

# 1 Social plasticity in the fish brain: 2 Neuroscientific and ethological aspects

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28

## 29 Abstract

30 Social plasticity, defined as the ability to adaptively change the expression of social  
31 behavior according to previous experience and to social context, is a key ecological  
32 performance trait that should be viewed as crucial for Darwinian fitness. The neural  
33 mechanisms for social plasticity are poorly understood, in part due to skewed reliance  
34 on rodent models. Fish model organisms are relevant in the field of social plasticity for  
35 at least two reasons: first, the diversity of social organization among fish species is  
36 staggering, increasing the breadth of evolutionary relevant questions that can be asked.  
37 Second, that diversity also suggests translational relevance, since it is more likely that  
38 “core” mechanisms of social plasticity are discovered by analyzing a wider variety of  
39 social arrangements than relying on a single species. We analyze examples of social  
40 plasticity across fish species with different social organizations, concluding that a “core”  
41 mechanism is the initiation of behavioral shifts through the modulation of a conserved  
42 “social decision-making network”, along with other relevant brain regions, by  
43 monoamines, neuropeptides, and steroid hormones. The consolidation of these shifts  
44 may be mediated via neurogenomic adjustments and regulation of the expression of  
45 plasticity-related molecules (transcription factors, cell cycle regulators, and plasticity  
46 products).

47 *Keywords:* Brain plasticity; cichlids; cleanerfish; social plasticity; social decision making  
48 network; zebrafish.



## 50 1. Introduction

51           The ability to adapt to changing social environments is a crucial characteristic of  
52 biological systems; social plasticity, defined “as the ability to adaptively change the  
53 expression of social behavior according to previous experience and to social context”  
54 (Teles et al. 2016) is a key ecological performance trait that should be viewed as crucial  
55 for Darwinian fitness (Taborsky and Oliveira 2012). The neural mechanisms for social  
56 plasticity are poorly understood, in part due to over-reliance on rodent models (e.g.,  
57 Krishnan et al., 2007 and Curley et al., 2011; but see important work on estrildid finches  
58 – e.g., Goodson and Kingsbury, 2011; Goodson et al., 2012) and examination of only a  
59 single sex within a species. In principle, these mechanisms involve the modulation of  
60 the activity of the social decision-making brain network (O’Connell and Hofmann 2012a)  
61 and other relevant brain nuclei on the short term - by neuromodulators (e.g.,  
62 neuropeptides and monoamines) and hormones (eg., sex steroids and glucocorticoids) -  
63 and on the long term - by modulating gene expression patterns across the network  
64 (Oliveira, 2009; Taborsky and Oliveira 2012; Cardoso et al. 2015).

65           The present review summarizes ongoing research on social plasticity in the fish  
66 brain. Fish model organisms are relevant and an ideal vertebrate group to examine  
67 social plasticity for at least two reasons: first, the diversity of social organization  
68 between fish species is staggering, increasing the breadth of evolutionary relevant  
69 questions that can be addressed. Second, that diversity also suggests translational  
70 relevance, since it is more likely that “core” mechanisms of social plasticity are

71 discovered by examining a wider variety of social arrangements than relying on a single  
72 species. Both issues are discussed in Sections 2 to 4. We proceed, in Sections 5 and 6,  
73 by discussing research on social and reproductive status as triggers for plasticity, and  
74 examining sensory and cognitive aspects of social plasticity in fishes. The specific  
75 example of cleanerfish, which exhibit mutualism but is currently under-studied in  
76 behavioral and molecular neuroscience, is analyzed further in Section 6, along with the  
77 role of brain size in social plasticity in guppies. We hope to demonstrate that, from  
78 cichlids to poeciliids (e.g., livebearers such as swordtails, mollies, and guppies), from  
79 zebrafish to cleanerfish, the variety of social interaction networks observed among  
80 fishes is of interest to both evolutionary neuroscientists and behavioral neuroscientists  
81 interested in describing the core mechanisms regulating and driving social plasticity.

82

## 83 2. Fish as models in the neurosciences

84 While a great deal of work on social plasticity of the brain has been made using  
85 rodents, this strict focus risks missing opportunities to answer questions on the  
86 evolution of social plasticity (Panksepp et al., 2002; Striedter et al., 2014; Taborsky and  
87 Oliveira, 2012), as well as the rich variety of social environments that fish occupy  
88 (Keenleyside, 1979). The use of rodents is certainly relevant due to the phylogenetic  
89 position occupied by these animals in relation to humans, but can overlook important  
90 variants of social organization that exist in fishes. Indeed, more than 30,000 species of  
91 fishes are estimated to occupy both marine and freshwater habitats

92 (<http://www.coml.org/>) (Nelson et al., 2016). These species occupy different social  
93 niches (Section 3), and include single fishes with solitary living and territorial mosaics,  
94 animals which establish male-female pairs, animals which live in small groups, animals  
95 which form shoals (individuals moving together as a group, but may orient in different  
96 directions) and schools (individuals in the shoal all oriented in the same direction), and  
97 many other varieties of social organizations (Keenleyside, 1979). Identifying how these  
98 different social societies impact brain and behavior, and how changing social  
99 environments alter these domains, is an important question to be exploited in the field of  
100 social plasticity (Figure 1).

101 It has been suggested (Gerlai, 2014; Kas et al., 2011) that increasing the breadth  
102 of species used in biomedical research “can robustly enhance our ability to identify  
103 biological features and mechanisms that are relevant to the studied behavioral  
104 phenomena” (Gerlai, 2014, p. 55). The choice of species and model organisms, in the  
105 case of the neurosciences, is usually guided by practical advantages (including fertility,  
106 throughput, and developmental speed), the existence of well-established research  
107 communities and data availability (including genomic and transcriptomic data), and the  
108 amenability to undertake genetic manipulations and relative simplicity of the nervous  
109 system (Maximino et al., 2015). In addition to using well-established model organisms,  
110 behavioral neuroscience can benefit from focusing on other, carefully chosen species to  
111 amplify the field of discovery and increase translational relevance (Gerlai, 2014; Hall et  
112 al., 2014; Maximino et al., 2015). In the context of evolutionary neuroscience, Striedter  
113 et al. (2014) used the term “reference species” that meant “carefully selected species  
114 from phylogenetically widely spaced vertebrate and invertebrate groups”. These

115 reference species are not “models for some other species, but [...] a basis for  
116 comparisons that may reveal both similarities and differences” (Striedter et al., 2014, p.  
117 5), ultimately increasing translational relevance by “allowing one to identify common  
118 features across species [that are likely to be] shared not just among the studied  
119 laboratory organisms but also with humans” (Gerlai, 2014, p. 55). In fact, historically,  
120 many of the most significant discoveries allowing the field of basic neuroscience to  
121 advance were made in diverse taxa ranging from invertebrates (e.g. squid, *Aplysia*,  
122 crustaceans) to vertebrates (e.g. fishes, frogs, mammals). A similar approach to other  
123 fields of neuroscience can benefit the field by comparing taxa to infer how variations in  
124 one domain (e.g., gene expression, connectivity, activation patterns) relates to variation  
125 in behavior. Of relevance to the question of social plasticity, fish species can be used to  
126 understand how variations in social environment impact variations in behavior and brain  
127 structure and function (Soares et al., 2018a).

128         One advantage of using fishes to better understand social plasticity of the  
129 vertebrate brain is the ability to study species in a naturalistic context; something rarely  
130 achieved in other social vertebrate models such as rodents. Studying fish social  
131 behavior in the wild or in laboratory settings that include salient sensory, environmental,  
132 and social factors is crucial for discovering accurate neurobiological mechanisms as  
133 well as the selective pressures leading to evolutionary adaptations. Because many  
134 aspects of neural function are conserved, investigations in amenable systems like fishes  
135 have and will continue to provide valuable insights for biomedical applications. Recent  
136 advances in genomic and genetic tools for different fish species also increase their  
137 utility in social neuroscience. Thus, by abiding to Krogh’s principle that for most



138 biological problems, there exists a species that is ideally suited (Krogh, 1929), the  
139 diversity of fish species becomes a cornucopia of possibilities for knowledge advances.  
140 This includes promise for better understanding mechanisms of and treatments for  
141 reproductive, endocrine, neuroendocrine, and neurological disorders in humans that can  
142 be influenced by the social environment.

143 Fish are also excellent reference species to study social plasticity because their  
144 brains are admirably plastic. Neural plasticity can involve structural changes, such as  
145 alterations in cell population size or connectivity between different nuclei by changing  
146 axonal growth and survival or dendritic synaptic connections (Cline, 2001). In contrast to  
147 mammals, in which neurogenesis is very limited in adulthood, the formation of new  
148 neurons continues throughout the fish's entire life (Zupanc and Sirbulescu, 2011).  
149 Continuing expression of *growth-associated protein-43 (gap-43)*, a marker of  
150 axonogenesis, in the brains of coho salmon *Oncorhynchus kisutch* (Ebbeson and  
151 Braithwaite, 2012), suggests that connectivity also changes throughout adulthood.  
152 Moreover, heightened plasticity is observed at critical periods of development, such as  
153 those associated with leaving fresh water and migrating to the ocean in salmon such as  
154 *Salmo salar* and *Onchorhynchus* sp. In these species, important behavioral  
155 preparations in this transition period include olfactory imprinting on their natal stream  
156 and switching from territorial to schooling behavior; these changes are accompanied by  
157 sequential changes in structure reorganization, and increased neuronal differentiation,  
158 neurogenesis, axonogenesis, and synaptogenesis (reviewed in Ebbeson and  
159 Braithwaite, 2012). Finally, the high adult neurogenesis in fish also facilitate high levels  
160 of neuronal regeneration: after injury of nervous tissue, a massive surge of apoptotic

161 cell death occurs at the lesion site, followed by a marked increase in cell proliferation  
162 and neurogenesis. There is also evidence for structural reorganization and  
163 neurogenesis related to the social environment, including social isolation, in several fish  
164 species (Sorensen et al., 2007; Maruska et al., 2012; Dunlap et al., 2013). The exquisite  
165 plasticity of the fish brain suggests that this group could represent interesting reference  
166 species and/or model organisms in the study of the social plasticity of the brain.

