Special features of neuroendocrine interactions between stress and reproduction in teleosts

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69 **Abstract**

70 Stress and reproduction are both essential functions for vertebrate survival, ensuring on one

71 side adaptive responses to environmental changes and potential life threats, and on the other

72 side production of progeny. With more than 25,000 species, teleosts constitute the largest

73 group of extant vertebrates, and exhibit a large diversity of life cycles, environmental

74 conditions and regulatory processes. Interactions between stress and reproduction are a

75 growing concern both for conservation of fish biodiversity in the frame of global changes and

76 for the development of sustainability of aquaculture including fish welfare. In teleosts, as in

77 other vertebrates, adverse effects of stress on reproduction have been largely documented and

78 will be shortly overviewed. Unexpectedly, stress notably *via* cortisol, may also facilitate

79 reproductive function in some teleost species in relation to their peculiar life cyles and this

80 review will provide some examples. Our review will then mainly address the neuroendocrine

81 axes involved in the control of stress and reproduction, namely the corticotropic and

82 gonadotropic axes, as well as their interactions. After reporting some anatomo-functional

83 specificities of the neuroendocrine systems in teleosts, we will describe the major actors of

84 the corticotropic and gonadotropic axes at the brain-pituitary-peripheral glands (interrenals

85 and gonads) levels, with a special focus on the impact of teleost-specific whole genome

86 duplication (3R) on the number of paralogs and their potential differential functions. We will

87 finally review the current knowledge on the neuroendocrine mechanisms of the various

88 interactions between stress and reproduction at different levels of the two axes in teleosts in a

89 comparative and evolutionary perspective.

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Introduction

The first definition of stress by Selye in 1973 as "… the non-specific response of the body to any demand made upon it", refers to a general adaptation syndrome as a response to a stressor, which is similar irrespective of its nature (Selye, 1973). Since then, various definitions have appeared in the literature but the most complete one proposed by Schreck defines stress as "the physiological cascade of events that occurs when an organism is attempting to resist death or re-establish homeostatic norms in face of an insult" (Schreck, 2000). In response to a stressful situation and the recognition of a threat by the central nervous system, an adaptive compensatory non-specific response takes place with an initial adrenergic response and a subsequent synthesis and secretion of cortisol due to activation of the corticotropic axis, hypothalamus-pituitary-adrenal (HPA) in mammals, birds and reptiles, and hypothalamus-pituitary-interrenal gland/head kidney (HPI) in amphibians and teleosts. Activation of these endocrine pathways constitutes the primary responses, which lead to make energy available for systems involved in the stress responses. Thus, activation of the cardiovascular and respiratory responses accompanied by osmoregulatory disfunctions favour oxygen and energy substrates distribution and constitute the secondary responses. Tertiary responses refer to aspects of whole-animal performance and generally are maladaptative; they include changes in growth, swimming capacity, and modified behavioral patterns (feeding, aggression) [for reviews: (Barton, 2002; Gorissen and Flik, 2016; Schreck and Tort, 2016; Wendelaar Bonga, 1997)].

Stress is, in most cases, reported to affect reproduction in a deleterious way, but may also induce positive outcomes and a substantial body of research has been dedicated to decipher the mechanisms underlying the complex relationships between stress and reproduction [for reviews: (Fuzzen et al., 2011; Leatherland et al., 2010; Milla et al., 2009; Pankhurst, 2016; Schreck, 2010)]. Since the first paper by Selye in 1939 (Selye, 1939) which proposed that

118 activation of the hypothalamo-pituitary-adrenal (HPA) axis inhibits the hypothalamo-

119 pituitary-gonads (HPG) axis, this paradigm has been established mainly in mammalian

120 species (Chand and Lovejoy, 2011) but also in fish for which numerous reports emphasizing

121 effects of corticosteroids on reproduction have been produced (Fuzzen et al., 2011;

122 Leatherland et al., 2010; Milla et al., 2009; Pankhurst, 2016; Schreck, 2010) . In this paper,

123 we will focus our interest on the relationships between stress and reproductive neuroendocrine

124 axes, trying to decipher direct stress effects and separate them from systemic effects on other

125 biological functions. Thanks to the recent progress brought by genomic studies, we will be

126 able to integrate the most recent informations provided by molecular phylogeny analyses and

127 describe effects of new actors, which appeared *via* different rounds of whole genome

128 duplications. This review will focus on teleost fish but with an evolutionary perspective

129 requiring comparison with other vertebrate species.

