

Social cognition in fishes

Redouan Bshary¹, Simon Gingins¹, and Alexander L. Vail²

¹ Department of Biology, University of Neuchâtel, Emile-Argand 11, 2000 Neuchâtel, Switzerland

² Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

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

Corresponding author: Bshary, R. (redouan.bshary@unine.ch).

Keywords: fish; social cognition; brain; physiology; behavior; ecological approach.

1364-6613/

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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

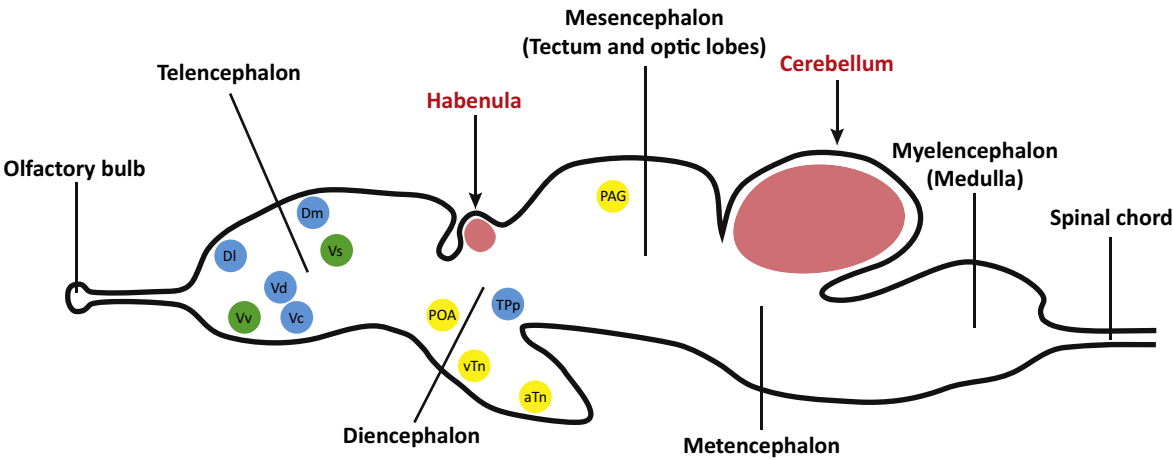
Comparative studies on brain evolution in mammals and birds have been criticized for various reasons, including failure to use multivariate methods to control for

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



The social decision-making network

Abbrev.	Name of brain nuclei for teleosts	Putative homolog structure in mammals
PAG	Periaqueductal gray	Periaqueductal gray
POA	Preoptic area	Preoptic area
vTn	Ventral tuberal nucleus	Anterior hypothalamus
aTn	Anterior tuberal nucleus	Ventromedial hypothalamus
Vs	Supracommissural part of the ventral pallidum	Extended amygdala
Vv	Ventral part of the ventral telencephalon	Lateral septum (and potentially pallidum)
Dl	Lateral part of the dorsal telencephalon	Hippocampus
Dm	Medial part of the dorsal telencephalon	Basolateral amygdala
TPp	Posterior tuberculum	Ventral tegmental area
Vc	Central part of the ventral telencephalon	Striatum and nucleus accumbens
Vd	Dorsal part of the ventral telencephalon	

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Figure 1. Regions of a fish brain involved in social cognition and conserved among vertebrates. Schematic representation of a sagittal section of a teleost brain (outline modified from [22]) that shows brain regions involved in social behavior that have recently been identified as conserved (i.e., homologous) within vertebrates. The teleost brain is divided into five large regions along the anteroposterior axis: telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon. The habenula (involved in controlling motor and cognitive behaviors) and the cerebellum (involved in associative learning) are represented in red. The social decision-making network comprises nuclei from the social behavior network (yellow) and the basal forebrain reward system (blue), with two nuclei involved in both the latter networks (green). The full name of each nucleus involved in the teleost social decision-making network and its putative mammalian homolog are given in the table below the figure. This figure recapitulates data on the social decision-making network and social behavior network from [15,16,18], but see [19] for a slightly different terminology.

reproductive behavior via the regulation of key fish hormones, such as 11-ketotestosterone, cortisol, and kisspeptin, in various brain areas, with changes taking place within a few hours to weeks [36]. Such changes increase the social competence of an individual [37]. Zebrafish offer similar opportunities as an experimental species, as well as great potential for genetic manipulations [17]. Understanding the brain physiology that underlies social behavior will be essential in unraveling the effects of brain structure and size differences among species.