167 Further, fishes are becoming valuable models to study impacts of anthropogenic  
168 noise, pollution, and climate change on sensory and brain function (Ashur et al., 2017;  
169 Braun, 2015; Fisher and Oleksiak, 2007; Lai et al., 2017), with important consequences  
170 for management and conservation. Sensory cues play an integral role in the daily lives  
171 and survival of marine and freshwater organisms, including influences on homing,  
172 settlement, predator detection and evasion, foraging, conspecific social interactions,  
173 and reproductive interactions. Ocean acidification, as a consequence of climate change  
174 and pollution, directly affects the performance of sensory systems of marine organisms,  
175 including chemosensation, acoustic detection, and vision (review in Ashur et al., 2017).  
176 Sound pollution (anthropogenic noise) disrupts both the octavolateralis systems of  
177 fishes (which include the vestibular, auditory, lateral line and electrosensory systems)  
178 and the sonic environment that provide ecological and ethological cues for fish behavior  
179 (review in Braun, 2015). These impacts on systems which show critical social plasticity  
180 are beginning to be understood, and studying these in diverse fish species have  
181 important ecological and economic consequences, particularly in identifying how fishes  
182 may or may not be able to adapt to a changing world.

183 In addition to increasing possibilities to understand social plasticity, fish models

184 can also increase translational relevance for research in social behavior (Oliveira, 2009;  
185 Soares et al., 2018a). This is relevant, because human sociality is crucial for mental  
186 health, and social stressors represent a very important source of suffering that can lead  
187 to mental disorders (Soares et al., 2018b). Moreover, alterations in social behavior are  
188 also observed in different disorders, including social anxiety disorder, autism, Williams  
189 syndrome, reactive attachment disorder, and disinhibited attachment disorder (Kennedy  
190 and Adolphs, 2012). One caveat to keep in mind when using a comparative approach is  
191 that fishes have different sensory abilities and live in an aquatic environment with  
192 sensory transmission characteristics that differ from those in air. Thus, the species  
193 sensory '*umwelt*' will influence their social behaviors and should be considered when  
194 making translational applications (von Uexkull, 1926). However, the use of relevant  
195 model organisms and reference species, including fish, is important to understand the  
196 value and expression of social behavior and the role of genes and the (social)  
197 environment interactions in shaping mental disorders (Huhman, 2006; Lim et al., 2005;  
198 McOmish et al., 2014; Soares et al., 2018ab).

199

### 200 3. The social brain of fish

201 Across vertebrates, social behavior is ultimately controlled by the brain. A neural  
202 "survival" circuit involved in both reward and sociality, termed the "social decision  
203 making network" (SDMN; Figure 2), was proposed as a framework for testing  
204 hypotheses on the neural control of context-dependent behaviors. This network

205 encompasses both the social behavior network and mesolimbic reward system, both of  
206 which include a series of brain regions that regulate and integrate responses to salient  
207 stimuli (including social and non-social stimuli) (O'Connell and Hofmann 2011). The  
208 SDMN involves, in mammals, the lateral septum, extended medial amygdala and bed  
209 nucleus of the stria terminalis, preoptic area/paraventricular nucleus (POA/PVN),  
210 anterior hypothalamus, ventromedial hypothalamus, and periaqueductal gray area, as  
211 well as six areas of the mesolimbic reward system – the striatum, nucleus accumbens,  
212 ventral pallidum, basolateral amygdala, hippocampus, and ventral tegmental area  
213 (Figure 2). This network is involved in multiple forms of social behavior, including sexual  
214 behavior and courtship, aggression, and parental care, and its nodes are reciprocally  
215 connected (Goodson 2005; O'Connell and Hofmann, 2011). By definition, these nodes  
216 also express sex hormone receptors (Forlano and Bass, 2011; O'Connell and Hofmann,  
217 2011, 2012).

218 Nodes of the SDMN are identified in teleost fish, although for many of them only  
219 partial homologies have been established and many remain undefined, debated, or  
220 controversial (cf. Soares et al. 2018a for a review; Goodson and Kingsbury, 2013)  
221 (Table 1). This is primarily due to the differences in forebrain development between  
222 teleosts (eversion) and tetrapods (evagination). In all ray-finned fishes, the outward  
223 folding, or eversion, of the solid telencephalic lobes results in positioning of pallial nuclei  
224 that border a single ventricular cavity (along midline and surrounding outside of  
225 hemispheres) rather than paired telencephalic hemispheres surrounding an internal  
226 ventricle (Nieuwenhuys, 2011). These developmental processes place many nuclei  
227 (particularly those of the dorsal telencephalon) in different locations between teleosts

228 and other vertebrates, making direct homologies more difficult. While the SDMN  
229 represents a starting framework to study neural mechanisms of social behaviors, it is  
230 becoming increasingly clear that many other brain regions (e.g. raphe nuclei, habenula,  
231 reticular nuclei, and many others) are also involved in both receiving sensory inputs  
232 critical for decisions, as well as choosing behaviors that are appropriate to the social  
233 context. Based on topology, hodology, expression of receptors for sexual hormones,  
234 and functional experiments, studies in several fishes have partially defined the  
235 mammalian homologs of the SDMN in teleosts (see Table 1). These neuroanatomical  
236 homologies between fishes and tetrapods will continue to be updated as more  
237 functional and connectivity studies are performed. As we will see, functional and  
238 structural changes in these socially-relevant regions, as well as in the connectivity  
239 among them, is an important consequence of social plasticity in fish.

240

## 241 4. Social organization in fish

242 Fish form a unique group, being the most numerous and diverse of the  
243 vertebrates, dominating the aquatic environment by showing a remarkable panoply of  
244 behavioral characteristics and adaptations (Moyle and Cech, 2000). Fish are still  
245 erroneously viewed as primitive and inflexible, controlled by fixed behavioral  
246 predispositions; however, the reality is very different. In the last three decades, scientific  
247 evidence has somewhat repaired these misconceptions, and reintroduced fish as an  
248 “equal” group of vertebrates, rich in all sort of behaviors, even those considered as

249 sophisticated or cognitively complex (Brown et al., 2006).

250 Fish occupy all aquatic niches, and their level of diversification and adaptation is  
251 remarkable. Behavioral traits maximize adaptation to the environment, giving access to  
252 food, reproductive opportunities, or social aggregation (which includes the whole social  
253 domain). The social environment of fish may have fitness consequences, as it is both a  
254 source of wellbeing as well as of conflict. In general, we may organize fish social  
255 systems into 3 categories: i) solitary, ii) individualized social units, and iii) collective  
256 social assemblages (Keenleyside, 1979, Bshary et al., 2002). Fish species living in  
257 individualized social units, may be found as pairs, harems, or in territorial neighbouring  
258 mosaics (which is the case of many fish from the pomacentrid family, a family of  
259 perciform fish from the suborder Labroidei that include damselfish and clownfish). In the  
260 case of collective social systems, these may vary in size, from smaller group units to  
261 large schools (Keenleyside, 1979). These social structures or networks may be based  
262 on distinct arrays of associations or behaviors; for instance, some are related to feeding,  
263 others to defense against predators or conspecifics, to mating, or even to cooperation  
264 (which may aggregate several of these functions) (Krause et al., 2008).

265 The variable functions of these social networks challenge individuals in multiple  
266 ways, with associated costs and benefits for different types of social and non-social  
267 information. The structure of each network will determine the value of each information  
268 source, thereby modulating the animals' capabilities. For example, the ability to  
269 recognize individuals within and outside the network and to gather information on  
270 relationships among group members affects the ability to make alliances, to participate  
271 in group activities, and to compete for access to food and mates (Croft et al., 2005).

272           There are some examples in the literature of solitary fish, including some  
273 butterflyfish, and pikes (*Esox lucius* and *Esox masquinongy*) - which are considered to  
274 be solitary and relatively sedentary carnivores showing little social interaction besides  
275 reproduction (Keenleyside, 1979). Most solitary fish studied so far are home-ranging,  
276 and not particularly territorial, but there are always exceptions (Keenleyside 1979). One  
277 interesting exception is *Betta splendens*, which show a marked territorial and  
278 aggressive behavior, especially in males (Simpson, 1968). Thus, even in solitary fish,  
279 social behaviors (agonistic encounters) are sometimes unavoidable.

280           Two marine families (Blenniidae and Pomacentridae) and one predominantly  
281 freshwater family (Salmonidae) are best representatives of fish living in territorial  
282 mosaics - that is, a system in which the home range is subdivided in a mosaic of  
283 contiguous territories (Keenleyside, 1979). The mosaic of contiguous territories  
284 occupied by these animals is a flat, two-dimensional system, with territory occupancy  
285 driven mainly by requirements of food and shelter: "Long-term utilization of benthic food  
286 can be assured by the mosaic system, each individual guarding its own resources. At  
287 the same time, thorough familiarity with escape routes and shelters within the territory  
288 reduces vulnerability to predators." (Keenleyside, 1979, p. 162). As a result, fish living in  
289 territorial mosaics have a highly fluctuating social environment as they are challenged  
290 for their territories by younger conspecifics.

291           Stable, long-term male-female pairs are rare among fish (Keenleyside, 1979).  
292 Some cichlid species, as those of the *Cichla* genus (Kullander and Ferreira, 2006),  
293 appear to form pair bonds for up to several weeks, with both parents collaborating in  
294 raising the brood until the young fish disperse (Gross and Sargent, 1985). Many species

295 of butterflyfish (*Chaetodon*) have been observed to form monogamous male-female  
296 pairs for up to three years (Fricke, 1973), as well as in some species of caribbean  
297 cleaning gobies *Elacatinus* spp, which live and engage in cleaning together, increasing  
298 the quality of service provided to visitors (Soares et al. 2009, Côté and Soares 2011).  
299 Interestingly, in convict cichlids (*Amatitlania nigrofasciata*) (Oldfield and Hofmann,  
300 2011), Daffodil cichlid (*Neolamprologus pulcher*) (Reddon et al., 2015), and  
301 Chaetodontid butterflyfishes (Dewan et al., 2011), social affiliation and mating system is  
302 associated with arginine vasotocin (AVT) and isotocin (IT) (homologues of the  
303 mammalian vasopressin and oxytocin systems) neuronal systems, highlighting one of  
304 the many links between the brain and social organization.