130

131 **1. Various interactions between stress, cortisol and reproduction in teleosts**

132 Many relationships between stress and reproduction, with the influence of environmental

133 conditions, have been documented in natural situation and in aquaculture. In this context, we

134 first consider in this section the effects of stressors on reproduction, which are frequently

135 associated with high cortisol levels.

136   **1.1. Negative interactions between stress and reproduction**

137 Early works in many teleost species reported the deleterious effects of stress and stress-related

138 increase of cortisol on gonadotropic axis and reproductive performance. Chronically-induced

139 stress such as by confinement or captivity and acutely-induced stress such as by predators or

140 by aquaculture practices (handling, frequent netting, tank draining, crowding, noise) result in

141 reduced plasma androgen and oestrogen levels [brown trout *Salmo trutta*: (Pickering et al.,

142 1987); wild spotted seatrout *Cynoscion nebulosus*: (Safford and Thomas, 1987); rainbow trout

143 *Oncorhynchus mykiss*: (Pankhurst and Dedual, 1994); red gurnard *Chelidonichthys kumu*:

144 (Clearwater and Pankhurst, 1997); striped trumpeter *Latris lineata*: (Morehead, 1998); roach

145 *Rutilus rutilus*: (Pottinger et al., 1999); black bream *Acanthopagrus butcheri*: (Haddy and

146 Pankhurst, 1999); sockeye salmon *Oncorhynchus nerka*: (Kubokawa et al., 1999); snapper

147 *Pagrus auratus*: (Carragher and Pankhurst, 1991; Cleary et al., 2000); spiny damselfish

148 *Acanthochromis polyacanthus*: (Pankhurst, 2001); striped bass *Morone saxatilis*: (Castranova

149 et al., 2005); jundia *Rhamdia quelen*: (Soso et al., 2008); tilapia *Oreochromis mossambicus*:

150 (Chabbi and Ganesh, 2012)]. Stress is also associated with reduced plasma vitellogenin (Vg)

151 levels [brown and rainbow trout: (Campbell et al., 1994)]. It also decreases plasma luteinizing

152 hormone (LH) levels [white sucker *Catostomus commersoni*: (Van Der Kraak et al., 1992)],

153 suppresses LH secreting cell activity [tilapia: (Chabbi and Ganesh, 2012)], as well as

154 decreases hypothalamic gonadotropin-releasing hormone 1 (GnRH1) mRNA levels [jack

155 mackerel *Trachurus japonicus*: (Imanaga et al., 2014)]. After applied stress, impacts on final

156 stages of reproduction are also observed such as delayed ovulation [rainbow trout: (Campbell

157 et al., 1992; Contreras-Sanchez et al., 1998)], reduced egg size in females [brown and

158 rainbow trout: (Campbell et al., 1994, 1992) ; *Neolamprologus pulcher*: (Mileva et al., 2011)]

159 and reduced sperm counts in males [brown and rainbow trout: (Campbell et al., 1994)],

160 increased gonadal atresia [(pike *Esox lucius*: (De Montalembert et al., 1978); red gurnard:

161 (Clearwater and Pankhurst, 1997); snapper: (Cleary et al., 2000); Atlantic bluefin tuna

162 *Thunnus thynnus*: (Corriero et al., 2011)], and reduced fecundity [rainbow trout : (Contreras-

163 Sanchez et al., 1998)]. Furthermore, impacts on progeny also occur such as reduced length

164 [tropical damselfish *Pomacentrus amboinensis*: (McCormick, 2009, 2006, 1999, 1998)],

165 decreased survival [brown and rainbow trout: (Campbell et al., 1994, 1992)] or occurrence of

166 abnormalities [Atlantic cod *Gadus morhua*: (Morgan et al., 1999)] [for reviews: (Billard,

167 1981; Pankhurst and Van der Kraak, 1997; Pankhurst, 2016; Pickering, 1989)].