A promising recent approach has been to select for larger and smaller brains and determine the associated behavioral effects. Apparently, brain size and functioning in fishes are flexible on individual, ecological, and evolutionary timescales [38–40]. Recently, Kotrschal *et al.* [33] showed that relative brain size diverged within one to two generations in response to artificial selection in guppies (*Poecilia reticulata*). Large-brained females outperformed small-brained females in a numerical-learning assay

designed to test cognitive ability, although effects on social cognition are currently unknown. An equally promising alternative approach would be to create selection lines exposed to different levels of social complexity to test whether brain size and structure evolve as a consequence.

Together, recent studies demonstrate generality among vertebrates in the brain features involved in social cognition. Fishes are suitable to investigate the physiological processes in the brain that underlie decision making, and to test hypotheses concerning the links between brain part size and/or structure evolution and ecological variables. In the remainder of this review, we evaluate the evidence that the cognitive abilities and processes facilitating fish social behavior may be similar to those in mammals and birds.

Cognitive performance of fishes in social contexts

The performance of humans and other animals in cognitive tasks is often used to infer the cognitive processes and decision rules that may underlie the behavior of subjects.

Behavioral tasks in the social domain have revealed various similarities between the decision rules and outcomes found in fishes and those in other vertebrates, including humans. The uses of fishes to develop and test hypotheses about group decision-making and collective cognition are presented in [Box 2](#). With respect to the decision rules underlying social learning, nine-spined sticklebacks have become a model system. Similar to humans, they use a ‘hill-climbing’ strategy whereby they compare their own success with that of a demonstrator, and base their decision to copy on the relative level of success observed [\[41\]](#). The decision from whom to learn is based on the success of potential demonstrators or a copy of the majority rule, using local enhancement [\[42–44\]](#). Studies on the use of social information to assess predation risk are revealing further abilities of fish to group closely related predators according to their smell [\[45,46\]](#), learn from heterospecifics [\[47\]](#), and incorporate multiple cues into decisions [\[48\]](#).

Counting abilities provide another example of similar cognitive mechanisms in fishes and mammals, including human infants. Shoaling fish typically prefer larger shoals over smaller shoals [\[49–52\]](#), allowing researchers to study their counting abilities in a social context. Mammals have two separate counting systems, one precise system for small numbers up to three or four, and one less precise for large quantities [\[53\]](#). Redtail splitfins [\[50\]](#), mosquitofish [\[49,51,54\]](#), guppies [\[55,56\]](#), and angelfish [\[52\]](#) match mammals in their performance on counting tasks, making it likely that the underlying mechanisms are similar.

Box 2. Collective cognition

Collective cognition is a young and dynamic field with a strong emphasis on theory, and models investigating the dynamics of group decisions continue to be developed (e.g., [\[88–90\]](#)). Collective behavior allows individuals to overcome their own cognitive limitations through emergent information-processing capabilities that are absent in individuals [\[91\]](#). The key point is that lack of knowledge would cause some individuals to make decision errors if alone. In a group, decision rules are in place so that knowledgeable individuals are followed preferentially [\[91–94\]](#). The importance of group cohesion for individual fitness prevents wrongly informed members from leaving the group and, thus, making an incorrect decision [\[93,95\]](#). A recent model proposes that following leaders might be more efficient for idiosyncratic decisions, whereas aggregating information is better for repeated decisions [\[90\]](#). Fishes have been instrumental to test various predictions from these recent theoretical models. First, it has been shown that collective behavior is beneficial in fishes, because the speed and accuracy of decisions increase with group size [\[94,96\]](#). Furthermore, not only the information available, but also group cohesion appear to have a role in group decisions, as was shown in golden shiner fish [\[95\]](#). Thus, group cohesion prevents wrongly informed individuals from committing their error. When information is unequally distributed, it appears that groups either aggregate the information and use quorum responses or follow a few informed individuals, referred to as ‘experts’ or ‘leaders’ (reviewed in [\[91,92\]](#)).