305 Several species live in small groups with moderate to high complexity. In the wild,  
306 the model organism zebrafish (*Danio rerio*) live in small groups that form shoals, which  
307 usually include small heterospecifics (Suriyampola et al., 2015). Shoaling behavior has  
308 been exploited as a tool to study the neurobiology of social behavior in zebrafish  
309 (Soares et al., 2018a). Within the shoal, dominant-subordinate relationships are  
310 established, a model of social plasticity that has also been exploited successfully (cf.  
311 section 4.1, below). However, many other important grouping schemes are observed  
312 across fish species that form small groups. For example, the freshwater African cichlid  
313 *Neolamprologus pulcher* lives on the rocky substrata of Lake Tanganyika, where it forms  
314 small groups made up of a dominant breeding pair and 0-20 smaller non-breeding  
315 subordinates called helpers (Wong and Balshine, 2011). These helpers are organized  
316 into size-based dominant-subordinate hierarchies, reflecting queues for breeding status:  
317 when the dominant female dies, helper females take its place; helper males are more



318 likely to disperse and take over a dominant position in other groups (Wong and  
319 Balshine, 2011). Importantly, both breeders and helpers defend the territory, do  
320 maintenance work (digging and removing debris), and care for the brood (Taborsky and  
321 Limberger, 1981). This system has been used to study the neural bases of cooperative  
322 behavior (e.g., Taborsky et al., 2013; Nyman et al., 2017; Kasper et al., 2018a, 2018b).

323 To navigate these complex social contexts, animals need a wide array of social  
324 skills (Soares, 2017; Soares et al., 2018a). For example, living in a territorial mosaic  
325 demands high investment in defense and competitive skills, while being a part of  
326 extended family groups will also demand defense capabilities but mostly in fine  
327 synchrony with others in the group (Bshary et al., 2002). Thus, social organization in  
328 fish take many forms, some of which exhibit complex social strategies and tactics,  
329 demands of advanced social learning capacities, elevated levels of communication, and  
330 even deception (Krause and Ruxton, 2002). Among these, cooperation and the  
331 expression of cooperative strategies among fish stands out in terms of sociality (Soares  
332 et al., 2018b). Some fish do cooperate, perhaps at lower frequencies when compared to  
333 birds and mammals (Balshine and Buston, 2008) but even so, this takes many forms:  
334 from the best-known conditional approach during predator inspection (Pitcher et al.,  
335 1986), to cooperative hunting (Bshary et al., 2006), cooperative breeding (Wong and  
336 Balshine, 2011), and finally to the notable cleaning mutualisms (Côté, 2000). Thus, the  
337 rich diversity in social organizations among fish species provides a plethora of suitable  
338 organisms to examine specific evolutionary and mechanistic hypotheses related to the  
339 brain and social behavior

340

## 341 5. Social status and plasticity

### 342 5.1 Social status and plasticity of the brain and behavior

343 Dominance hierarchies are an integral part of the social structure in many animal  
344 societies. As such, an individual's position or rank in the population has profound effects  
345 on their reproductive potential, access to food and other resources, overall health, and  
346 survival (Sapolsky, 2005; Wingfield and Sapolsky, 2003). Fish show diverse social  
347 societies, with examples ranging from solitary living species to group-living species that  
348 exist in either constant or ephemeral (e.g. during breeding season) hierarchies.  
349 Because of their great diversity in social, reproductive, and parental strategies, fish are  
350 powerful taxa to examine interactions between the brain and behavior. Specifically,  
351 zebrafish and cichlids are used extensively to address broad questions related to neural  
352 mechanisms of social plasticity and dominance hierarchies, and some of the main  
353 findings revealed from these species are summarized below.

354 Establishment of dominance hierarchies often leads to specialized social  
355 interactions and behaviors, resulting in each individual of the group occupying a specific  
356 rank in the population. This social position is constantly evaluated and reinforced by  
357 aggressive and reproductive interactions with other individuals of both higher and lower  
358 rank. In zebrafish (*Danio rerio*), dominant–subordinate relationships occur both between  
359 males and between females (Paull et al., 2010), and dominant males and females are  
360 more aggressive and bolder (Paull et al., 2010; Dahlbom et al., 2011). Moreover,  
361 dominance is associated with higher gonadosomatic indices and higher mRNA levels of

362 the androgen receptor *ar* (in males) and estrogen receptor 1 *esr* (in females) in the  
363 gonads (Filby et al., 2010). These gonad differences result in a greater total  
364 reproductive success in males but not in females, but dominant females sire more  
365 offspring with the dominant male (Paull et al., 2010).

366 In zebrafish, much of the work on social status has been done targeting stress  
367 and arousal pathways. The establishment of a hierarchy increases cortisol levels in both  
368 dominants and subordinates, but no differences are found between dominant and  
369 subordinate fish after dominance (Pavlidis et al., 2011; Filby et al., 2010). These  
370 changes are associated with an upregulation of molecules associated with arousal (e.g.,  
371 catecholaminergic, histaminergic, and orexinergic systems) in dominants, and an  
372 upregulation of the stress axis during establishment of status in subordinates that is  
373 switched to an hypocortisolemic profile when the hierarchy is established (Larson et al.,  
374 2006; Filby et al., 2010; Pavlidis et al., 2011). While 'reverse inference' should be  
375 approached with caution, it can be speculated that increased arousal is needed to patrol  
376 territories and maintain a high level of aggression in dominants, while the stress profile  
377 in subordinates is important for social plasticity of submissive behaviors.

378 Zebrafish also offer the opportunity to force social interactions and status  
379 transitions to discover underlying mechanisms. In one zebrafish study (Teles et al.  
380 2016), four social phenotypes were experimentally induced: winners and losers of a  
381 real-opponent interaction; mirror-fighters, which fight their own image in a mirror and  
382 thus do not experience a change in social status despite the expression of aggressive  
383 behavior; and non-interacting fish. By analyzing the expression of plasticity genes  
384 (*wnt3*, *neurod*, *npas4*, *bdnf*, and *nlg1* and *nlg2*) in regions of the SDMN, authors

385 identified markers of social plasticity associated with social status changes: winners  
386 were characterized by greater expression of neurogenesis genes (*wnt3* and *neurod*) in  
387 Dm, and of *neuroligin* genes in Vv and Vs (see Table 1 for homologies); and losers were  
388 characterized by greater expression of *bdnf* in DI and of *wnt3* in Vv, and by lower  
389 expression of *nlg2* in Vs (Teles et al. 2016). These results suggest the participation of  
390 mechanisms of neural plasticity in the establishment of social hierarchies in zebrafish.

391 Cichlid fish of the African (e.g. Haplochromines, *Oreochromis* spp.) and  
392 Neotropical (e.g. *Cichlasoma* spp.) clades are also ideally-suited to address questions  
393 related to the interactions between neural function and social status for several reasons.  
394 They are socially diverse, easy to manipulate, show remarkable plasticity in behavior,  
395 physiology, and brain function, and have evolved the ability to not only assess their  
396 social environment via multiple sensory channels, but also to be deceptive and  
397 determine both their own position and that of others within the hierarchy (Grosenick et  
398 al., 2007; Maruska and Fernald, 2018). Thus, cichlids display a level of social plasticity  
399 that rivals or exceeds that of many other vertebrates. In fact, they have already revealed  
400 many important discoveries about how the brain regulates and is influenced by social  
401 interactions at levels from behavior to molecular mechanisms.

402 There has been considerable focus on social status-specific differences in the  
403 brain of *Astatotilapia burtoni* (formerly *Haplochromis*). For example, cell proliferation  
404 (Maruska et al., 2012), neural activation in decision centers (revealed by markers such  
405 as immediate early genes), distribution, abundance, or activation of cells expressing  
406 neuromodulatory substances or their receptors (Loveland et al., 2014; Maruska et al.,  
407 2013b; O'Connell and Hofmann, 2012b; Renn et al., 2008), and aspects of the stress

408 response system (Carpenter et al., 2014; Chen and Fernald, 2008) can all differ  
409 between dominant and subordinate males. These factors are also well known to  
410 modulate the expression of diverse social behaviors in fish as well as other vertebrates,  
411 including species like rodents and primates that are closer in phylogenetic position to  
412 humans. Similar types of social status differences are also observed in other fish  
413 species [e.g. zebrafish, as mentioned above; other cichlids, electric fish, salmonids, and  
414 others; (Gilmour et al., 2005; Maruska, 2014; Miller et al., 2017; Perrone and Silva,  
415 2018; Teles et al., 2016)], and in some cases result in a change in an individuals' sex  
416 (male to female, or vice versa) that is accompanied by plasticity in neural circuits (Black  
417 et al., 2005; Semsar et al., 2001; Todd et al., 2018). These examples support the broad  
418 relevance of fish for addressing questions related to how an animal's social rank  
419 impacts their brain and reproductive fitness, health, and survival. Thus, by taking  
420 advantage of controlled status transitions and natural dominance hierarchies, fish have  
421 and will continue to reveal insights on neural plasticity that can inform studies in other  
422 taxa.

423 While much of the focus on dominance hierarchies is in males, in *A. burtoni*,  
424 establishment of dominant-subordinate hierarchies in females also induces  
425 neurotranscriptomic differences across ranks. Using cDNA microarray, Renn et al.  
426 (2016) found that several hormonal and neuropeptide genes showed higher expression  
427 in dominant compared to subordinate females, including *prolactin*, *avt*, *brain aromatase*,  
428 and *glycoprotein alpha polypeptide subunit*, a necessary precursor step in the  
429 production of active gonadotropin-releasing hormone (GnRH), luteinizing hormone,  
430 follicle-stimulating hormone, and thyrotropin. Interestingly, *prolactin*, *avt*, and

431 *glycoprotein alpha polypeptide subunit* are also upregulated in the brains of dominant  
432 male *A. burtoni* (Renn et al. 2008). Neuroplasticity genes were also found to be  
433 differentially regulated by female social rank: *FK506-binding protein 1*, *cell cycle*  
434 *associated protein 1*, *neuromodulin*, and *dynammin-1* were up-regulated in dominant  
435 females, while *voltage-dependent N-type calcium channel subunit alpha-1B* was  
436 expressed at higher levels in subordinate females (Renn et al. 2016). While some of  
437 these rank-specific gene expression patterns are similar between males and females,  
438 others are not. It is well established that there are differences in neural and behavioral  
439 mechanisms between males and females in many species, which highlights the  
440 importance of conducting studies in both sexes. For comparative translational science  
441 to be effective, however, increased attention must be given to sex-differences in  
442 mammals as well.

