

# Complexity and the evolution of the social brain

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Our long-term goal is to understand the relationship between complex behaviors and complex brains. Here, we explore the effects of social organization, specifically monogamy versus polygamy, on the brains and behavior of African cichlid fishes. Since cichlids process social information visually, we began by behaviorally comparing the visual acuity of monogamous and polygamous fish. We then explored the next level, where social meaning is extracted from the sensory information, by comparing the size of the telencephalon and amygdalar homologue, area Dm. We also explored integrative brain areas and neuropeptides implicated in social behavior by comparing the number of AVT-immunoreactive cells in the preoptic area of the brain. Finally, we explored the role of social experience in visual behavior in a monogamous species by comparing isolated fish with those from a normal social group. This paper details the preliminary results of our investigation.

## **1 Introduction**

How do social forces sculpt complex brains? Complex brains and behaviors such as social behavior have arisen throughout vertebrate evolution, likely reflecting developmental forces, adaptation, and drift [Striedter, 2005]. However, the

underlying selective forces remain poorly understood, hampered by our lack of understanding of phylogenetic, behavioral, allometric, and developmental constraints [Macphail, 2001; Deacon, 1990; Finlay & Darlington, 1995; Rehkämper et al., 2001]. Using the comparative method, we study how social organization shapes brain structure and function in a model evolutionary system, African cichlid fish [Dobberfuhl et al., 2005; Pollen et al., 2006]. In this study, we compare brain and behavior of closely related species differing in social organization (monogamy versus polygamy). The species share habitat preference and feeding behavior. Our goal is to understand the neural and molecular building blocks of complex brains and behavior, and how they are shaped over developmental and evolutionary time.

### 1.1 Exploring the Social Brain

Comparative studies have helped us begin to understand the social brain [Insel & Young, 2001]. Two productive approaches include:

**A) *Exploring the relationship between social complexity and brain size.*** These studies compare size of brain regions across species as a function of some measure of social complexity, assuming that size is related to the area's functional potential. While several correlations have been found, such a relationship does not always hold [Brodin, 2005].

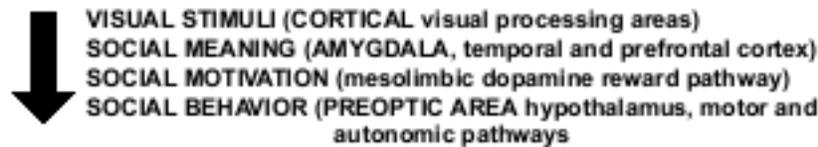
**B) *Exploring the role of neuropeptides in social behavior.*** Neuropeptide hormones (e.g., vasopressin/vasotocin (AVP/AVT), oxytocin/isotocin) are implicated in diverse complex social behaviors, including affiliative behavior (parental care, pair-bonding, social recognition), aggression, fear behavior and reproduction [Young & Wang, 2004; Carter, 2002]. While the presence of AVP/AVT is highly conserved across vertebrates, variations in the system may contribute to both interspecific and intraspecific variation in social behavior [Insel & Fernald, 2004].

### 1.2 The role of Plasticity in creating Different Social Brains

Do species differences in complex brains and behavior simply arise over the course of evolution, or does experience contribute to such changes? Vertebrate phenotypic change is associated with remarkable changes in social behavior and brain structure [Lott, 1991]. Many studies have shown experience-dependent plasticity in sensory areas, hippocampus, and on learning and memory in developing animals and adults [Shumway et al., 1999, 2005; Clayton, 1994]. In mammals, songbirds, and fish, social manipulations can affect neurogenesis, neuronal survival, and spine density in forebrain and midbrain areas [Fowler et al., 2002; Lipkind et al., 2002; Castellano et al., 2005; Coss & Globus, 1978].

## 2 Information Processing in the Social Brain

In this study, we explore the effects of social organization on the brains and behaviors of cichlid fishes, using the Insel and Fernald [2004] framework for information processing of social information (Figure 1).