A powerful tool to test empirically the emerging theories is ‘robofish’, whose movement patterns are experimentally programmed and towards which real fish react relatively naturally [\[93,97\]](#). It has been used to show that, whereas singleton sticklebacks are susceptible to a leader behaving in a maladaptive way (going towards a predator), larger groups avoid this pitfall by using a quorum response [\[93\]](#). Similarly, in mosquitofish, the accuracy and speed of decision at choosing the predator-free arm of a Y-maze, despite a robofish leading them towards the predator-inhabited arm, increased with group size [\[94\]](#).

Cooperation between unrelated individuals is a topic where fish research has provided major contributions by showing that decision rules and partner control mechanisms that humans use to stabilize cooperation, in particular reciprocity, are found in other animals. The economists’ standard assumption that humans behave rationally, combined with the difficulty to prove reciprocal strategies in nonhuman animals [\[57,58\]](#), led to the conclusion that reciprocity is complex without scientists aiming to identify its underlying processes. It is often assumed that it relies on ‘quantitative abilities’, such as a precise memory of past interactions [\[10,57\]](#).

As a consequence, most research in nonhuman animals has focused on the ability of the subject to use various forms of reciprocity, and fishes have provided some of the best examples. Classic studies provide strong evidence that partner prey fish reciprocate when sharing the risks of inspecting a nearby predator [\[59\]](#). More recently, it was shown that guppies choose a partner that cooperates similarly to themselves for such inspections [\[60\]](#), and cooperation with specific partners stabilizes over time, because guppies are more cooperative with familiar partners [\[61\]](#). Cleaner wrasse have provided evidence for various important concepts developed to explain human cooperation. ‘Client’ reef fish visit cleaners to have ectoparasites removed, but cleaners prefer client mucus. The resulting conflict has led to various adaptations. For example, bystander clients pay close attention to the service quality that cleaners provide to current clients, and the cleaner *Labroides dimidiatus* is in return more cooperative if observed [\[62\]](#). Such audience effects have also been described in a competitive context in Amazonian mollies and the cichlid *A. burtoni*, where males alter courtship and aggressive behavior if observed by another male [\[63,64\]](#) and depending on their familiarity with the bystander [\[65\]](#). Furthermore, pairs of the cleaner wrasse *L. dimidiatus* solve the problem of remaining cooperative during co-inspections of clients where the one who cheats first benefits while both share the costs of a client leaving in response. The solution is asymmetric punishment: the larger males pay a cost to chase female partners when the latter cheat a client, a behavior that yields future benefits to both males and clients because females will behave more cooperatively [\[66\]](#). Males adjust punishment levels flexibly based on their relationship quality with the female and the value of the client [\[67,68\]](#). The various decision rules of the cleaner wrasse appear to be linked to rather unique cognitive challenges because they perform better in tasks replicating problems in natural client interactions than do closely related wrasse or primates [\[69,70\]](#). The underlying cognitive processes are poorly understood. Nevertheless, it has been shown that cleaners quickly relearn in reversal conditions (whereby the previously unsuccessful option becomes the successful option) [\[69\]](#), which demonstrates a flexibility that was proposed to be a key selection factor for the evolution of large brains [\[71\]](#). Furthermore, cleaners remember the ‘when’ and ‘what’ of their interactions [\[72\]](#), allowing them to choose clients with a greater parasite build-up because their last visit was longer ago. This performance comes close to the episodic-like memory described in food-caching jays (that, in

addition, remember where they hid food [73]). Finally, the roving cleaner wrasse *L. bicolor*, is more cooperative in core areas of its home range where the chances of repeated interactions are higher [74], a phenomenon called ‘the shadow of the future’ in the human literature.