443         Position in a social society has profound impacts on behavior, physiology, brain  
444 function, survival, and reproductive success across vertebrates. Fishes such as  
445 zebrafish and cichlids are amenable to manipulations that control an individuals'  
446 transition in social rank, which have revealed many genes, brain nuclei, and other  
447 physiological correlates associated with this social plasticity. With recent advancements  
448 in genetic technologies (e.g. CRISPR, transgenics), these fish species are now poised  
449 to advance the field of social neuroscience with targeted and functional hypothesis  
450 testing to better link neural mechanisms to behavioral outcomes.

451

## 452 5.2. Social status and sensory plasticity

453 Studies in fish have also revealed important neural mechanisms involved in  
454 sensory plasticity. Because the ability to assess the social environment is critical,  
455 particularly for species living in dominance hierarchies, conspecific communication and  
456 sensory perception is of paramount importance. For example, social rank or alternative  
457 reproductive phenotypes (e.g. nesting vs satellite/sneaker males) within a species are  
458 often associated with differences in the ability to detect auditory, olfactory, and visual  
459 information that is necessary for their status-specific behaviors such as reproduction,  
460 territory defense, feeding, and growth. In *A. burtoni*, dominant males have higher levels  
461 of modulatory receptors (e.g. steroid receptors) in the ear (Maruska and Fernald,  
462 2010b) and olfactory bulbs (Maruska and Fernald, 2010c), as well as a greater  
463 response of the olfactory epithelium to food-related odorants (Nikonov et al., 2017)  
464 compared to subordinate males. This may facilitate detection of acoustic social signals  
465 and prey/food to support their territorial status, which comes with an associated trade-  
466 off of reduced feeding time and growth (Hofmann et al., 1999). Further, conspicuous  
467 dominant males show an increased startle response probability compared to less  
468 conspicuous subordinate males, possibly mediated by serotonin at the Mauthner  
469 neurons, that may allow them to better escape from predators (Neumeister et al., 2010;  
470 Whitaker et al., 2011). In plainfin midshipman fish, in which males are either large  
471 nesting type I or small satellite type II, there are status-dependent differences in both  
472 the vocal and auditory systems that are crucial to the reproductive fitness of this species  
473 that relies heavily on acoustic signaling (Forlano et al., 2016; Maruska and Sisneros,

474 2015). Sensory plasticity can be modulated both at peripheral sensory structures (i.e.  
475 ear, olfactory epithelium, retina), as well as centrally in the brain, and in most cases is  
476 controlled by plasticity in signaling of neuromodulatory molecules such as steroids,  
477 neuropeptides, and biogenic amines. Social communication in fish is often multisensory,  
478 but also depends on the reproductive strategies employed by the species, and the  
479 habitat and environmental conditions where they live, which can dictate the  
480 transmission properties and effectiveness of information sent via different sensory  
481 channels. Because modulation of sensory systems is common across vertebrates,  
482 including in humans, the diversity of sensory dependence seen in fish (i.e. species that  
483 rely on multisensory information, such as many reef fishes, vs. those relying heavily on  
484 a single sense to reproduce, such as midshipman) provides unique opportunities to  
485 uncover basic mechanisms of sensory function. The conservation of sensory structures  
486 across taxa allows research in fish to also reveal how perception of social information  
487 can be modulated by neurochemicals that change with their social rank. As mentioned  
488 above, however, sensory abilities of fishes and transmission properties of aquatic  
489 habitats can differ from those found in terrestrial organisms. Because these factors  
490 influence social behaviors, they should be considered when making comparisons  
491 across vertebrates. Nevertheless, fish are becoming valuable models to study impacts  
492 of anthropogenic noise, pollution, and climate change on sensory and brain function,  
493 opening opportunities to study the interaction of those factors with ecologically relevant  
494 sensory plasticity.

495



### 496 5.3. Is the establishment of social rank inherently stressful?

497 Social stressors are powerful activators of the hypothalamus-pituitary-adrenal  
498 (interrenal) axis in many species, and in rodents are even used as a model for  
499 depression (Beery and Kaufer 2015). Initial studies on rodents increased the  
500 comprehension regarding how stressor type, timing, and other factors affect physiology  
501 and behavior (see Sgoifo et al., 1999, for a review). Studies in fishes demonstrate that  
502 an animal's social status affects its access to feeding, mates, and shelter, and different  
503 studies showed the consequences of rank-related stress to the physiology and health of  
504 dominant and subordinate individuals (Francis et al., 1993; Qvarnström and Forsgren,  
505 1998; Valdimarsson & Metcalfe, 2001; Iwata et al., 2008). Models for social stress in  
506 zebrafish revealed that subordinate animals show a higher brain expression of genes  
507 associated with the activation of the hypothalamus-pituitary-interrenal (HPI) axis, higher  
508 cortisol levels, peripheral expression of pro-inflammatory cytokines, and compromised  
509 reproductive activity immediately after hierarchy establishment (Filby et al. 2010).

510 Higher cortisol levels, however, are not always observed in subordinates  
511 compared to dominants, however. Pavlidis and collaborators (2011) also established a  
512 model for social rank stress in zebrafish, forcing a dyadic interaction for five days - after  
513 which dominance was successfully established. After the establishment of dominance,  
514 both subordinates and dominant males showed higher whole-trunk cortisol  
515 concentrations than control animals; no differences were observed, however, between  
516 dominant and subordinate animals. Teles et al. (2016) showed a significant increase in  
517 cortisol in winner animals (that is, animals which win a 30 min fight against a

518 conspecific) and in animals fighting against a mirror (that is, animals which display  
519 aggression without establishing dominance), but not in loser animals.

520         These results suggest that, at the initiation of a social rank interaction, cortisol is  
521 more associated with aggression levels than with classical stress responses (i.e.,  
522 behavioral inhibition, hypoaggressiveness, etc). However, these relationships between  
523 cortisol and stress or other behaviors like aggression are not always consistent across  
524 species. For example, the circulating cortisol levels in the cichlid *A. burtoni* are quite  
525 sensitive to experimental paradigms, with some studies showing higher levels in  
526 subordinate males, while others detect no differences between dominant and  
527 subordinates (Fox et al., 1997; Maruska 2015). This illustrates a caveat of these results:  
528 cortisol levels are not very reliable as a measure of stress, especially in a comparative  
529 context. This results from the fact that the matrix in which cortisol is measured (whole  
530 body, brain, plasma), as well as timing and method of extraction, are very likely to alter  
531 the results. For example, in zebrafish cortisol is usually measured in whole-body, which,  
532 although relatively sensitive, lacks specificity. Moreover, cortisol release in the plasma is  
533 expected to produce faster physiological adjustments than, e.g., effects in the brain. As  
534 a result, it is difficult to compare data on small fish (such as zebrafish) vs. larger  
535 animals, including cichlids and trouts.

536         In rainbow trout subjected to stressful social interactions, dominant animals show  
537 higher aggressive behavior immediately after rank establishment, but only subordinate  
538 animals have elevated plasma cortisol levels associated with other signs of chronic  
539 stress, such as reduced feeding and reduced serotonergic activity in the brainstem  
540 (Sørensen et al. 2012). Moreover, subordinates had reduced proliferation of adult brain

541 cells than controls, and cell proliferation was negatively correlated with the intensity of  
542 aggression received at the end of the social rank establishment (Sørensen et al. 2012).  
543 A study in the cichlid *A. burtoni* examined the behavioral consequences and neural  
544 activation patterns of repeated social defeat from the same aggressor and showed that  
545 individual males will switch between proactive and reactive coping behaviors over time,  
546 and each coping behavior is associated with distinct activation patterns in the brain (e.g.  
547 reactive had greater activation in raphe nuclei, while proactive had greater activation in  
548 Dm, Vs, Vc, Vd, Vp, Vv, TPa, ATn) (Butler et al., 2018).

549         These data in fish reaffirm the literature that was built on rodents, which show  
550 links between the neurobiology of stress and behavior, with social interactions  
551 sometimes acting as a stressor. In rodents, social stressors are used as models for  
552 depression, taking into consideration how social plasticity – including social  
553 subordination, crowding, social isolation, and social instability – influences stress  
554 responses (Beery and Kaufer 2015). Fish are increasingly used as models for better  
555 understanding human mental health disorders, many of which are associated with  
556 stress responses, such as anxiety, depression, and post-traumatic stress disorder  
557 (PTSD) (see Kalueff et al., 2014; Stewart et al., 2014, 2015, for reviews discussing the  
558 possibility of using fish as models in biological psychiatry). For this translational  
559 approach to be effective and informative, studies in fish are necessary because it is  
560 important to understand the evolution and conservation of neural networks underlying  
561 the behaviours typically displayed in these neurological conditions.

562

## 563 5.4. Reproductive status and plasticity

564 One of the most important consequences of an individual's social status is their  
565 reproductive potential. Within a population, dominant individuals typically have an up-  
566 regulated reproductive axis and more mating opportunities compared to subordinate  
567 individuals. Studies in the African cichlid *A. burtoni* in particular have revealed important  
568 insights on how social rank impacts the reproductive brain [see Fernald and Maruska,  
569 2012; Maruska, 2014; Maruska and Fernald, 2014; Maruska and Fernald, 2018, for  
570 reviews]. In this species, males form hierarchies in which a small percentage of  
571 dominant individuals hold territories that they aggressively defend from rivals and use to  
572 court and spawn with females. Subordinate males comprise the majority of the  
573 population, but lack territories and therefore have minimal chances to reproduce. Their  
574 shallow habitats along the shores of Lake Tanganyika, however, are dynamic and there  
575 are frequent opportunities for males to rise or fall in social rank, thereby switching  
576 between subordinate and dominant status. These social transitions are associated with  
577 many dramatic changes in the brain and sensory structures that allow them to better  
578 adapt to their status-specific lifestyles (see references cited above).