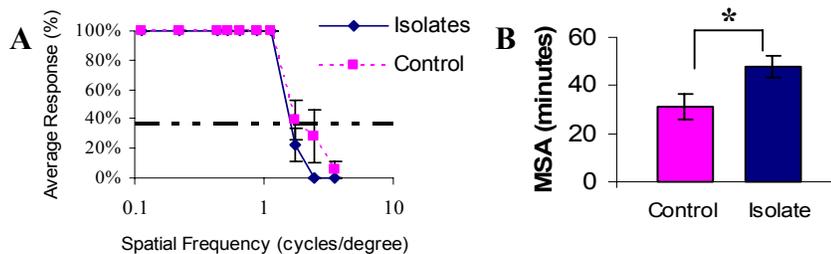


**Figure 1.** Information processing in the social brain [modified from Insel & Fernald, 2004].

## 3 Visual Processing

The social behavior of cichlid fishes relies upon visual signals. Several species can recognize conspecifics by visual cues alone (e.g., Jordan et al., 2003). We previously found that social organization is associated with differences in visual acuity [Doberfuhl et al., 2005]. We compared the visual acuity of adults from two species that differ solely in social organization (monogamy versus polygamy). These sand-dwelling species share the same beaches, feeding behavior, light levels, water quality, predators, and heterospecifics [our field data; Konings, 1996]. The polygamous species (*Enantiopus melanogenys*) detected spatial frequencies more than 2X greater than the monogamous one (*Xenotilapia flavipinnis*,  $p=0.0002$ ), and a minimal separable angle (MSA) one-half the size ( $p<0.05$ ) [Doberfuhl et al., 2005].

We then compared the effects of social experience on visual acuity, by comparing acuity of the monogamous species raised under two different social conditions: isolated and normal social groups. At 4 months, the visual acuity of the isolated fish was significantly decreased at the higher spatial frequencies (fig. 2;  $p < 0.05$ ). These results suggest that social experience contributes to the differences in visual behavior observed across species. Previous studies have demonstrated cichlid phenotypic plasticity for social and visual behavior, and brain and retinal structure [Insel & Fernald, 2004; Hofmann & Fernald, 2001; Kröger et al., 2001].

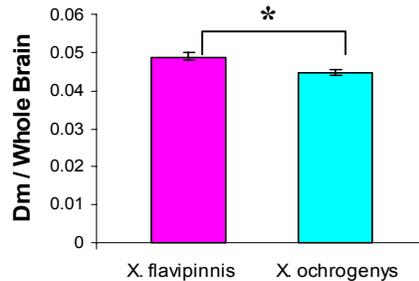


**Figure 2:** Visual acuity differs with social manipulations. **A.** Average response. Dashed line: 37% response level. (N = 4 isolates; 6 control). **B.** Minimal Separable Angle (N = 4 isolates; 6 control).

## 4 Social Meaning (Telencephalon and Amygdala)

Telencephalic size is correlated with social complexity, social learning, enhanced visual cognition, and innovation [Reader & Laland, 2002; Burish et al., 2004, but see Beauchamp & Fernandez-Juricic for an opposing view [2004]. In fish, the telencephalon is involved in a variety of social and cognitive behaviors, including courtship, parenting and learning [review: Demski & Beaver, 2001]. We previously showed that the telencephalon of monogamous species is 15-20% larger than that of polygamous species [Pollen et al., 2006], suggesting enhanced cognitive needs in monogamous fish.

In mammals, the amygdala has been implicated in both pair-bond formation and social recognition [Curtis & Wang 2003; Ferguson, et al. 2001]. In fish, area Dm is believed to be the amygdalar homologue [Northcutt 2006]. To determine what telencephalic structure is responsible for this expansion, we sectioned brains (50 $\mu$ m) and obtained volumetric measures of telencephalic regions with image analysis software (Image Pro). We found that area Dm was 9.4% larger in the monogamous, pair-bonding *X. flavipinnis* than the polygamous *X. ochrogenys* (Fig 3;  $p = .04$ ,  $n = 3$  fish/species, normalized for total brain volume). These results suggest that the task of social recognition required in these pair-bonding monogamous animals may be driving amygdalar expansion.