168   Socially mediated stress response and downregulated reproductive function are observed in

169   some teleosts, such as in cichlids. For example, subordinate (non-territorial) males of

170   *Astatotilapia (Haplochromis) burtoni* display high expression of hypothalamic and pituitary

171   corticotropin-releasing hormone (CRH) receptor as well as high plasma cortisol levels, but

172   low mRNA levels of hypothalamic GnRH1 and of pituitary GnRH receptor, LH and FSH, as

173   well as low plasma levels of LH and FSH, and androgens, compared to dominant (territorial)

174   males [for review: (Maruska, 2014)].

175   **1.2. Positive interactions between cortisol and reproduction related to peculiar**

176   **life cycles**

177   **1.2.1. Cortisol and environmentally-related spawning activity in some**

178   **teleosts**

179   The catfish, *Heteropneustes fossilis*, awaits the onset of the monsoon rainfall for spawning in

180   order to get favorable environmental conditions. Interestingly, in this species, plasma cortisol

181   levels exhibit a peak at monsoon (Lamba et al., 1983; Sundararaj and Goswami, 1966a,

182   1966b), and glucocorticoids are effective both *in vivo* and *in vitro* in inducing ovulation

183   (Sundararaj and Goswami, 1977). *In vivo* administration of an ovulatory dose of LH in this

184   species induces an increase in plasma levels of cortisol followed by an increase in sex steroid

185   (T and E2) levels, while ACTH injection only stimulates cortisol levels. The authors suggest

186   that gonadotropin acts at two loci, the interrenal and the ovary (Goswami et al., 1985). All

187   these data indicate a potential positive role of cortisol in the induction of spawning in the

188   catfish. Another striking example is the killifish *Fundulus heteroclitus* which exhibits

189   synchronized spawning with the semilunar cycle of spring tides and a peak of plasma cortisol

190   level coincides with spawning (Bradford and Taylor, 1987).

191   **1.2.2. Cortisol and upstream reproductive migration in salmonids**

192 Upstream migration and spawning require high energy reserve mobilization; in Atlantic

193 salmon *Salmo salar*, for example, between 60% and 70% of the body reserves are spent

194 during upstream migration and spawning (Jonsson et al., 1997). High plasma cortisol levels

195 and interrenal hyperplasia have long been reported during the later stages of the spawning

196 migration and at the time of spawning in various salmonids [Pacific sockeye salmon:

197 (Donaldson and Fagerlund, 1972; Hane and Robertson, 1959; Idler et al., 1959); migratory

198 (steelhead) rainbow trout: (Robertson et al., 1961); Atlantic salmon: (Schmidt and Idler,

199 1962); kokanee salmon, landlocked form of sockeye salmon: (Carruth et al., 2000)]. However,

200 one study in sockeye salmon reports that sexual maturation is not necessarily accompanied by

201 elevated plasma cortisol levels (Fagerlund, 1967). Increased cortisol level is also described at

202 spawning in non-migratory rainbow trout (Bry, 1985; Robertson et al., 1961). Altogether

203 these studies indicate that high cortisol levels in salmonids are, at least, not deleterious to

204 sexual maturation and spawning.

