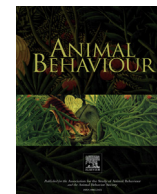




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Social behaviour: can it change the brain?



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Dominance hierarchies are ubiquitous in social species. Social status is established initially through physical conflict between individuals and then communicated directly by a variety of signals. Social interactions depend critically on the relative social status of those interacting. But how do individuals acquire the information they need to modulate their behaviour and how do they use that information to decide what to do? What brain mechanisms might underlie such animal cognition? Using a particularly suitable fish model system that depends on complex social interactions, we report how the social context of behaviour shapes the brain and, in turn, alters the behaviour of animals as they interact. Animals observe social interactions carefully to gather information vicariously that then guides their future behaviour. Social opportunities produce rapid changes in gene expression in key nuclei in the brain and these genomic responses may prepare the individual to modify its behaviour to move into a different social niche. Both social success and failure produce changes in neuronal cell size and connectivity in key nuclei. Understanding mechanisms through which social information is transduced into cellular and molecular changes will provide a deeper understanding of the brain systems responsible for animal cognition.

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In all social systems, animals must interact to survive and thrive in their social and physical environments. Remarkably diverse social systems have evolved repeatedly across phylogeny during the course of evolution, reflecting adaptations to the environment constrained by intrinsic capacities of the species. Perhaps animal groups initially arose from times when animals aggregated around food sources and from these caloric encounters came organized social interactions. All such social groups are believed to continue in a population because individuals derive a genetic benefit for themselves by being members of a group. Since behaviour is the key interface between an animal and its environment, animals respond to novel situations first through behavioural change, whereas adaptations in morphology, physiology and life history take longer. While ethologists have tended to focus on the mechanisms and development of behaviour, behavioural ecologists have concentrated generally on the causes and consequences of social behaviour. In this review, I will show how integrating these ways of thinking in a single system allows a mechanistic understanding of an animal's behaviour from its ecosystem to its social brain (Robinson, Fernald, & Clayton, 2008). I will also discuss the

cognitive challenges of living socially and some examples of how social behaviour influences the brain to shape cognitive skills.

In his prolific and prescient writing, Aristotle identified four causes for behaviour that should be studied (Hladký and Havlíček, 2013). About 2300 years later, Tinbergen in a classic paper 'rediscovered' Aristotle's four causes, situating them in two more modern categories: proximate explanations that were directly causal such as hormones and neural activity, and ultimate, or evolutionary explanations such as adaptations that conferred fitness and the phylogenetic trajectory of the species (Tinbergen, 1963). In this review, we have used the Aristotle/Tinbergen level of explanations to understand social behaviour and in particular to gain insight into the cognitive demands social living places on animals.

To understand social behaviour in a naturalistic context, I wanted a model organism that allows natural conditions to be replicated in a laboratory setting with sufficient fidelity to assure realistic results. Fish species are a natural choice because they allow construction of a semi-naturalistic setting in which careful experimentation can be done without compromising the behaviour of the animal. More specifically, because social information is essential, we need to allow animals to live in normal social groups. Fish make up ~50% of all vertebrate species and are increasingly appreciated as models for understanding the complexities of social behaviour (reviewed in Brown, Laland, & Krause, 2011). Moreover, they represent more than 400 million years of vertebrate evolution, and their taxonomic dimensions exceed the phylogenetic distance

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from frogs to humans (Romer, 1959). Fish species have evolved sensory systems exquisitely tuned to their particular environment, including the usual suspects (e.g. vision, olfaction, taste and hearing), but also mechanosensory detection (e.g. lateral line), external taste buds and numerous electroreceptor systems that have driven evolution of specialized brain structures (reviewed in Collin & Marshall, 2003). It is also known that among fish species, every known kind of social system has evolved from monogamy to harems to sex-changing animals (Desjardins & Fernald, 2009; Keenleyside, 1979).

Cognitive skills in various fish species have been shown in several domains including acquisition of foraging skills (Brännäs & Eriksson, 1999), tool use (Pasko, 2010; Timms & Keenleyside, 1975), spatial memory and manipulation of the environment (Hughes & Blight, 1999). Examples of social intelligence in fish have been measured by how they interact in group-living environments (Balshine-Earn, Neat, Reid, & Taborsky, 1998), enhance offspring survival with biparental care (Alonzo, McKaye, & van den Berghe, 2001; Gross & Sargent, 1985; Hourigan, 1989; Van den Berghe & McKaye, 2001), cooperate in hunting (Diamant & Shpigel, 1985; Vail, Manica, & Bshary, 2013) and share information about predator inspection (Pitcher, Green, & Magurran, 1986).

Among fish species, the cichlid species flocks in the rift valley lakes of East Africa offer an unparalleled adaptive radiation of species with many different social systems represented. The ~2000 species have diversified into widely different ecological systems in a relatively short time (Brawand et al., 2014). African cichlids have been studied since the end of the 19th century, most notably in Lake Tanganyika by Boulenger (1898), who published four volumes cataloguing the freshwater fishes of Africa. The colonization of Africa by European countries led to further exploration focused on fish as a potential resource and were particularly well studied by Max Poll (1956), who performed a comprehensive analysis of cichlid fish species and other organisms in Lake Tanganyika and wrote several definitive volumes describing his findings. The radiations in some East African lakes have the highest rates of speciation known in vertebrates (McCune, 1997); cichlid phenotypic diversity includes variation in behaviour, body shape, colour and trophic specialization. Exactly how cichlids evolved their highly varied phenotypes remains unexplained, but close examination of one species described here suggests that unique adaptations to highly social lives might be a partial explanation.

