is likely that this network of social behavior will play an important role in response to changes in social environment and the reception of social information. More recently, this social behavioral network has been modified to apply to birds and fish (Goodson 2005). Using the plainfin midshipman (*Porichthys notatus*), a species of fish that uses vocal social communication, Goodson and Bass (2002) were able to show that afferent and efferent connections of brain loci were active when engaged in vocalizations distributed throughout the basal forebrain, midbrain tegmentum, and hindbrain. The patterns of activation showed remarkable resemblance to those suggested by Newman (1999). However, this research is the only test of this hypothesis for the social behavior in fish. By manipulating the social environment and by capitalizing on the plasticity of social status in *A. burtoni*, the influence of available social information on the hypothalamic–pituitary–gonadal (HPG) axis has been established. *Astatotilapia burtoni* males transitioning from NT to T show large increases in GnRH1-containing neuron cell-body size (White et al. 2002), the production of GnRH1 mRNA in the pre-optic area (White et al. 1994; White and Fernald 1998), and the production of the immediate early gene *egr-1* in the POA (Burmeister et al. 2005). In this last case, social opportunity led to an extremely rapid genomic response in the GnRH1-containing neurons of the pre-optic area accompanied by the rapid adoption of coloration and behaviors associated with dominance.

### The hippocampus and the amygdala

While brain areas related to the social behavioral network have been shown to be involved in social behavior in fish (Goodson and Bass 2002; Goodson 2005), other brain regions in the telencephalon have been implicated in more cognitive abilities (Salas et al. 1996a, 1996b; López et al. 2000a, 2000b;

Salas et al. 2006). These areas include the fish homologues to the hippocampus and the amygdala. Substantial evidence shows that cognitive mapping abilities depend on the forebrain in teleost fish and immunocytochemical, developmental, and connectivity studies suggest that teleost areas dorsolateral telencephalon (Dl) and dorsomedial telencephalon (Dm) are homologous to the mammalian hippocampus and amygdala, respectively (Northcutt 1995; Salas et al. 1996a, 1996b; López et al. 2000a, 2000b; Wullimann and Mueller 2004). Ablation studies have demonstrated the importance of Dl in spatial learning and of Dm in emotional (fear) learning (Portavella et al. 2002, 2003; Salas et al. 2003). In addition, both of these brain areas receive multimodal sensory input, including visual input (Northcutt 2006). Given the importance of areas Dl and Dm in spatial and emotional learning, it is possible that these brain areas may also be involved in the reception and integration of cues associated with solving complex cognitive tasks. To date, a number of researchers have examined how full ablation of these telencephalic regions impacts learning and memory in fish (Portavella et al. 2002, 2003; Salas et al. 2003). While these studies elucidate the role these brain areas have in learning and memory, to our knowledge, no research has been conducted on nonprimates in which specific patterns of activation in Dl or Dm have been examined while animals are solving complex cognitive tasks. Given that *A. burtoni* males are able to solve complex cognitive tasks and rely heavily on social information for reproduction, they are an ideal model species to use to resolve the importance of areas Dl and Dm in the communication and reception of social information.

### The cerebellum

The cerebellum is one of the most variable parts of the vertebrate brain in terms of shape and size and is used to control how individuals move in space. However, despite this variability, the cerebellum of every vertebrate species shows similar cellular organization, neural circuits, and neurophysiological mechanisms (Rodríguez et al. 2005). Known as a center for motor control and coordination of movement, experimental evidence from mammals suggests that the cerebellum is also involved in multiple cognitive processes that were previously thought to be located exclusively in the telencephalon, particularly language processing, spatial memory, and learning by observation (Lalonde and Botez 1990; Thompson and Krupa 1994; Petrosini et al. 1998). More recent anatomical evidence for this

relationship between the cerebellum and cognitive function lies in the telencephalon–cerebellar connections (Vonderschen et al. 2002).

In teleosts, the cerebellum has often been implicated in the detection of, and the response to, electrical signals (Bombardieri and Feng 1977). Bombardieri and Feng (1977) found that the cerebellum of the electric fish *Apteronotus albifrons* is essential for recognizing and/or the tracking of approaching electrical stimuli. Other aspects of cerebellar function in teleosts have received less attention than has cerebellar involvement in electroreception. Experiments on cerebellar ablation in teleosts have provided equivocal and sometimes contradictory evidence about the involvement of the cerebellum in control of movement, with some authors reporting disturbances of equilibrium and others reporting no effect (Paul 1982). While relational memory processes, such as spatial cognition, are based on the function of the hippocampus, some of the implicit learning processes, such as classical conditioning of simple motor reflexes and emotional responses, depend on the cerebellum and the amygdala, respectively (Salas et al. 2006). Given this, it is likely that, in solving complex cognitive tasks, both the telencephalon and the cerebellum may play roles in the integration of inputs from a variety of brain areas.

## Conclusions

In this review, we discussed how social information can influence reproduction, cognition, and the brain. In *A. burtoni*, social information from multiple sensory systems impacts complex behavioral patterns and the entire HPG axis from the expression and secretion of GnRH1 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 GnRH1 neurons are connected to produce the requisite pulsatile secretion and how the effects of GnRH1 are coordinated with other body systems.

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

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