579 The brain controls both the activity of the reproductive axis, as well as the  
580 expression of behaviors and must be inherently plastic to accommodate social change.  
581 In *A. burtoni*, dominant males have larger gonadotropin-releasing hormone (GnRH1)  
582 neurons in the preoptic area with distinct cell and firing properties (Davis and Fernald,  
583 1990; Ma et al., 2015; Maruska and Fernald, 2013) compared to subordinate males,  
584 which leads to increased pituitary and testes activity to promote greater reproductive

585 potential, higher circulating sex steroids, and increased territorial and reproductive  
586 behaviors [see (Maruska and Fernald, 2013; Maruska and Fernald, 2014; Maruska and  
587 Fernald, 2018) for reviews]. When subordinate males perceive an opportunity to gain a  
588 territory and rise in social rank, within minutes, they begin looking and behaving like  
589 dominant males (Burmeister et al., 2005; Maruska and Fernald, 2010a). This social  
590 ascent is also associated with numerous rapid (minutes to days) cellular and molecular  
591 changes from the brain to the testes (Maruska and Fernald, 2014; Maruska and  
592 Fernald, 2018), and similar changes occur on a slower timescale (days to weeks) when  
593 males fall in rank (Maruska et al., 2013a; Maruska, 2015). Because changes in social  
594 position occur across invertebrate and vertebrate taxa, this rapid neural and behavioral  
595 plasticity in cichlids provides unique opportunities to test functional, mechanistic, and  
596 evolutionary hypotheses. For example, a study in haplochromine cichlids of Lake  
597 Victoria demonstrated that competition for breeding sites between males promotes male  
598 nuptial color diversification that can lead to speciation (Seehausen & Schluter, 2004).  
599 One neuroendocrine system that links body pigmentation to fish behavior is the  
600 melanocortin system. In *A. Burtoni*, studies showed that yellow males are more  
601 aggressive, with higher circulating levels of 11-ketotestosterone (fish-specific androgen)  
602 than their blue counterparts (Korzan et al., 2008). However, while exogenous  $\alpha$ -  
603 melanocyte-stimulating hormone ( $\alpha$ -MSH) increases yellow coloration in both yellow  
604 and blue males, only the blue morph-type individuals increased their aggressiveness  
605 (Dijkstra et al., 2018). Thus, by combining tests of evolutionary and functional  
606 hypotheses in cichlids, we can begin to unravel the mechanisms and drivers of social  
607 plasticity.

608            Important work on sexual conflict and social plasticity has been done in poeciliids  
609 (see Cummings, 2018, for a review), due to the variety of reproductive strategies and  
610 levels of sexual conflict found across species. Conflict levels vary across poeciliid  
611 species mainly as a result of variation in male mating systems, given that females of  
612 most species have long gestation periods and, being able to store sperm, are rarely  
613 sperm-limited; males, on the other hand, vary from systems dominated by male  
614 coercion (about half of the species) to systems that include both courtship and coercive  
615 tactics. The result is a sex ratio that is male-biased, with the optimal mating rate for  
616 males being several times a day, while for females less than one mating episode per  
617 month is optimal. Interesting species differences are observed, with guppy (*Poecilia*  
618 *reticulata* Peter 1859) and mosquitofish (*Gambusia affinis* Baird & Girard 1853) males  
619 attempting mating more than once per minute, and Panuco swordtail (*Xiphophorus*  
620 *nigrensis* Rosen 1960) males attempting mating between 0.25 and 5 times per minute  
621 (Magurran and Maciás Garcia, 2000). Thus, the relative investment in a single  
622 reproductive event varies between males and females across poeciliid species, but  
623 females always allocate more resources towards foraging and avoiding male  
624 harassment (Houde 1997; Magurran 2011), while males allocate most of their resources  
625 towards mating attempts (Magurran and Seghers 1994).

626            The resulting selective pressures described above produced species in which  
627 males and females display sexual dimorphism in social behavior and cognition  
628 (Cummings, 2018). In guppies and mosquitofish, females that experience a high degree  
629 of sexual coercion exhibited a greater tendency to shoal in the presence of male  
630 conspecifics relative to the absence of a male, while females from the *X. hellerii* or *X.*

631 *mayae* do not shoal together in response to male conspecifics (Dadda, 2015). This  
632 increased aggregation in females can be interpreted as an adaptive strategy to reduce  
633 the costs of male sexual behavior. Moreover, females from species with high sexual  
634 conflict also occupy different habitats, inhabiting areas with higher predation risks to  
635 avoid male harassment (Croft et al. 2006; Darden and Croft 2008); as a result, females  
636 from species with high sexual conflict show less exploratory behavior and increased  
637 anxiety-like behavior (Cummings, 2018). Interestingly, in *G. affinis*, a species with high  
638 sexual conflict, males that showed less neophobia and anxiety performed better on a  
639 numerosity discrimination task, whereas females showed no relationship between  
640 exploration and learning performance (Etheredge et al., 2018). No differences were  
641 found between *G. affinis* males and females in learning performance, but high-  
642 performance learner males exhibited different behavioral attributes than high-  
643 performance learner females: while high-performance females showed higher mate  
644 choice, activity, and anxiety (key responses to social conflict), high-performance males  
645 do not show higher levels of any behavioral trait (Etheredge et al., 2018).

646 In an interesting approach, Cummings and colleagues analyzed gene expression  
647 in whole brains or in the dorsolateral telencephalon (DI, a putative homologue of the  
648 hippocampus in teleosts) of females species with low conflict (*X. nigrensis*) or high  
649 conflict (*G. affinis*) that varied in levels of preference for courting vs. coercive male  
650 conspecifics (Cummings et al., 2008; Lynch et al., 2012; Wong et al., 2012; Wang et al.,  
651 2014). In *X. nigrensis*, the expression of *neuroligin-3* and *neuroserpin*, genes associated  
652 with synaptic plasticity, is positively associated with preference for courting males in  
653 both the whole-brain and DI samples; however, in *G. affinis*, these genes are negatively

654 associated with preference for courting males in whole-brain samples. When *G. affinis*  
655 females are exposed to a courting heterospecific male (a large *Poecilia latipinna*), a  
656 positive correlation is observed between preference and *neuroserpin* brain levels, while  
657 a negative correlation is observed when females are exposed to a coercing *P. latipinna*  
658 (Cummings et al., 2008; Lynch et al., 2012; Wong et al., 2012; Wang et al., 2014).  
659 These results suggest that different expression of neuroplasticity genes across species  
660 is not due to species differences *per se*, but that females are responding more to male  
661 reproductive tactics than species identity. Finally, in *X. nigrensis*, females exposed to  
662 two courting males show a high correlation in the expression of *neuroligin-3* in regions  
663 that are associated with social decision making than females exposed to a courting and  
664 a coercive male, and little correlation is observed across these regions when females  
665 are exposed to two coercive males (Wong and Cummings, 2014), suggesting that  
666 interaction with courting phenotypes, more than coercive phenotypes, demand  
667 engagement of brain plasticity (Figure 3).

668 The most remarkable expression of social plasticity, however, is the sex change,  
669 an adaptive strategy that has already been observed for 27 teleost families (Sadovy de  
670 Mitcheson and Liu, 2008). Most of them are marine species, such the Epinephelidae  
671 groupers *Epinephelus akaara* and *E. awoara*, both functional protogynous  
672 hermaphrodites (Liu et al., 2016), in which individuals first function as female and then  
673 males, and in the protandrous hermaphrodites Amphiprioninae, as in *Amphiprion*  
674 *melanopus* (Choi et al., 2016) and *A. ocellaris* (Khoo et al., 2018), in which animals  
675 are first males and then females. Theoretically, these strategies evolved to ensure a



676 high mating success. In protogynous hermaphrodites, for example, larger males tend to  
677 be dominant, commonly monopolizing mating, either by defending spawning sites that  
678 females visit or by controlling a harem of females. Thus, if an individual acts as a female  
679 when small and as male after achieving a large size, it would have a greater offspring in  
680 comparison to a gonochoristic (unisexual) individual (Warner, 1984). Moreover, usually  
681 a protogynous male also controls the emergence of other males by aggressive  
682 dominance over females. The former tendency was demonstrated by Lo Nostro and  
683 Guerrero (1996) in the swamp eel *Synbranchus marmoratus*, in which the so-called  
684 primary male, which directly develops as male, were smaller (13 cm), while the larger  
685 ones (91 cm) were found to be secondary males, which develop from functional  
686 females. Contrary to the general findings in protogynous hermaphrodite species, in  
687 which female individuals are the majority, in this study the authors showed that most of  
688 the population (80%) was composed of secondary males. That occurrence might be a  
689 result of the survival strategy adopted by the species, since it inhabits streams and  
690 swamps that periodically dry out leaving the individual isolated. Thus, protogynous  
691 specimens are hypothetically more efficient to establish new colonies (Lo Nostro and  
692 Guerrero, 1996). The authors suggested that sex differentiation in this sex-changing  
693 species can be triggered by an initiating event in the brain, rather than directly on the  
694 gonad. Indeed, chronic administration of salmon GnRH analogue or the dopamine  
695 receptor antagonist domperidone induced sex change in female *S. marmoratus* and  
696 spermiation in males (Ravaglia et al 1997).

697 Bluehead wrasses (*Thalassoma bifasciatum*) are dyandric protogynous labrids,  
698 presenting both smaller, drab, non-aggressive primary males, a certain percentage of

699 which will change to a large, brightly-coloured, highly aggressive terminal male. Removal  
700 of a terminal phase male from a patch reef induces aggressive behavior in the largest  
701 female, targeted towards other females, as well as courtship towards smaller females,  
702 suggesting that one important control of sex change is dominance hierarchies (Warner  
703 and Swearer 1991). In this species, sex change is accompanied by increases in the  
704 expression of GnRH in the POA (Grober et al. 1991), and terminal phase individuals  
705 show higher GnRH expression than intermediate phase individuals (Grober and Bass  
706 1991). The closely-related *T. duperrey* is also diandric, but females have a larger home  
707 range and do not always mate with the same male; the presence of smaller individuals  
708 promotes sex reversal and the presence of larger individuals inhibits sex reversal (Ross  
709 1986). In this species, norepinephrine appears to stimulate gonadal sex reversal, while  
710 dopamine exerts inhibitory action on the initiation of sex reversal and serotonin inhibits  
711 both initiation and completion of sex reversal (Larson et al. 2003a). During sex change  
712 in females, monoamine metabolism changes in the SDMN, as well as in the locus  
713 coeruleus and raphe nucleus (Larson et al. 2003b); during the first week of sex change,  
714 when animals undergo behavioral changes, serotonergic activity in the Dm is increased,  
715 while in the POA it is decreased (Larson et al. 2003b). Norepinephrinergic activity is  
716 decreased, and dopaminergic activity is increased, in the VMH; in the locus coeruleus,  
717 norepinephrinergic activity is increased, while in the raphe nucleus, there is a decrease  
718 in serotonergic activity at the time of behavioral sex reversal (Larson et al. 2003b). Both  
719 studies suggest that behavioral sex reversal is under the control of serotonin in the  
720 raphe, while gonadal sex change is mediated by serotonergic effects on norepinephrine  
721 in the POA. In addition to sex-change, there are numerous other examples of alternative

722 reproductive phenotypes across fish species, all showing plasticity in behavior, the  
723 brain, and physiology that can be useful for revealing core neural mechanisms across  
724 taxa (for reviews see Maruska et al, 2018; Oliveira et al., 2008).

