

Social cognition in fishes

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Brain evolution has often been correlated with the cognitive demands of social life. Further progress depends on our ability to link cognitive processes to corresponding brain part sizes and structures, and, ultimately, to demonstrate causality. Recent research suggests that fishes are suitable to test general hypotheses about vertebrate social cognition and its evolution: brain structure and physiology are rather conserved among vertebrates, and fish are able to perform complex decisions in social context. Here, we outline the opportunities for experimentation and comparative studies using fish as model systems, as well as some current shortcomings in fish social cognition research.

Introduction

In its broadest sense, social cognition refers to the mechanisms by which animals acquire, process, store, and act on information from other individuals [1]. Many apparently complex social interactions, such as those found in humans, may rely on specialized cognitive processes, including joint attention and sharing intentions, the ability to attribute beliefs and desires to other individuals ('theory of mind'), or the learning of behaviors through imitation of knowledgeable individuals [2,3]. Recent research has focused on emotional processes that may underlie more complex forms of cooperation, such as the ability to keep close stable bonds [4,5], the role of empathy [6], and inequity aversion (a negative response to receiving a smaller reward than that of a partner [7]). A general underlying assumption is that the use of such seemingly complex cognitive processes may only be possible with the evolution of specific brain areas and/or circuits. The standard approach to this assumption has been to correlate species differences in cognitive performance, in social organization and in other aspects of life considered cognitively demanding (e.g., extractive foraging) with brain size and/or brain part size [8]. Although a potentially valuable starting point, this approach has its shortcomings [2,9]. It cannot necessarily tell us much about the importance of sophisticated cognitive processes, because larger brains may often mean 'more of the same' rather than an improvement in the sophistication and number of possible cognitive processes [9,10]. There is also considerable debate concerning the links between variables that have been used as proxies for brain performance and cost, that is, absolute brain size,

brain size relative to body size, the absolute or relative size of specific brain parts known to be involved in cognitive processes, and precise brain structure such as cell density, connectivity, and so on [2,9,11]. This is beginning to be addressed in studies linking cognitive processes to the size of brain parts in primates [12]. Nevertheless, we need new independent samples (including groups of species other than birds and mammals) using a multivariate approach to control for potentially confounding ecological and/or life-history variables (such as climate or longevity) to explore the repeatability of published post-hoc interpretations of results [2].

In this context, fishes have begun to provide major insights concerning vertebrate social cognition, with some projects explicitly integrating the study of behavior, brain anatomy, and brain physiology. Since the publication of a book on fish social cognition and behavior that covers the literature until 2010 [13], various breakthroughs have been achieved in studies on fish brain anatomy and socio-cognitive abilities that will offer new possibilities for future research linking brain size and structure to environmental variables, social structure, and cognitive processes. Here, we evaluate the following points: (i) the discovery of important similarities in brain structure between fishes and other vertebrates suggests that various results obtained with fishes can be generalized; (ii) fish biologists are now studying the causes and consequences of variations in brain (part) size, applying concepts that were initially developed for primates, other mammals and birds; and (iii) increasing behavioral evidence indicates that at least some fish species may solve complex problems using fast learning, precise memory, and cognitive processes that go beyond conditioning.

Fish brains are remarkably similar in organization to those of other vertebrates

For any comparison of sociocognitive abilities between fishes and other vertebrate groups, it is important to know whether fish brains are similar or different to those from other groups with respect to organization and function. Classic studies emphasized the differences, such as the fact that fish have small brains relative to body size and a relatively small and unstructured forebrain (telencephalon) compared with birds and mammals [14]. However, recent studies emphasized similarities with respect to brain structures involved in social decision-making (Box 1). Most importantly, a large network of nuclei that is essential for learning and social behavior is highly conserved within vertebrates [15–18] (Figure 1). The hippocampus and amygdala (centers for memory formation

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Box 1. Social decision-making in vertebrate brains

Across vertebrates, a conserved (i.e., putatively homologous) social decision-making network (SDM) in the brain regulates social interactions (Figure 1, main text). It comprises the social behavior network (SBN) consisting of six mutually interconnected nuclei and/or brain areas [15], and the mesolimbic reward system (MRS) [16,18] consisting of seven mutually interconnected nuclei and/or brain areas. Two of the MRS nuclei are also part of the SBN, thus linking them into the SDM [16,18] (Figure 1, main text). The expression of hormones, neurohormones, enzymes, and receptors in these areas is similar among vertebrate groups [16].