205   **1.2.3. Cortisol and oceanic reproductive migration in eels**

206 The downstream and oceanic migrations of eels (*Anguilla* species), as well as their whole

207 gonadal development from prepubertal stage to full sexual maturation, require both metabolic

208 energy and metabolites that come exclusively from body stores [for review: (Palstra and van

209 den Thillart, 2010)]. Clevestam and collaborators report that 45% of European eel (*Anguilla*

210 *Anguilla*) from Baltic sea would be within 90% of complete energy depletion after migration

211 and reproduction and 20% would have completey exhausted their initial fat reserves

212 (Clevestam et al., 2011). Eel, at the silver prepubertal, downstream migratory, stage and

213 during their subsequent reproductive oceanic migration and sexual migration, are fasting and

214 all their metabolic stores, accumulated during the juvenile growth (yellow stage) phase, will

215 be mobilized. In silver eels, an elevation of plasma cortisol levels is observed prior to

216 downstream migration (Van Ginneken et al., 2007). Early studies of hypophysectomy and

217   adrenalectomy report the need of an intact pituitary-interrenal axis for maintenance of liver

218   glycogen levels in eels [*Anguilla anguilla*: (Hatey, 1951); American eel *Anguilla rostrata*:

219   (Butler, 1968)]. Cortisol induces mobilization of lipid and protein stores and stimulates

220   hepatic neoglucogenesis [for review: (Butler, 1973); Japanese eel *Anguilla japonica*: (Chan

221   and Woo, 1978); *Anguilla anguilla*: (Dave et al., 1979); *Anguilla rostrata*: (Butler, 1968;

222   Foster and Moon, 1986)]. Cortisol also induces eel vertebral demineralization, by promoting

223   both osteocytic osteolysis and osteoclastic resorption, allowing mobilization of phospho-

224   calcic stores necessary for vitellogenin synthesis (Sbaihi et al., 2009). Besides these actions

225   on metabolism necessary for the eel migratory and reproductive processes, cortisol may also

226   directly stimulate the gonadotropic axis, as shown by its positive effect on pituitary *lhβ*

227   mRNA and LH protein content *in vivo* and *in vitro* [*Anguilla anguilla*: (Huang et al., 1999)].

228   Thus, in the eel, cortisol may both coordinate storage mobilization and participate in the

229   induction of sexual maturation during reproductive migration.

230   **1.3. Cortisol and gonadal sex differentiation**

231   In some teleost fish species, gonadal sex determination and/or sex change are under the

232   regulation of environmental factors. An increasing number of data proposes cortisol as a key

233   factor integrating environmental cues (such as temperature or social status) to induce male sex

234   determination/sex change [for reviews: (Fernandino et al., 2013; Fernandino and Hattori,

235   2019; Goikoetxea et al., 2017; Liu et al., 2017; Perry and Grober, 2003; Solomon-Lane et al.,

236   2013; Todd et al., 2016)]. Cortisol administration or stress-induced cortisol release (including

237   high temperature-induced effects) promotes masculinization in a number of teleosts [rainbow

238   trout: (van den Hurk and van Oordt, 1985); pejerrey *Odontesthes bonariensis*: (Hattori et al.,

239   2009); Japanese flounder *Paralichthys olivaceus*: (Yamaguchi et al., 2010); Southern flounder

240   *Paralichthys lethostigma*: (Mankiewicz et al., 2013); three-spot wrasse *Halichoeres*

241   *trimaculatus*: (Nozu and Nakamura, 2015); black sea bass *Centropristis striata*: (Miller et al.,

242   2019); medaka *Oryzias latipes* (Hayashi et al., 2010); orange spotted grouper *Epinephelus*

243   *coioides* (Chen et al., 2020)]. Several potential pathways are described for cortisol triggering

244   maleness: cross-talk between glucocorticoid and androgen metabolism (11β-hydroxysteroid

245   dehydrogenase, 11βHSD, and 11β-hydroxylase, Cyp11b, enzymes) promoting the synthesis

246   of 11-ketotestosterone (11KT); inhibition of aromatase (*cyp19a1a*) expression, leading to a

247   shift in steroidogenesis from estrogens to androgens; and upregulation of anti-Müllerian

248   homone (*amh*) expression [for reviews: (Fernandino et al., 2013; Fernandino and Hattori,

249   2019; Goikoetxea et al., 2017; Liu et al., 2017; Perry and Grober, 2003; Solomon-Lane et al.,

250   2013)]. In the pejerrey, cortisol increases the expression of *hsd11b2*, the gene for 11βHSD, an

251   enzyme which deactivates cortisol to cortisone and catalyzes the final step in 11-KT synthesis

252   (Fernandino et al., 2012). Typical DNA binding sites of glucocorticoid receptor (GR) *i.e.*

253   glucocorticoid response elements (GRE) are identified in the *cyp19a1a* promoter in the goby

254   *Gobiodon histrio* (Gardner et al., 2005) and in the black sea bass (Miller et al., 2019).