A cooperative context in fishes where the interest is on coordination rather than on strategies is cooperative hunting, where individuals work together to catch prey. Yellow goatfish have been described to hunt in groups such that there are chasers and blockers, and all coordinate to pry out prey hiding in crevices [75]. By coordinating different complementary roles, they perform what is considered the most complex form of cooperative hunting: collaboration [76]. Groupers not only hunt collaboratively with Napoleon wrasse and moray eels, but also use referential gestures (i.e., signals used to draw the attention of the receiver to an external entity) to direct the attention of their partner towards hidden prey, fulfilling criteria used to classify communication as intentional (goal-directed) in apes and a corvid [77].

Taken together, the behavioral examples presented here show that fishes can exhibit sophisticated social behavior; that is, they solve problems suggested to involve complex coordination, precise memory, and decision making. Furthermore, some behaviors may involve cognitive processes that go beyond conditioning learning. The clearest evidence of a more complex cognitive process in fishes is the demonstration of transitive inference in the cichlid *A. burtoni*: by observing fights between males, they infer their rank order and, thus, who is dominant in pairs that they have never seen fighting each other [78]. Nevertheless, it has to be acknowledged that many cognitive processes that are currently focuses of interest in mammals and birds (typically in the context of stable individualized groups) have not yet been studied in fishes. Of particular interest are potential fish analogies of processes that, in anthropoid primates, apparently involve specialized regions, such as the frontal lobe of the neocortex, which is found only in this group [79]. Negative results, such as the apparent absence of inequity aversion in cleaner wrasse [80], would also be of value for the comparative approach. Likewise, complex communication and the evolution of language [81] is a subject that is rarely addressed in fishes (but see [77]).

Concluding remarks

Our main conclusion from the current literature on fish social cognition is that the brains and social behavior of fish are more similar to those of mammals and birds than previously appreciated. This conclusion yields various key topics for future research, including gaps that require closing (Box 3). Given that associative learning appears to be of paramount importance for fish [13], they seem particularly suitable to test how differences in performance (speed, precision, and volume of information learned, duration of its retention, and flexibility of use) translate into brain differences [9,10]. Complex cognitive processes, such as transitive inference, occur in fishes, but the diversity and taxonomic extent of these is poorly understood, despite fish already being used to study stress and psychological diseases with applications for human medical research [82–84]. The differential expression of complex cognitive

Box 3. Potential future avenues for fish social cognition research

One future line of research should build on recent progress, aiming at the full integration of research on brain structure, decision-making processes, and cognitive performance. The social decision-making network (SDM) appears to be of key importance and should be checked for connections to brain areas known to be involved in higher cognitive processes, because this is a likely source of variation in cognitive performance among taxa. Knowledge of the SDM should be combined with more classic measures of brain size, brain part size, structure, and interconnectivity. All of this should be applied to species living in a variety of environments and social systems, taking advantage of independent species radiations (e.g., cichlids) to determine the repeatability of results. On the behavioral side, we need to develop standardized tests that allow the comparison of cognitive performance among taxa. Suitable starting topics are those already well studied in fishes, such as swarm intelligence, social learning, and cooperation. Integrating disciplines would allow the cognitive performance of a species to be correlated with brain features and emerging predictions tested using lesions or immediate early gene methods.

Important insights will also be achieved by focusing on largely underexplored challenges. On the behavioral level, fish biologists should emulate the research of colleagues working on mammals and birds to test to what extent fishes have variants of supposedly advanced human cognitive processes: communication with aspects of human language, processes linked to a theory of mind, social bonds, and emotions. Furthermore, studies that link cognitive performance with brain evolution should include fish species that are primitive in the sense that they represent ancient lineages that have diverged the least from the common fish ancestor. Candidates include the bichirs (*Polypterus*) and reedfish (*Erpetoichthys*) (two genera of predatory bony fish inhabiting African rivers) and many of the 1200 species of cartilaginous fishes [98,99] (sharks, rays, skates, chimaeras, and elephant sharks). Studying such species will help to understand the ancestral form of the vertebrate brain and its subsequent adaptations.

processes in closely related species will potentially allow the neural causes and/or consequences of such cognitive tools to be identified.

Acknowledgments

We thank the reviewers and Klaus Zuberbühler for their helpful comments on a previous version. We further thank the Neuchâtel behavioural ecology group and the comparative cognition group for discussion. R.B. is funded by the Swiss Science Foundation and A.L.V. by a Gates Cambridge Scholarship.

