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.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
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 electrosensory 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 studied in several domains including acquisition of foraging skills (Branäs & 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, McKay, & van den Berghe, 2001; Gross & Sargent, 1985; Hourigan, 1989; Van den Berghe & McKay, 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 of his catalogue of the freshwater Lake Tanganyika by Boulenger (1898), who published four volumes of his catalogue of the freshwater

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).
دریافت فوری متن کامل مقاله

امکان دانلود نسخه تمام متن مقالات انگلیسی
امکان دانلود نسخه ترجمه شده مقالات
پذیرش سفارش ترجمه تخصصی
امکان جستجو در آرشیو جامعی از صدها موضوع و هزاران مقاله
امکان دانلود رایگان ۲ صفحه اول هر مقاله
امکان پرداخت اینترنتی با کلیه کارت های عضو شتاب
دانلود فوری مقاله پس از پرداخت آنلاین
پشتیبانی کامل خرید با بهره مندی از سیستم هوشمند رهگیری سفارشات