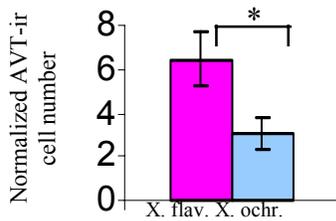
**Figure 3.** Amygdalar homologue, Dm, significantly differs in size with social organization ( $\pm$  SE,  $n = 3$ /species).

## 5 Social Behavior (Preoptic Area and AVT)

In mammals, both the amygdala and the integrative area called the preoptic area (POA) are implicated in pair-bond formation [Curtis & Wang, 2003]. The POA receives multimodal sensory information and may regulate telencephalic activity. It contains diverse neuropeptides, including AVT/AVP. AVP mediates social recognition: transgenic V1a knockout mice cannot recognize familiar conspecifics [Bielsky et al., 2004]. While a role for AVT in pair bonding or mate choice in fishes has not been demonstrated, expression levels of AVT mRNA and the abundance of AVT-mRNA producing cells correlate with mating behaviors [Perry & Grober, 2003]. AVT injections also inhibit social approach in highly social, but not asocial, goldfish [Thompson & Walton, 2004].

We sectioned the brains of monogamous *X. flavipinnis* and the polygamous *X. ochrogenys*, and stained them with an AVT antibody. An observer blind to species-

type compared the number of AVT-ir cells in the POA and found that there are significant differences in the number of AVT-ir cells in the POA with respect to mating system. Corrected for body size [Miranda et al., 2003], monogamous male *X. flavipinnis* had over 2X more AVT-ir cells than polygamous male *X. ochrogenys* (fig. 4; n=4 fish/species; p<0.05). These results, which corroborate differences in the AVT system between monogamous and polygamous voles [Insel & Fernald, 2004], support the notion that the AVT/AVP pathway is fundamental to vertebrate affiliation.



**Figure 4:** Normalized AVT-ir cell number (# cells/brain vol.) ± SE.

## 6 Conclusion

This paper shows a number of associations between brain/behavior and social organization. For us to better understand the relationship between complex brains and social behaviors, however, we will need to resolve how to quantify social complexity. Should a unitary measure be obtained, and is this valid for comparison across species? The problem is that researchers have not agreed on the best social measure. For example, monogamous, social voles have larger brains [Shapiro et al., 1991]. However, the social force (sociality or other aspect of monogamy such as biparenting) remains unknown, and the species' ecological differences may confound the results. In primates, brain size correlates with group size, range, and home range [Sawaguchi, 1988], but neocortex size correlates only with group size [Dunbar, 2002a,b]. In our research to date, we have compared numbers of species, abundance, social organization, and focal behaviors, and found differences for all measures. Another approach, originating from social anthropologists, is to compare groups of social traits across populations or species [Carneiro, 2003], using a scaleogram. Scaleograms incorporate both the number and frequency of social traits; more complex groups exhibit more traits.

A second issue is whether social forces cause qualitative changes in information processing, very different from environmental effects. Several lines of evidence support qualitative shifts during social evolution. In birds, no change is seen in telencephalic size with group size until the complexity of the social interactions is increased [Burish et al., 2004]. Similarly, in bower birds, brain size does not change with the complexity of the bower until the bower reaches a certain level of complexity [Madden, 2001]. In humans, the size of communities stays small unless the community has a second axis for classification among its members [Carneiro, 2000]. In our system, we find that social forces have very selective effects on brain structure, affecting far fewer structures than environmental forces [Pollen et al.,

2006]. Future effort in understanding complex brains and behaviors should be directed at understanding the differences in information processing for social and environmental tasks.

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