References

- Shettleworth, S.J. (2009) *Cognition, Evolution, and Behavior*, Oxford University Press
- Healy, S.D. and Rowe, C. (2007) A critique of comparative studies of brain size. *Proc. Biol. Sci.* 274, 453–464
- Zuberbühler, K. and Byrne, R.W. (2006) Social cognition. *Curr. Biol.* 16, R786–R790
- Silk, J.B. *et al.* (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. Biol. Sci.* 276, 3099–3104
- Seyfarth, R.M. and Cheney, D.L. (2013) Affiliation, empathy, and the origins of theory of mind. *Proc. Natl. Acad. Sci. U.S.A.* 110, 10349–10356
- De Waal, F.B.M. (2012) The antiquity of empathy. *Science* 336, 874–876
- Brosnan, S.F. (2013) Justice and fairness-related behaviors in nonhuman primates. *Proc. Natl. Acad. Sci. U.S.A.* 110, 10416–10423
- Dunbar, R.I.M. and Shultz, S. (2007) Evolution in the social brain. *Science* 317, 1344–1347
- Chittka, L. and Niven, J. (2009) Are bigger brains better? *Curr. Biol.* 19, R995–R1008

- 10 Bshary, R. *et al.* (2011) How intelligent is Machiavellian behavior? In *Animal Thinking: Contemporary Issues in Comparative Cognition* (Menzel, R. and Fisher, J., eds), pp. 209–221, MIT Press
- 11 Shultz, S. and Dunbar, R.I.M. (2010) Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biol. J. Linn. Soc.* 100, 111–123
- 12 Shultz, S. and Dunbar, R.I.M. (2010) Species differences in executive function correlate with hippocampus volume and neocortex ratio across nonhuman primates. *J. Comp. Psychol.* 124, 252–260
- 13 Brown, C. *et al.*, eds (2011) *Fish Cognition and Behavior* (2nd edn), John Wiley & Sons
- 14 Jerison, H. (1973) *Evolution of the Brain and Intelligence*, Elsevier
- 15 Goodson, J.L. (2005) The vertebrate social behavior network: evolutionary themes and variations. *Horm. Behav.* 48, 11–22
- 16 O'Connell, L.A. and Hofmann, H.A. (2012) Evolution of a vertebrate social decision-making network. *Science* 336, 1154–1157
- 17 Oliveira, R.F. (2013) Mind the fish: zebrafish as a model in cognitive social neuroscience. *Front. Neural Circuits* 7, 131
- 18 O'Connell, L.A. and Hofmann, H.A. (2011) The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis. *J. Comp. Neurol.* 519, 3599–3639
- 19 Demski, L.S. (2013) The pallium and mind/behavior relationships in teleost fishes. *Brain Behav. Evol.* 82, 31–44
- 20 Amo, R. *et al.* (2010) Identification of the zebrafish ventral habenula as a homolog of the mammalian lateral habenula. *J. Neurosci.* 30, 1566–1574
- 21 Hibi, M. and Shimizu, T. (2012) Development of the cerebellum and cerebellar neural circuits. *Dev. Neurobiol.* 72, 282–301
- 22 Hutardo-Parrado, C. (2010) Neuronal mechanisms of learning in teleost fish. *Univ. Psychol.* 9, 663–678
- 23 Arnott, G. *et al.* (2011) Lateralization of lateral displays in convict cichlids. *Biol. Lett.* 7, 683–685
- 24 Moscicki, M.K. *et al.* (2011) Lateralized behaviour of a non-social cichlid fish (*Amatitlania nigrofasciata*) in a social and a non-social environment. *Behav. Processes* 88, 27–32
- 25 Karenina, K.A. *et al.* (2012) Eye as a key element of conspecific image eliciting lateralized response in fish. *Anim. Cogn.* 16, 287–300