255   Interestingly, GR is also shown to directly interact with cAMP-responsive element (CRE) on

256   *cyp19a1a* promoter of Japanese flounder, down-regulating the expression of aromatase

257   (Yamaguchi et al., 2010). Temperature-dependent sex determination (TSD) is shown to

258   involve regulation of DNA methylation of the *cyp19a1a* promoter [European sea bass

259   *Dicentrarchus labrax*: (Navarro-Martín et al., 2011)], and such epigenetic modifications may

260   also be a mechanism by which cortisol regulates aromatase expression.

261   All these studies highlight the role of cortisol as a mediator between environmental conditions,

262   especially temperature, and male sex determination in various teleost species. This confers to

263   cortisol a key-role in the potential impact of global climatic change on the modification of sex

264   ratio in some teleost species and its consequences on population sustainability.

265   **1.4. Animal welfare, environment, stress and reproduction**

266 Concerns about fish welfare have increased considerably during the recent years owing to the

267 growing public interest for the negative impacts of intensification in aquaculture and for

268 scientific debate about pain in fish. Many authors agree on a definition for which welfare is

269 not only based on physical health but also lack of mental suffering and presence of positive

270 feelings (Huntingford et al., 2006; Segner et al., 2012; Sneddon et al., 2016; Stevens et al.,

271 2017; Toni et al., 2019). In this context, most of the welfare issues are related to stress

272 responses, experience of pains, growth problems, incidence of disease, abnormal behaviors

273 and less frequently to degradated breeding with negative impact on male or female

274 reproduction. These effects observed in aquaculture environment are not only the

275 consequence of exposure of adult fish to stressors (*e.g.* confinement, handling, hypoxia or

276 poor water quality) but also associated with abnormal behavior or impossibility to develop a

277 normal behavior created by captive environment (Sneddon et al., 2016). Thus, one potential

278 consequence of confinement is irregular spawners which suffer from a low fertilisation rate

279 and a broken ovulatory rhythm (Kjesbu, 1989; Patterson et al., 2004). Intense swimming

280 activity during chase and capture can also be sufficient to compromise reproduction

281 (Pankhurst and Van der Kraak, 1997). Repeated acute confinement stress during the spawning

282 season as well as poor body condition or food deprivation have also negative effects on

283 fecundity in cod, all effects which have been suggested to be related to altered energy

284 allocation (Bogevik et al., 2012; Kjesbu et al., 1991; Kjesbu, 1989; Lambert and Dutil, 2000).

285 Behavioral needs can also be a welfare issue, not only by preventing maltreatment but also by

286 providing adult fish resources to perform natural behavioural repertoire necessary for

287 reproduction, accommodations which are species specific (Sneddon et al., 2016). Sometimes

288 also, search for optimal performance in aquaculture can lead to welfare issue in relation to

289 reproduction. In salmon aquaculture, early maturation can be a significant welfare issue. The

290 maturation process is energetically expensive which is reflected in early maturing salmon by

291   decreased growth rate and increased mortality through susceptibility to pathogens (Gjerde,

292   1984; Thorpe, 1994). Selection for both fast growth and late sexual maturation has been

293   considered problematic as it has been suggested that there is a correlation between the

294   phenotypes fast growth and early sexual maturation (Thorpe et al., 1983). The importance of

295   energy cost for reproduction also appears when considering exercised female sockeye salmon

296   compared to non-exercised fish: they displayed lower lipid content, delayed maturity, lower

297   egg deposition rate and higher egg mortality prior to ovulation (Chellappa and Huntingford,