## 725 6. Cognitive plasticity and social interactions

726 By definition, cognitive social plasticity refers to the ability to change patterns of  
727 cognition and behavior in the context of social engagement. This field, as with many  
728 others, was initially developed to tackle “human questions”, as part of social psychology,  
729 and later applied to other vertebrates including fish. Indeed, the diversity of fish species,  
730 social systems and cognitive abilities, together with the variety of adaptive contexts in  
731 which these species evolved, stirred the interest to generate new behavioral and  
732 cognitive paradigms with higher ecological validity (Hall et al., 2014). Recently, the use  
733 of fish in neurosciences, mostly zebrafish, and the development of new molecular tools,  
734 has created new possibilities and consequently, taken many more model fish species  
735 into the spotlight. However, when thinking about social behavior and cognition, not  
736 many fish species or families come to mind, except for a few well studied examples as  
737 the cichlids (Grosnick and Fernald, 2007; Greenwood et al., 2008; Oldfield and  
738 Hofmann, 2011; Winberg et al., 2008) and the cleaner wrasses (Bshary and Côté, 2008;  
739 Soares 2017); with a few others coming as runner-up candidates, such as zebrafish  
740 (Oliveira 2013), poeciliids (Dugatkin, 1988, 1991), or cleaning gobies (Côté and Soares,  
741 2011).

742 In this section, we will focus on the cleanerfish example, as it is possibly the best

743 studied fish system in terms of complex social behavior and includes both interspecific  
744 and conspecific components (Soares, 2017). Cleaners are suitable candidates as model  
745 organisms to study the role of social plasticity in contextual social cognition and decision  
746 making; moreover, they are also putative models for more “organizational” questions, as  
747 those focusing on the evolutionary emergence of cleaning behavior (between species,  
748 Soares et al., 2018a), ontogenetic changes in cleaning behavior (the case of facultative  
749 cleaners, Soares et al., 2018a), and of alternative strategies (adaptive behavioral  
750 ecotypes, as with the Caribbean cleaning goby *Elacatinus prochilos*) (Côté and Soares,  
751 2011). Neuroendocrine trade-offs are assumed to play a crucial role on cleaners’ highly  
752 plastic social performance, enabling a successful navigation within and across  
753 challenges posed by the social environment (Soares, 2017, Soares et al., 2018ab).  
754 Recent research, while still just beginning, has provided us with a few good potential  
755 candidates regarding the proximate mechanisms, such as the nonapeptides AVT and IT,  
756 the stress steroid cortisol, and the monoamines dopamine and serotonin.

757

## 758 6.1. Social plasticity and the special case of the cleaner fish 759 system

760 Fish, as other vertebrates, need to use previously acquired information and  
761 combine it with the current social environment, if they are to avoid putative costs. For  
762 instance, these include being eaten by a predator while inspecting it, or being expelled  
763 from the social group (Oliveira, 2009). According to Oliveira (2012), the ability to

764 appropriately adjust social behavior relies on social plasticity mechanisms that occur in  
765 different temporal scales: the first is associated with *changes* to life-history, with those  
766 being reversible (breeding vs non-breeding) or irreversible (juvenile cleaners vs adult  
767 non-cleaners); the second occurs *during* the same life-history stage, described as  
768 punctual or short term behavioral fluctuations (behavioral flexibility). Here, we prefer to  
769 envision these categories in a non-fixed manner, using them to virtually differentiate the  
770 multiple domains of social plasticity, some working between irreversible life stages,  
771 others seasonally, and some punctually; the first two being mostly modulated by non-  
772 social factors (like diet, reproduction), and the latter by contextual changes of the social  
773 environment.

774 Fish are remarkable examples of social plasticity and behavioral flexibility. A  
775 notable case of a highly social and cooperative species, the indo-pacific bluestreak  
776 cleaner wrasse *Labroides dimidiatus*, has been exploited as a model for sociality and  
777 cooperation. Individuals of this species are known to exhibit complex cognitive skills,  
778 such as predisposition to approach partners, impulsivity and deception, social  
779 recognition and inference, learning and memory, communication and levels of  
780 investment, and bonding (Soares 2017). These skills make them good examples of  
781 strategic sophistication in decision making in teleosts, which ultimately translates into a  
782 unique demonstration of fish social plasticity (Bshary, 2001, Bshary and Côté, 2008,  
783 Soares, 2017). Naturally, the cleaning system has developed strong interest, since the  
784 very idea that fish could repeatedly move away from all their activities just to visit a  
785 specific and territorial, smaller and colourful other species, is still puzzling (Côté, 2000).

786 The discovery of conflict in what seemed as harmless ectoparasite gleaning

787 behavior, was a massive step forward in understanding the social complexity of this  
788 system: Grutter and Bshary (2003) showed that these cleaners, while foraging on  
789 ectoparasites, preferred to feed directly on client mucus, which is energetically costly for  
790 the client fish to produce and constitutes cheating. In our view, this was the starting  
791 point that enabled the accumulation of evidence on the social and cooperative building  
792 blocks of this system. Cleaners and clients are involved in a challenging network of  
793 interactions, based on behavioral and physiological costs and benefits (Soares, 2017).  
794 Clients were discovered to make use of partner control mechanisms aiming to reduce  
795 the frequency of cheating events; these mechanisms include close monitoring of  
796 cleaner behavior, for instance, in choosing beforehand (eavesdropping) and reacting  
797 with termination, switching to other cleaners, or retaliating when bites occur during the  
798 cleaning (Bshary and Côté, 2008). Thus, clients not only gain from successful parasite  
799 removal, but also with a whole neuroendocrine cascade of wellbeing derived from  
800 physical and visual contact (Ros et al., 2011, Soares et al., 2011, Soares et al., 2017a,  
801 Abreu et al., 2018). As a dynamic biological “market”, cleaners are challenged to  
802 respond in flexible way, changes that may occur in relation to clients’ species and  
803 identity (familiarity – previous recognition, Tebbich et al., 2002, Soares et al., 2017b);  
804 these cognitive modules and physiological mechanisms will be further discussed below.

805 Adding to all this behavioral plasticity, most cleaner species undergo seasonal  
806 variations, mostly related to reproduction, which have significant dietary physiological  
807 impact (Soares et al., 2014), and hence impact on cleaners’ cooperative levels (Bshary  
808 2002). Temperature and other environmental fluctuations also influence cleaners’ social  
809 plasticity, especially when these tend to be extreme. This was firstly documented in a

810 recent study by Trickett and colleagues (2017), which found that, following the extreme  
811 weather events affecting the Great Barrier Reef (consecutive cyclones and the 2016 El  
812 Niño event), cleaners failed to display the previously documented strategic abilities  
813 (lower ability to manage their reputation and to learn to prioritize food sources as to  
814 maximize food intake). These changes were mostly due to a change in clientele  
815 densities, which means that the contextual social environment is crucial to the  
816 development of cleaners high-end social and interspecific abilities, cognitive differences  
817 that had been previously noted by Wismer et al. (2014) in cleaner wrasses from  
818 different reefs, and in other species of dedicated (full time) cleaners (the Caribbean  
819 cleaning gobies *Elacatinus* spp., Soares et al., 2008a).

820 It's also relevant to note that cleaners are found in many different fish families  
821 and most of which only do so in a specific life stage (during the juvenile phase; Côté  
822 2000, Vaughn et al., 2016). These transitions are of significant social relevance, as  
823 these facultative cleaner species stop interacting with heterospecifics to focus  
824 exclusively on their conspecific networks (frequently during adulthood). Finally, some  
825 species of cleaning gobies (most notably the case of *Elacatinus prochilus*, Côté and  
826 Soares, 2011) show alternative mixed strategies, which seem to adaptably express  
827 cleaning behavior, with the absence of cleaning being associated with the sponge-  
828 dwelling habitat and the presence of cleaning associated with living on substrata other  
829 than sponge (Rüber et al., 2003; Taylor and Hellberg, 2005). Whether this is exclusive  
830 to *Elacatinus* spp cleaning gobies or something observed in certain socio-environmental  
831 conditions or species, is yet to be discovered. But even in systems other than *L.*  
832 *dimidiatus*, variations of behavioral output are cumulatively being documented: for

833 instance, with the effects of competition in cleaning gobies (Soares et al., 2008b), or the  
834 effects of uneven habitat use to cleaner-client familiarity and to cleaners' cheating levels  
835 (Oates et al., 2010). At this point much have been done in terms of behavior, ecology,  
836 and physiology of cooperative behavior in cleaner fish, however, the cleaner-client  
837 mutualism is still a promising system, most especially in matters of social plasticity and  
838 the underlying brain mechanisms.