- 26 Gonzalez-Voyer, A. *et al.* (2009) Brain structure evolution in a basal vertebrate clade: evidence from phylogenetic comparative analysis of cichlid fishes. *BMC Evol. Biol.* 9, 238
- 27 Shumway, C.A. (2010) The evolution of complex brains and behaviors in African cichlid fishes. *Curr. Zool.* 56, 144–156
- 28 Pollen, A.A. *et al.* (2007) Environmental complexity and social organization sculpt the brain in lake Tanganyikan cichlid fish. *Brain Behav. Evol.* 70, 21–39
- 29 Gonzalez-Voyer, A. *et al.* (2009) Social fishes and single mothers: brain evolution in African cichlids. *Proc. Biol. Sci.* 276, 161–167
- 30 Gonzalez-Voyer, A. and Kolm, N. (2010) Sex, ecology and the brain: evolutionary correlates of brain structure volumes in Tanganyikan cichlids. *PLoS ONE* 5, e14355
- 31 Kubo, D. *et al.* (2013) Brain size of *Homo floresiensis* and its evolutionary implications. *Proc. R. Soc. B* 280, 20130338
- 32 Székely, T. *et al.* (2010) *Social Behaviour: Genes, Ecology and Evolution*, Cambridge University Press
- 33 Kotrschal, A. *et al.* (2013) Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. *Curr. Biol.* 23, 168–171
- 34 Maruska, K.P. *et al.* (2013) Social descent with territory loss causes rapid behavioral, endocrine and transcriptional changes in the brain. *J. Exp. Biol.* 216, 3656–3666
- 35 Fernald, R.D. and Maruska, K.P. (2012) Social information changes the brain. *Proc. Natl. Acad. Sci. U.S.A.* 109, 17194–17199
- 36 Huntingford, F.A. (2012) The physiology of fish behaviour: a selective review of developments over the past 40 years. *J. Fish Biol.* 81, 2103–2126
- 37 Taborsky, B. and Oliveira, R.F. (2012) Social competence: an evolutionary approach. *Trends Ecol. Evol.* 27, 679–688
- 38 Gonda, A. *et al.* (2012) Brain development and predation: plastic responses depend on evolutionary history. *Biol. Lett.* 8, 249–252
- 39 Ebbesson, L.O.E. and Braithwaite, V.A. (2012) Environmental effects on fish neural plasticity and cognition. *J. Fish Biol.* 81, 2151–2174
- 40 Wismer, S. *et al.* (2014) Variation in cleaner wrasse cooperation and cognition: influence of the developmental environment? *Ethology* 120, 519–531
- 41 Kendal, J.R. *et al.* (2009) Nine-spined sticklebacks deploy a hill-climbing social learning strategy. *Behav. Ecol.* 20, 238–244
- 42 Pike, T.W. *et al.* (2010) Learning by proportional observation in a species of fish. *Behav. Ecol.* 21, 570–575
- 43 Pike, T.W. and Laland, K.N. (2010) Conformist learning in nine-spined sticklebacks' foraging decisions. *Biol. Lett.* 6, 466–468
- 44 Webster, M.M. and Laland, K.N. (2013) The learning mechanism underlying public information use in ninespine sticklebacks (*Pungitius pungitius*). *J. Comp. Psychol.* 127, 154–165
- 45 Brown, G.E. *et al.* (2011) Generalization of predators and nonpredators by juvenile rainbow trout: learning what is and is not a threat. *Anim. Behav.* 81, 1249–1256
- 46 Mitchell, M.D. *et al.* (2013) Generalization of learned predator recognition in coral reef ecosystems: how cautious are damselfish? *Funct. Ecol.* 27, 299–304
- 47 Manassa, R.P. *et al.* (2013) Socially acquired predator recognition in complex ecosystems. *Behav. Ecol. Sociobiol.* 67, 1033–1040