298   1989; Hansen et al., 2010). Methods used in aquaculture for egg collection from female is

299   also a crucial procedure for fish reproduction in salmonid aquaculture: comparison between

300   various methods (massage of the fish abdomen versus pressure of gas) in rainbow trout

301   indicated that air stripping led to better quality of eggs and better juvenile survival rate

302   (Kowalski et al., 2018). In recreational fisheries, studies on angling and release of nesting

303   species during the spawning season reported decreased progenity survival and paternal nest

304   abandonment and impaired care (Cooke et al., 2000; Hanson et al., 2007; Philipp et al., 1997).

305   However, specific investigations on gonadal development of final maturation find very few

306   adverse effects (Booth et al., 1995; Hall et al., 2009; Lowerre-Barbieri et al., 2011).

307   Moreover, when testing effects of mild angling and release on golden perch *Macquaria*

308   *ambigua*, normal gonadal development is observed in angled fish, a result attributed to the

309   flexible reproductive strategy of that species and benigness of the mouth hooking (Hall et al.,

310   2017). These results illustrate the complexity of welfare questions related to reproduction,

311   which certainly need to take into account the specificity of the fish species and/or the

312   characterisitics of the environment and stressors.

313

314   **2. Overview of neuroendocrine stress and reproductive axes in teleosts**

315   **2.1. Teleost specific traits compared to other vertebrates**

316   In mammals, brain-pituitary-peripheral glands axes are a classical schema when describing

317   the endocrine regulation of major physiological functions, such as reproduction with the

318   gonadotropic axis or stress with the corticotropic axis. Similar structures are observed in

319   teleost fish which also present specificities which need to be considered for understanding

320   stress/reproduction relationship in these species.

321   **2.1.1. Anatomo-functional specificities**

322   **2.1.1.1. Pituitary regionalisation and direct innervation**

323   The pituitary gland is a vertebrate innovation [for reviews: (Dufour et al., 2020; Sower,

324   2018)]. In all vertebrates, the pituitary consists of the adenohypophysis and the

325   neurohypophysis. The adenohypophysis has been subdivided by early studies into the *pars*

326   *distalis* and the *pars intermedia*, with in tetrapods, an additional *pars tuberalis* [for reviews:

327   (De Beer, 1923; Dores, 2017)]. In contrast to tetrapods in which cells of the *pars distalis* seem

328   widely distributed, in teleosts, the different types of cells of the *pars distalis* are regionalised

329   [*Poecilia formosa* and *latipinna* (Olivereau and Ball, 1964); European eel (Olivereau, 1967);

330   Atlantic halibut *Hippoglossus hippoglossus* (Weltzien et al., 2004); zebrafish *Danio rerio*

331   (Pogoda and Hammerschmidt, 2007)*;* for reviews: (Schreibman et al., 1973; Trudeau and

332   Somoza, 2020; Zohar et al., 2010)]. This allowed an anatomical subdivision of the *pars*

333   *distalis* (PD), in teleosts, into an anterior region, the rostral *pars distalis* (RPD) composed of

334   lactotropes (prolactin cells) and corticotropes (corticotropin, ACTH cells), and a posterior

335   region, the proximal (or caudal) *pars distalis* (PPD) composed of somatotropes (growth

336   hormone cells), thyreotropes (thyrotropin TSH cells) and gonadotropes (luteinizing hormone

337   LH and follicle stimulating hormone FSH cells). Interestingly, in teleosts, the two

338   gonadotropins, LH and FSH, are expressed in different pituitary cells, in contrast to the

339   situation observed in mammals which produce LH and FSH in the same pituitary cell [for

340   review: (Kanda, 2019)]. This feature allowed Golan and collaborators to investigate in

zebrafish the differential organization of LH and FSH cells and they reported that LH cells are coupled *via* strong gap-junction, while FSH cells show long cytoplasmic extension to maintain contact, possibly explaining their differential release patterns (Golan et al., 2016). In teleosts as in tetrapods, the *pars intermedia* of the pituitary contains melanotrope cells which produce MSH (melanocyte-stimulating hormone) from the same precusor as ACTH.