I study the social behaviour of a cichlid species from Lake Tanganyika, *Astatotilapia burtoni* (formerly *Haplochromis burtoni*). While developing this species as a model organism, it became clear that the male hierarchical social system required particular social skills and, furthermore, that social interactions could change the brain. *Astatotilapia burtoni* offers unique opportunities for discovering how social behaviour changes the brain because (1) the social system, based on resource guarding, can be reliably and accurately replicated in the laboratory, (2) male status is signalled phenotypically via bright coloration, including a dark bar through the eye making animals easy to distinguish and behaviour readily quantifiable, (3) in this species, as in all vertebrates, GnRH1 neurons in the brain ultimately control reproduction, but in *A. burtoni*, are directly regulated by male social status, (4) *A. burtoni* allows measurement of behaviour, circulating hormones, tissues, cells and molecular expression and (5) the *A. burtoni* genome has been sequenced (Brawand et al., 2014), enabling experiments at the genetic level not previously possible.

SOCIAL SYSTEM OF *A. BURTONI*

Astatotilapia burtoni males live as one of two quickly reversible, socially controlled phenotypes: reproductively competent

dominant males and reproductively incompetent nondominant males (see Fig. 1). Dominant males are brightly coloured, aggressively defend territories and actively court females (Fernald & Hirata, 1977). In striking contrast, nondominant males have a dull coloration, mimic female behaviour and school with females and other nondominant males, except when fleeing from an attacking dominant male.

These obvious external differences reflect major physiological differences due to social status. As animals transition from one phenotype to the other, some changes including expression of the black bar through the eye, brightening of the body colour and switch in behaviours expressed occur in minutes.

A nondominant male that previously performed only two behaviours begins to express 17 distinct behaviours rapidly upon social ascent (Burmeister, Jarvis, & Fernald, 2005; Fernald & Hirata, 1977). Over a few days, the reproductive system is remodelled as can be observed at several levels along the hypothalamic–pituitary–gonadal (HPG) axis (Maruska & Fernald, 2014). In *A. burtoni*, as in all vertebrates, reproduction is controlled by gonadotropin-releasing hormone (GnRH) containing neurons in the hypothalamus that deliver the eponymously named GnRH decapeptide to the pituitary. When a male ascends (nondominant → dominant), delivery of this molecule sets in motion a cascade of actions ultimately resulting in reproductive competence. The GnRH neurons increase in volume by eight-fold (Davis & Fernald, 1990), extend their dendrites (Fernald, 2012) and rapidly increase production of GnRH mRNA (Burmeister, Kailasanath, & Fernald, 2007) and GnRH peptide (White, Nguyen, & Fernald, 2002). However, when a dominant male is moved into a social system with larger dominant males (>5% longer), it abruptly loses its colour (<1 min) and joins other nondominant males and females in a school. Its GnRH-containing neurons in the preoptic area (POA) shrink to one-eighth their volume and produce less GnRH mRNA and peptide, causing hypogonadism and loss of reproductive competence (~2 weeks) (Davis & Fernald, 1990; Francis, Soma, & Fernald, 1993). Similarly, androgen, oestrogen and GnRH receptor mRNA expression levels depend on social status (Au, Greenwood, & Fernald, 2006; Burmeister et al., 2007; Harbott, Burmeister, White, Vagell, & Fernald, 2007), as do electrical properties of the GnRH neurons themselves (Greenwood & Fernald, 2004).

CHANGES IN THE BRAIN

While the changes in GnRH neuron size and concomitant changes in GnRH production and in hormone receptors are part and

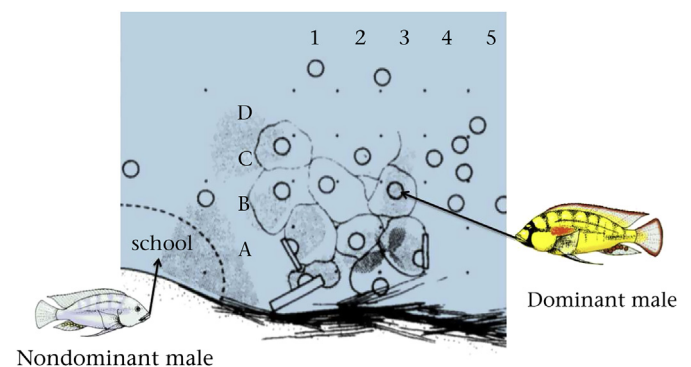


Figure 1. Sketch of an observation area in Lake Tanganyika, Burundi, Africa. Solid dots are grid stakes spaced ~50 cm and labelled (1–5; A–D) for identification. Circles represent spawning pit locations of dominant males. Lighter coloured outlines circumscribe the territories of individuals. Nondominant males and females school near the territorial area. (Based on Fernald & Hirata, 1977).

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