- 48 Manassa, R.P. *et al.* (2013) Coral reef fish incorporate multiple sources of visual and chemical information to mediate predation risk. *Anim. Behav.* 86, 717–722
- 49 Agrillo, C. *et al.* (2008) Do fish count? Spontaneous discrimination of quantity in female mosquitofish. *Anim. Cogn.* 11, 495–503
- 50 Stancher, G. *et al.* (2013) Discrimination of small quantities by fish (redtail splitfin, *Xenotoca eiseni*). *Anim. Cogn.* 16, 307–312
- 51 Dadda, M. *et al.* (2009) Spontaneous number representation in mosquitofish. *Cognition* 112, 343–348
- 52 Gómez-Laplaza, L.M. and Gerlai, R. (2011) Can angelfish (*Pterophyllum scalare*) count? Discrimination between different shoal sizes follows Weber's law. *Anim. Cogn.* 14, 1–9
- 53 Feigenson, L. *et al.* (2004) Core systems of number. *Trends Cognit. Sci.* 8, 307–314
- 54 Agrillo, C. *et al.* (2009) Use of number by fish. *PLoS ONE* 4, e4786
- 55 Piffer, L. *et al.* (2012) Small and large number discrimination in guppies. *Anim. Cogn.* 15, 215–221
- 56 Piffer, L. *et al.* (2013) Large number discrimination in newborn Fish. *PLoS ONE* 8, e62466
- 57 Hammerstein, P. (2003) Why is reciprocity so rare in social animals? a protestant appeal. In *Genetic and Cultural Evolution of Cooperation* (Hammerstein, P., ed.), pp. 83–93, Cambridge, MA, MIT Press
- 58 Raihani, N.J. and Bshary, R. (2011) Resolving the iterated prisoner's dilemma: theory and reality. *J. Evol. Biol.* 24, 1628–1639
- 59 Milinski, M. *et al.* (1990) Tit for tat: sticklebacks (*Gasterosteus aculeatus*) "trusting" a cooperating partner. *Behav. Ecol.* 1, 7–11
- 60 Croft, D.P. *et al.* (2006) Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* 59, 644–650
- 61 Granroth-Wilding, H.M.V. and Magurran, A.E. (2013) Asymmetry in pay-off predicts how familiar individuals respond to one another. *Biol. Lett.* 9, 20130025
- 62 Pinto, A. *et al.* (2011) Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Curr. Biol.* 21, 1140–1144
- 63 Bierbach, D. *et al.* (2011) Male fish use prior knowledge about rivals to adjust their mate choice. *Biol. Lett.* 7, 349–351
- 64 Desjardins, J.K. *et al.* (2012) Social context influences aggressive and courtship behavior in a cichlid fish. *PLoS ONE* 7, e32781
- 65 Dziewieczynski, T.L. and Perazio, C.E. (2012) I know you: familiarity with an audience influences male-male interactions in Siamese fighting fish, *Betta splendens*. *Behav. Ecol. Sociobiol.* 66, 1277–1284
- 66 Raihani, N.J. *et al.* (2010) Punishers benefit from third-party punishment in fish. *Science* 327, 171
- 67 Raihani, N.J. *et al.* (2011) Male cleaner wrasses adjust punishment of female partners according to the stakes. *Proc. R. Soc. B* 279, 365–370
- 68 Raihani, N.J. *et al.* (2012) Female cleaner fish cooperate more with unfamiliar males. *Proc. Biol. Sci.* 279, 2479–2486
- 69 Salwiczek, L.H. *et al.* (2012) Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orang-utans in a complex foraging task derived from cleaner–client reef fish cooperation. *PLoS ONE* 7, e49068
- 70 Gingins, S. *et al.* (2013) Power and temptation cause shifts between exploitation and cooperation in a cleaner wrasse mutualism. *Proc. Biol. Sci.* 280, 20130553