In tetrapods, brain hypophysiotropic neurons project to the median eminence at the basis of the hypothalamus and release their neurohormones into the hypophyseal portal vascular system, which carries them to the *pars distalis*. Differently, in teleosts, the axonal endings of the brain hypophysiotropic neurons terminate in close vicinity to the cells of the adenohypophysis providing a direct innervation [for review: (Trudeau and Somoza, 2020; Zohar et al., 2010)].

2.1.1.2. Caudal neurosecretory system

The caudal neurosecretory system (CNSS) is unique to some non-mammalian vertebrates such as teleosts (Osteichthyes) and elasmobranchs (Chondrichthyes). It is situated in the posterior region of the spinal cord and it comprises large neurosecretory neurons named after their discoverer, the Dahlgren cells (Dahlgren, 1914). These neurons project their axons to a neurohaemal organ, the urophysis, where neuropeptides are released into the renal portal system *via* the caudal vein to the head kidney [for reviews: (Bern and Takasugi, 1962; McCrohan et al., 2007; Winter et al., 2000)]. Two of these neuropeptides were first isolated from CNSS and named urotensins: urotensin I in white sucker *Catostomus commersoni* (Lederis et al., 1982) and common carp *Cyprinus carpio* (Ichikawa et al., 1982) and urotensin II in the goby *Gillichthys mirabilis* (Pearson et al., 1980). Urotensin I is related to CRH [for review: (Lovejoy et al., 2014)] and urotensin II to somatostatin [for review: (Tostivint et al., 2014)]. Apart from these urotensins, the CNSS produces two other neuropeptides, CRH and parathyroid hormone-related protein, as well as a neurotransmitter, acethylcholine [for

review: (McCrohan et al., 2007)]. In teleosts, together with the preoptic area of the brain, the CNSS is the major source of CRH and urotensins [European flounder *Platichthys flesus*: (Lu et al., 2004); rainbow trout: (Bernier et al., 2008; Craig et al., 2005); zebrafish: (Alderman and Bernier, 2009)], two neuropeptides which are involved in the stress axis (cf § 2.2.2.1).

2.1.2. Teleost specific whole genome duplication

Two whole genome duplications (WGD) likely occurred in ancestral vertebrates and are named 1R and 2R for first and second round of WGD, respectively [for review: (Dehal and Boore, 2005)]. An additional WGD specifically occurred at the basis of the teleost lineage, referred to as teleost specific WGD (TWGD) or as 3R for third round of WGD [for review: (Meyer and Van De Peer, 2005)]. WGD events led to the expansion of gene numbers. This additional WGD in teleosts would have favored the evolutionary success and the remarkable biological diversity of teleosts, the largest vertebrate group. Concerning the neuroendocrine axes, the 3R is at the origin of additional paralogs for a number of actors of both gonadotropic and corticotropic axes in teleosts. Further additional WGD occurred more recently independently in some teleost groups, such as in salmonids (Lien et al., 2016; Robertson et al., 2017) and in carps (Larhammar and Risinger, 1994; Wang et al., 2012) and are referred to as 4R for fourth round of WGD. Conservation of duplicated paralogs may be related to amplification of function, sharing of multiple preexisting functions (subfunctionalization) or acquisition of new function (neofunctionalization) [for review: (Dufour et al., 2020)].