839

## 840 6.2. Nonapeptides in social plasticity of cleaner fish

841 The nonapeptides, arginine-vasotocin (AVT) and isotocin (IT), have a well-conserved  
842 structure and core functions across vertebrate taxa (Acher and Chauvet, 1995,  
843 Goodson and Bass, 2001), and are implicated in great number of social and  
844 reproductive behaviors in fishes (Godwin and Thompson, 2012). In teleosts, AVT and IT-  
845 immunoreactive (ir) neurons of the preoptic area (POA) are the main source of these  
846 nonapeptides, have neuronal projections both to the pituitary and to extrahypothalamic  
847 brain regions, which include the diencephalon, telencephalon, optic tectum cerebellum  
848 and brain stem; Holmgvist and Ekström, 1995, Saito et al., 2004). A comparative study  
849 found that obligate cleaners *L. dimidiatus* have smaller and less numerous AVT-ir  
850 neurons in the gigantocellular preoptic area (gPOA) compared to non-cleaners, the  
851 corallivorous *Labrichthys unilineatus* (Mendonça et al., 2013). As such, differences in  
852 bio-active AVT and IT quantitative levels are expected to occur selectively, in  
853 accordance to species, social behaviour and brain regions involved, as we will further



854 develop bellow.

855 Arginine-Vasotocin has been found to have tremendous effects on the cleaning  
856 predisposition of cleaner wrasses. Intramuscular injection of AVT made cleaners cease  
857 inspecting clients and instead turned their focus to conspecific activities, while those  
858 injected with V1a receptor antagonists were stimulated to clean (Soares et al., 2012a).  
859 Similar learning and cooperative deficits were subsequently found after exogenous AVT  
860 injections (Cardoso et al., 2015a, 2015b). AVT appears to work as a switch, turning “on”  
861 or “off” the expression of interspecific cooperative behavior of cleaner wrasses,  
862 indicating that lower levels of AVT could be a prerequisite for approaching and  
863 interacting with clients while higher AVT activity could predispose cleaners into mating  
864 activities (Cardoso et al., 2015a). Interestingly, examination of brain active nonapeptide  
865 levels of mixed sex pairs of cleaner wrasse *L. dimidiatus* demonstrated that in males,  
866 forebrain isotocin (IT) levels increased with the level of pair association, but no  
867 relationship was found for females (Figure 4B; Cardoso et al., 2015c). These males  
868 were found to receive more tactile stimulation from female partners, but seem to  
869 contribute to an overall decrease of cleaning service quality given to clients (i.e. cheated  
870 more often; Cardoso et al., 2015c). Recently, male cleaner forebrain IT levels have been  
871 found to increase when introduced to clients (visual-only or full contact), compared to  
872 conspecifics (Abreu et al., 2018b; Figure 5).

873 This evidence pointed towards the need for comparative studies. Kulczykowska  
874 and colleagues (2015) looked at biologically available nonapeptide levels (measured via  
875 liquid chromatography-tandem mass spectrometry) in different brain regions of four  
876 species of closely related Labrid fish, and found that in the cerebellum of the obligate

877 cleaners *L. dimidiatus* and *L. bicolor*, AVT and IT levels were higher than those of  
878 facultative cleaner *L. australis* (in which juveniles are cleaners and adults are  
879 corallivorous) and of a non-cleaner species *L. unilineatus*, suggesting that AVT levels at  
880 the cerebellum may be associated with the expression of cleaning behavior (Figure 4A).  
881 Thus at this point, it's safe to say that the nonapeptides AVT and IT are implicated in  
882 decision-making in cleaner wrasse, but with AVT strongly mediating structural and  
883 perhaps life-history changes between cleaning and non-cleaning, however much is yet  
884 to be discovered.

### 885 6.3. Cortisol in social plasticity in cleaner fish

886 Cortisol was described as a strong candidate modulator of cleaners and clients'  
887 behavioral decisions (Soares et al., 2014, Binning et al., 2017, Soares 2017). The  
888 involvement of cortisol was more obvious in clients, as these visit cleaners to have their  
889 parasites removed, and these parasites may cause discomfort, itching, disease, and  
890 immune dysfunctions (Côté 2000). On the other hand, for cleaners, cortisol should have  
891 a role as a mediator of stress and antipredator responses, since some clients are  
892 dangerous piscivores, which cleaners graze around and inside their mouths and leave  
893 unharmed (Soares et al., 2007a). Interaction of cleaners and clients increase cortisol  
894 levels in the first, causing them to attend these clients faster and during longer bouts of  
895 time (Soares et al., 2007a, 2012b). Indeed, it has been hypothesized that variations in  
896 cortisol levels work to "fine-tune" cleaners' behavioral profiles by contributing to  
897 behavioral shifts (Soares 2017).

898 Bshary (2002) proposed a description of two non-fixed cleaner behavioral  
899 strategies: the first is adopted by the great majority of cleaners, which show low interest  
900 in small clients and focus on the best treatment of larger clients, and the second -  
901 known as “biting”, in which cleaners behave in the opposite manner and bite (“cheat”)  
902 the larger and most valuable non-predatory clients. Cortisol plays a decisive role in  
903 these behavioral shifts, which occur in stages of higher metabolic demands (and as a  
904 consequence, increased glucocorticoid expenditure), such as during stages of high  
905 reproductive effort, high growth effort, or during stages of change in female social rank  
906 (see Soares et al., 2014). However, the scope of influence by cortisol variations seems  
907 to be set by the social environment inhabited by cleaners. For instance, only cleaner  
908 wrasses inhabiting highly complex social environments seem to respond to exogenous  
909 cortisol injections with strategy shifts (e.g. tactical deception of clients: more tactile  
910 stimulation to small clients and more bites to large clients; Binning et al., 2017). Another  
911 good example is the case of ecotype differences in cleaning gobies (Soares and Côté  
912 2011), as the absence of cleaning is related to sponge-dwelling habitat and the  
913 presence of cleaning is associated with living on substrata rather than sponge (Rüber et  
914 al., 2003; Taylor and Hellberg, 2005). Stress mechanisms are involved in this system,  
915 with species that show both cleaner and non-cleaner strategies (*E. prochilos*)  
916 responding more to stressful events and in this way enabling the necessary robustness  
917 that allows for them to develop in one of these social environments: one more  
918 hierarchical and aggressive (sponges), and another more tolerant and riskier  
919 (substratum) (White et al., 2007, Soares et al., 2018a). There is also a high degree of  
920 behavioral flexibility; for instance, sponge dwellers have been observed to inspect

921 clients (Côté and Soares, 2011). However, species of cleaning gobies that are  
922 specialized in cleaning (such as *E. evelynae*), depending exclusively on the client-  
923 derived food and inspecting dangerous clients often, seem to depend on more precise  
924 cortisol responses that enable them to react to smaller trophic differences between  
925 clients (Soares et al 2012b, Soares et al 2018a). These results suggest that cortisol  
926 work to “fine-tune” cleaners’ behavioral profiles by contributing to behavioral shifts and  
927 flexibility.

928

#### 929 6.4. Monoamines in social plasticity in cleaner fish

930 Cognitive function in cleaner fish (and other teleosts) requires flexible  
931 coordination of multiple specialized areas of the brain; some of these regions are part of  
932 the SDMN. A participation of monoamines in learning and cognition has already been  
933 demonstrated in *L. dimidiatus*, as dopamine D1 receptor agonists improves learning of  
934 both a cue discrimination task and a side discrimination task (Messias et al., 2016),  
935 while serotonin 1A receptor antagonists delays learning of a cue discrimination task  
936 (Soares et al., 2016) Recently, efforts have been made to understand how the main  
937 brain areas respond, in terms of serotonergic and dopaminergic signalling, during the  
938 processing of complex social and mutualistic information (Abreu et al., 2018c, Maximino  
939 et al., 2018 [<https://doi.org/10.1101/326843>]). Abreu and colleagues (2018c)  
940 demonstrated that diencephalon serotonergic activity is particularly responsive in a  
941 situation of visual stimulation even in absence of actual physical contact (Figure 5),

942 suggesting that this region processes the cleaner's intrinsic motivation to interact  
943 regardless of the outcome (but see Paula et al 2015). While the decrease of  
944 dopaminergic activation was expected in the case of social reward omission, this was  
945 seemingly only observed when cleaners were prevented to interact with novel  
946 conspecifics rather than clients (Figure 5). The importance of cleaners' conspecific  
947 relationships, the value of couple dynamics to the overall expression of a series of  
948 "bilateral" behaviors between pair partners (conspecifics) and clients, and how these are  
949 modulated by cleaners' brain mechanisms, leaves plenty to look forward to in future  
950 studies. Interestingly, it was the actual cleaning engagement that resulted in significant  
951 change of dopaminergic activity, this time at the cerebellum (Abreu et al., 2018c; Figure  
952 5). As is the case with reproductive plasticity and choice in poeciliids, then, the  
953 cerebellum appears as a main area for processing mutualistic information  
954 (Kulczykowska et al., 2015), as it is strongly implicated in cognitive and emotional  
955 functions, namely in those linked to associative learning and memory processes  
956 (Rodriguez-Ortiz, 2005).

957

## 958 6.5. Social plasticity and brain size in guppies

959 The association of plasticity-related molecules and social plasticity is also of  
960 interest because it raises the question of whether brain morphology is altered by  
961 different social contexts, since many of these molecules are also involved in early brain  
962 differentiation, brain size, and gross morphology. Interesting studies have been  
963 developed in the guppy *P. reticulata* to investigate whether general and specific brain

964 morphology is associated with navigating complex social environments. A relationship  
965 between social plasticity and brain size was found by Kotrschal et al. (2012), who  
966 observed that male brains were larger in guppies that interacted with females, while the  
967 optic tectum was larger in females in female-only groups, suggesting that, while  
968 differences in brain sizes between sexes can be attributed to differences in emotional  
969 and foraging behavior, cognitive demands associated with courtship can also be  
970 responsible for brain size plasticity. Similar changes are seen after multiple generations  
971 of breeding guppies for large and small brain size relative to body size: after only two  
972 generations of selection, Corral-López et al. (2018) found that non-selected and large-  
973 brained males, but not small-brained males, showed context-dependent preferences for  
974 larger females that depend on the difference in female size; similarly non-selected and  
975 large-brained *females* show a strong preference for males with color traits that predict  
976 attractiveness in *P. reticulata* (Corral-López et al., 2017). That social complexity  
977 changes brain size has also been observed in the cooperatively breeding cichlid *N.*  
978 *pulcher*, in which the size of the rearing group influences both the development of  
979 aggressive and submissive behavior and the size of the optic tectum, hypothalamus,  
980 and cerebellum (Fischer et al., 2015). Finally, social competence is also associated with  
981 brain size, with dominance being established earlier in contests with losers which were  
982 selected for large brain size, whereas the brain size of the winner had no effect (van der  
983 Bijl et al., 2018).