- 71 Van Schaik, C.P. *et al.* (2012) Explaining brain size variation: from social to cultural brain. *Trends Cognit. Sci.* 16, 277–284
- 72 Salwiczek, L.H. and Bshary, R. (2011) Cleaner wrasses keep track of the “when” and “what” in a foraging task. *Ethology* 117, 939–948
- 73 Clayton, N.S. and Dickinson, A. (1998) Episodic-like memory during cache recovery by scrub jays. *Nature* 395, 272–274
- 74 Oates, J. *et al.* (2010) The shadow of the future affects cooperation in a cleaner fish. *Curr. Biol.* 20, R472–R473
- 75 Strübin, C. *et al.* (2011) On group living and collaborative hunting in the yellow saddle goatfish (*Parupeneus cyclostomus*). *Ethology* 117, 961–969
- 76 Boesch, C. and Boesch, H. (1989) Hunting behavior of wild chimpanzees in the Taï National Park. *Am. J. Phys. Anthropol.* 78, 547–573
- 77 Vail, A.L. *et al.* (2013) Referential gestures in fish collaborative hunting. *Nat. Commun.* 4, 1765
- 78 Grosenick, L. *et al.* (2007) Fish can infer social rank by observation alone. *Nature* 445, 429–432
- 79 Passingham, R.E. and Wise, S.P. (2012) *The Neurobiology of the Prefrontal Cortex: Anatomy, Evolution, and the Origin of Insight*, Oxford University Press
- 80 Raihani, N.J. *et al.* (2012) Are cleaner fish, *Labroides dimidiatus*, inequity averse? *Anim. Behav.* 84, 665–674
- 81 Zuberbühler, K. (2013) Primate communication. In *New Perspectives on the Origins of Language* (Lefebvre, C. *et al.*, eds), pp. 187–210, John Benjamins Publishing Company
- 82 Formella, I. *et al.* (2012) Transient knockdown of tyrosine hydroxylase during development has persistent effects on behaviour in adult zebrafish (*Danio rerio*). *PLoS ONE* 7, e42482
- 83 Sørensen, C. *et al.* (2013) Neural plasticity and stress coping in teleost fishes. *Gen. Comp. Endocrinol.* 181, 25–34
- 84 Spinello, C. *et al.* (2013) Acute ethanol administration affects zebrafish preference for a biologically inspired robot. *Alcohol* 47, 391–398
- 85 Soares, M.C. *et al.* (2011) Tactile stimulation lowers stress in fish. *Nat. Commun.* 2, 534
- 86 Field, T. *et al.* (2005) Cortisol decreases and serotonin and dopamine increase following massage therapy. *Int. J. Neurosci.* 115, 1397–1413
- 87 Dunbar, R.I.M. (2010) The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neurosci. Biobehav. Rev.* 34, 260–268
- 88 Torney, C. *et al.* (2009) Context-dependent interaction leads to emergent search behavior in social aggregates. *Proc. Natl. Acad. Sci. U.S.A.* 106, 22055–22060
- 89 Grunbaum, D. (2012) A spatially explicit Bayesian framework for cognitive schooling behaviours. *Interface Focus* 2, 738–745
- 90 Katsikopoulos, K.V. and King, A.J. (2010) Swarm intelligence in animal groups: when can a collective out-perform an expert? *PLoS ONE* 5, e15505
- 91 Couzin, I.D. (2009) Collective cognition in animal groups. *Trends Cognit. Sci.* 13, 36–43
- 92 Conradt, L. and Roper, T.J. (2005) Consensus decision making in animals. *Trends Ecol. Evol.* 20, 449–456
- 93 Ward, A.J.W. *et al.* (2008) Quorum decision-making facilitates information transfer in fish shoals. *Proc. Natl. Acad. Sci. U.S.A.* 105, 6948–6953
- 94 Ward, A.J.W. *et al.* (2011) Fast and accurate decisions through collective vigilance in fish shoals. *Proc. Natl. Acad. Sci. U.S.A.* 108, 2312–2315
- 95 Miller, N. *et al.* (2013) Both information and social cohesion determine collective decisions in animal groups. *Proc. Natl. Acad. Sci. U.S.A.* 110, 5263–5268
- 96 Sumpter, D.J.T. *et al.* (2008) Consensus decision making by fish. *Curr. Biol.* 18, 1773–1777
- 97 Faria, J.J. *et al.* (2010) A novel method for investigating the collective behaviour of fish: introducing “Robofish.”. *Behav. Ecol. Sociobiol.* 64, 1211–1218
- 98 Yopak, K.E. (2012) Neuroecology of cartilaginous fishes: the functional implications of brain scaling. *J. Fish Biol.* 80, 1968–2023
- 99 Collin, S.P. (2012) The neuroecology of cartilaginous fishes: sensory strategies for survival. *Brain Behav. Evol.* 80, 80–96