The SBN brain nuclei and/or areas have sex-steroid receptors that help to regulate key social behaviors, such as parental care, aggression, mating and sexual behaviors, response to social stressors, and communication [15,16,34]. The SDM includes regions responsible for memory formation and for emotional assessment; that is, the fish equivalents of the mammalian hippocampus and amygdala (hippocampus: the ventral part of the dorsolateral region of the telencephalon; amygdala: the dorsal part of the dorsomedial area of the telencephalon [16,18,19]). The structural similarities fit well with a recent study that demonstrated that regular access to massage-like physical stimulation lowers stress levels in fish [85], as previously reported in humans [86] and proposed for other primates [87]. Thus, this fish reward system apparently functions such that a purely hedonistic experience without material benefits might positively affect survival and reproduction [85]. Regarding potential differences among vertebrate groups, the SDM will interact with other brain areas [16,34] and, if it does so with areas in the telencephalon and/or neocortex, this may have important implications for comparative social cognition.

and emotional assessment, respectively), form part of this network and have the same functions for all vertebrates investigated [19].

Other areas of fish and mammal brains also have important similarities in organization and function. In both groups, aversive stimuli or inappropriate outcomes lead to activation of the lateral habenula (a mesencephalic nucleus), which then affects motor and cognitive behaviors by inhibiting the activity of mesencephalic dopaminergic and serotonergic neurons [20]. Furthermore, the anatomy, development, and function of the cerebellum are conserved between mammals and bony fishes [21], and cerebellum lesions in both groups prevent associative learning in various contexts [22]. Also, the lateralization of brain functions (i.e., the selective processing of information in one hemisphere of the brain [23]) is now known to be widespread in fishes, as it is in birds and mammals [23–25]. Lateralization can reduce distance between connected brain parts and, thus, increase the speed of decision making [9]. Similarities between fish, mammal, and bird brains make it more likely that results on social cognition in fishes can be generalized to other vertebrates, and that concepts developed with mammals and birds can be tested on fishes. Regarding the latter, patterns include correlations between the relative size of key brain parts (such as the neocortex) and group size and extractive foraging (as found in primates), and correlations between pair bonding and brain measures (as found in birds and various mammalian groups) [8]. In the next section, we present recent findings linking brains and ecology in fishes.

Links between ecology and brain evolution in fishes

Comparative studies on brain evolution in mammals and birds have been criticized for various reasons, including failure to use multivariate methods to control for

potentially confounding ecological and life-history variables, and the analysis of overall brain size rather than brain part sizes [2]. These criticisms have been addressed in most of the fish studies presented here. Many studies on potential links between social cognition and brain evolution examine cichlids because their adaptive radiations with niche specialization have occurred repeatedly on local scales in the African Great Lakes. Ecological factors may cause selective adjustments to the size of relevant brain areas in cichlids, given that, in lake Tanganyika species, overall brain size explains only 86% of the variance in size of major brain areas [26]. This would be predicted if the size of each brain part can evolve at least in part independently of the other parts, rather than all brain parts being constrained to change in an entirely allometric manner with each other [2]. In the Ectodini cichlids of Lake Tanganyika, monogamy correlates with larger relative telencephalon size [27,28]. In a more diverse sample of Lake Tanganyika cichlid species, female parental care correlates with a larger brain overall [29], whereas the relative size of hypothalamus and cerebellum is decreased [30]. Habitat complexity, which is linked to interspecific social complexity, also seems to have major effects on the telencephalon and overall brain size in these cichlids [26–30]. This conclusion mirrors evidence for brain size reduction in island-dwelling birds and mammals, including hominids, as an adaptation to reduced ecological challenges [31]. A key point that emerges from these studies is that social cognition should not be restricted to interactions with conspecifics (i.e., [32]), but should extend to between-species competition, mutualism, and predator–prey relations, as also suggested for primates [3].

The correlative approach to the link between sociality and brain evolution may yield important insights when applied to fishes. Nevertheless, a more powerful approach would be to conduct experiments to infer brain–behavior links. A variety of potential tools has been used for such studies in vertebrates, such as functional magnetic resonance imaging (fMRI), lesions, methods for looking at immediate early gene action [2], and more recently, selection experiments for brain size [33]. In the next section, we discuss experimental approaches linking brains and behavior in fishes.

Brain parts as causal agents for social behavior in fishes

Recent investigations of immediate early gene expression have provided important insights concerning the functioning of the social decision-making network in the model cichlid species *Astatotilapia burtoni* [34]. Dominant males are easily recognizable by their color pattern, which differs from that of subordinate males. Dominance changes in both directions can easily be induced in the lab [35] to document the consequences on behavioral repertoire and gene expression. If an individual gains dominance, the mRNA levels of two immediate early genes (*cfos* and *egr-1*) are upregulated within minutes. Losing dominance causes the upregulation of only one of these genes [34]. The increased immediate early gene expression linked to the acquisition of dominance seems to cause an increase in the production of gonadotropin-releasing hormone (GnRH) [35], which has cascading effects on aggression and

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