984

985 

## 7. Conclusions

986 Social plasticity represents a challenging, yet evolutionarily and translationally  
987 relevant field of investigation across species. The over-reliance on a few “choice  
988 species”, under the assumption that they more closely model the human organism, not  
989 only does not make evolutionary sense, but also risks missing translationally relevant  
990 mechanisms (Gerlai 2014) of social plasticity. The wide range of social organizations  
991 across fish species makes them ideal model organisms to study the relationship  
992 between social plasticity and brain plasticity.

993 Patterns of modulation emerge when species and situations are compared. For  
994 example, a role for nonapeptides is observed during the establishment of dominance  
995 hierarchies; given the relationships between AVT and aggression in fish, this is not  
996 surprising, as behavioral shifts towards more aggressive phenotypes are advantageous  
997 when establishing dominance. A limitation of using fish, in this sense, is that brain  
998 contents cannot typically be analyzed without killing the animal, and therefore it is not  
999 yet possible to know whether nonapeptide levels are already high before the  
1000 establishment of hierarchies (and therefore predict dominance), or whether they  
1001 increase to shift behavior. Interestingly, however, in the Indo-Pacific cleaner wrasses  
1002 nonapeptides are implicated in decision-making, with AVT acting as an ontogenetic and  
1003 punctual switch between cleaning and non-cleaning; since cleaning is not expected to  
1004 involve aggression, these results underline the role of nonapeptides not only on

1005 aggression-based social dynamics, but also on cooperation and mutualism.

1006 Monoamines are also implicated in neural plasticity, especially in the contexts of  
1007 motivation, arousal, and emotional behavior (Forlano and Bass, 2011). Serotonin is a  
1008 “pleiotropic” neurotransmitter, being involved in aggression, antipredator defense, fear  
1009 and anxiety, and social behavior (Herculano and Maximino 2014). In fish, changes in  
1010 the serotonergic system were associated with behavioral sex reversal, with serotonin  
1011 mediating decreased aggression and dominance. Social status changes also mediate  
1012 sensory plasticity by modulating the serotonergic system, and diencephalic serotonin is  
1013 important for the establishment of interspecific cooperation in cleaner wrasses. Thus,  
1014 social plasticity of the serotonergic system appears to be important to induce behavioral  
1015 shifts associated with aggression and antipredator behavior. Also, the raphe nucleus  
1016 which contains serotonergic neurons was implicated in regulating reactive coping  
1017 behaviors associated with repeated social defeat in an African cichlid (Butler et al.,  
1018 2018). Peptides and monoamines, as well as cortisol, appear to act as “initiators” of  
1019 brain plasticity in a context of social plasticity.

1020 Not surprisingly, changing social status, reproduction, or behavioral strategy  
1021 warrants structural and functional changes in the SDMN. The work reviewed here  
1022 showed that markers of neuroplasticity and cell proliferation are stimulated by social  
1023 status changes, as well as by reproductive status changes (including sex reversal and  
1024 mate choice). Interestingly, these effects appear to be restricted to dominants, in the  
1025 case of social status. Whether the absence of effects in subordinates results from  
1026 technical limitations (e.g., lack of sensitivity), stress effects (which can impair memory,  
1027 for example), or other reason is still unknown. However, the breadth of species and



1028 contexts in which these plastic changes take place points to these molecules as “core”  
1029 mechanisms in consolidating brain plasticity in a context of social plasticity.

1030         The work discussed here also underlines potentialities and limitations of the  
1031 SDMN approach. Not surprisingly, social plasticity appears to be associated with neural  
1032 plasticity across regions of the SDMN; thus, in principle, focusing on these regions can  
1033 improve the power of comparative research to find conserved mechanisms of social  
1034 plasticity across species and social contexts, as well as to help in the discovery of  
1035 context-specific changes. Focusing on the role of specific neurotransmitters and  
1036 neuromodulators (e.g., monoamines and nonapeptides) on these changes seems to be  
1037 the obvious way forward. At the same time, changes are also observed in areas not  
1038 usually associated with the SDMN, including the cerebellum, optic tectum, and regions  
1039 of the hindbrain associated with escape responses and prey capture. This suggest that  
1040 a too narrow focus on the SDMN can create blind spots, as other regions involved in  
1041 social plasticity and context-dependent behaviors are ignored.

1042         Fish are also valuable for understanding the neural substrates and circuitry that  
1043 govern social behaviors, particularly in an evolutionary context. While the SDMN  
1044 provides a useful framework for investigating brain regions involved in social plasticity,  
1045 many other brain nuclei are implicated in context-dependent behaviors that should also  
1046 be considered. The everted teleost telencephalon also limits translation of fish studies to  
1047 other vertebrates until the homologies are better established. Nevertheless, it appears  
1048 as though some brain regions (and neural circuits) are common to broad behavioral  
1049 contexts like the POA in reproduction and the ATn (homolog of ventromedial  
1050 hypothalamus) in aggression, but how these circuits were co-opted for distinct

1051 behaviors in different species remains an intriguing question.

1052 Overall, fish represent an under-studied but promising taxon in the field of social  
1053 plasticity. In addition to zebrafish, which have been introduced in the neuroscience  
1054 literature, many other species are associated with vibrant research communities,  
1055 important “base” knowledge to ground neurobehavioral studies on neuroethology, and  
1056 species-specific social organizations which beget the need to understand commonalities  
1057 and differences in terms of social plasticity in the brain. The future awaits more  
1058 neuroscientists working with these animals to increase both evolutionary neuroscience  
1059 and translational studies.

1060

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1458 **Table captions**1459 **Table 1. Putative homologous brain regions between teleost fishes and mammals.**

1460 Note that putative mammalian homologs are only “in part” for many nuclei and are  
 1461 based on the following references: . The teleost homolog of the mammalian ventral  
 1462 pallidum is unclear and not listed. Abbreviations: ATn, anterior tuberal nucleus; DI,  
 1463 lateral part of dorsal telencephalon; Dm, medial part of dorsal telencephalon; PAG/CG,  
 1464 periaqueductal gray/central gray; POA, preoptic area; TPs, periventricular nucleus of  
 1465 posterior tuberculum; Vc, central part of ventral telencephalon; Vd, dorsal part of ventral  
 1466 telencephalon; Vp, postcommissural part of ventral telencephalon; Vs,  
 1467 supracommissural part of ventral telencephalon; Vv, ventral part of ventral  
 1468 telencephalon; VTn, ventral tuberal nucleus.

Teleost Region	Putative Mammalian Homolog
Dm	Pallial amygdala
DI	Medial pallium/hippocampus
Vv	Septum/External globus pallidus
Vd	Striatum/basal ganglia/nucleus accumbens
Vc	Striatum
Vs/Vp	Basal/central/extended amygdala
POA	Preoptic area
VTn	Anterior hypothalamus
ATn	Ventromedial hypothalamus
TPp	Ventral tegmental area
PAG/CG	Periaqueductal gray/central gray

1469

1470 **Figure captions**

1471 **Figure 1: Selected fish species used in behavioral neuroscience and ethology and**  
 1472 **their social organizations.** Different species occupy different social niches, showing  
 1473 potential to investigate one aspect of social plasticity.

1474

1475 **Figure 2: The social decision-making network (SDMN) of rodents (top) and fish**  
1476 **(bottom).**

1477 Abbreviations: LS – lateral septum; BNST – bed nucleus of the stria terminalis; meAMY  
1478 – medial amygdala; VMH – ventromedial hypothalamus; AH – anterior hypothalamus;  
1479 PAG – periaqueductal gray area; Dm – medial zone of the dorsal telencephalon; DI –  
1480 lateral zone of the dorsal telencephalon; Vs – supracommissural zone of the ventral  
1481 telencephalon; Vd – dorsal zone of the ventral telencephalon; Vv – ventral zone of the  
1482 ventral telencephalon; VI – lateral zone of the ventral telencephalon; POA – preoptic  
1483 area; Hv – ventral hypothalamus; ATN – anterior tuberal nucleus; TPp – posterior  
1484 tuberculum

1485

1486 **Figure 3: Sexual conflict and mate choice induce neuroplasticity between areas of**  
1487 **the SDMN in female *X. nigrensis*.** Adapted from Cummings (2018)

1488 Abbreviations: Dm – medial zone of the dorsal telencephalon; DI – lateral zone of the  
1489 dorsal telencephalon; Vs – supracommissural zone of the ventral telencephalon; Vd –  
1490 dorsal zone of the ventral telencephalon; Vv – ventral zone of the ventral telencephalon;  
1491 VI – lateral zone of the ventral telencephalon; POA – preoptic area; Hv – ventral  
1492 hypothalamus; ATN – anterior tuberal nucleus; TPp – posterior tuberculum

1493

1494 **Figure 4: Role of brain nonapeptides arginine-vasotocin (AVT) and isotocin (IT) in**  
1495 **mutualism in cleanerfish.** (A) Differences in nonapeptide levels between closely-  
1496 related cleanerfish species: 1 and 2) obligatory cleaners *Labroides dimidiatus* and

1497 *Labroides bicolor*; 3) facultative cleaner *Labropsis australis* and 4) non-cleaner species,  
1498 *Labrichthys unilineatus* (adapted from Kulczykowska et al., 2015). (B) Differences  
1499 between male and female *Labroides dimidiatus* couples, in accordance to their  
1500 association index – proportion of time spent cleaning together (adapted from Cardoso et  
1501 al. 2015).

1502

1503 **Figure 5: Cleaner brains presents different neuroendocrine shifts that are related**  
1504 **to contextual treatments** at 3 levels: A) non-social, B1 and B2) conspecific, and C1  
1505 and C2) interspecific. At different macro-areas: forebrain, diencephalon, optic tectum,  
1506 cerebellum, and brainstem. Experimental setup, individual cleaner *Labroides dimidiatus*  
1507 exposed to A) a ball, B) another conspecific, and C) a client. Abbreviations: Dopamine  
1508 (DA) and Serotonin (5-HT; 5-hydroxytryptamine), 3,4-dihydroxyphenylacetic acid  
1509 (DOPAC), 5-hydroxy indole acetic acid (5-HIAA), isotocin (IT).  
1510 (Adapted from Abreu et al. 2018a,b)