2.2. The corticotropic axis

2.2.1. Main actors of the corticotropic axis in vertebrates

In all vertebrates, stress response is regulated by the corticotropic axis (HPA in mammals and sauropsids and HPI in amphibians and teleosts) [for review: (Gorissen and Flik, 2016)]. The neurohormone, corticotropin-releasing hormone (CRH), as its name indicates, controls the production and release of corticotropin (also named adrenocorticotropic hormone, ACTH), at

391   the pituitary level. ACTH is the result of tissue-specific post-translational processing of

392   proopiomelanocortin (POMC), together with melanocyte stimulating hormone (MSH), and β-

393   endorphin (β-END). ACTH and MSH, called melanocortins (MC) act *via* MC receptors

394   (MCR), while β-END acts *via* opioid receptors. ACTH from the corticotrophs of the *pars*

395   *distalis* of the pituitary controls via type 2 MCR (melanocortin-2 receptor, MC2R),

396   glucocorticoid production and release from adrenal cortex cells in amniotes or interrenal cells

397   in amphibians and teleosts. Major glucocorticoids are cortisol in most mammals and ray

398   finned fish and corticosterone in most birds, amphibians and reptiles [for review: (Aerts,

399   2018)]. MC2R, in teleosts as in tetrapods, is ligand selective as it can only be activated by

400   ACTH and not by MSH, and requires coexpression with an accessory protein, melanocortin-2

401   receptor accessory protein (MRAP) for trafficking to the cell surface [for reviews: (Dores,

402   2016; Dores et al., 2016)]. Glucocorticoids negatively feedback on the brain (hypothalamic

403   CRH) / pituitary (ACTH) corticotropic axis [for reviews: (Bernier et al., 2009; Faught et al.,

404   2016; Gorissen and Flik, 2016)]; this negative feedback regulation of the HPI axis involves

405   glucocorticoid receptor (GR) signaling pathway.

406   **2.2.2. Specific features of the corticotropic axis in teleosts**

407   The hypothalamic regulation of corticotropes and melanotropes in teleosts has already been

408   extensively reviewed by Bernier and collaborators (Bernier et al., 2009).

409   **2.2.2.1. CRH and related peptides and their receptors**

410   CRH, first isolated from sheep hypothalamus, together with urotensin I (UI) isolated from the

411   CNSS of the white sucker (Lederis et al., 1982) and the common carp (Ichikawa et al., 1982),

412   and with sauvagine (SVG) isolated from the skin of the amphibian *Phylomedusa sauvagei*

413   (Montecucchi et al., 1980), form a large family of peptides. Later on, urocortins were

414   identified in mammals and also found to be related to CRH: urocortin 1 (Ucn1), ortholog of

415   UI and SVG (Vaughan et al., 1995); urocortin 2 [Ucn2: (Reyes et al., 2001)] and urocortin 3

416 [Ucn3: (Lewis et al., 2001)] [for review: (Lovejoy and Balment, 1999)]. All these peptides,

417 CRH and urocortins in mammals and CRH and UI/SVG in teleosts and amphibians, represent

418 the CRH/urocortin family.

419 The complex evolutionary scenario of this family was recently clarified by Cardoso and

420 collaborators (Cardoso et al., 2016). As previously suggested by Hwang and collaborators,

421 two ancestral *crh/ucn1* and *ucn2/ucn3* genes likely arose by specific gene duplication before

422 vertebrate WGD events (Hwang et al., 2013). Both ancestral genes were duplicated twice in

423 ancestral vertebrates *via* 1R and 2R, followed by some paralog losses, leading to up to 5

424 genes (*crh1, crh2, ucn1* issued from ancestral *crh/ucn1*; *ucn2, ucn3*, issued from ancestral

425 *ucn2/ucn3*) in extant representative species of some vertebrate lineages such as

426 chondrichthyans, holosteans and actinistians (Cardoso et al., 2016). Teleost specific 3R

427 resulted in the duplication of *crh1* into two paralogs *crh1a* and *crh1b* conserved in many

428 species [for review: (Cardoso et al., 2016)]. *Crh2* may have been lost in recent teleosts

429 (Cardoso et al., 2016), while one 3R-*crh2* paralog has been conserved in basal groups of

430 teleosts [(Maugars et al., 2016) and Maugars et al. unpublished data].

431 The involvement of CRH in the stress response in teleosts is well-documented [for reviews:

432 (Flik et al., 2006; Gorissen and Flik, 2016)]. Teleost *crhb* (*crh1b*) paralog is widely expressed

433 in the brain of various teleost species [goldfish *Carassius auratus*: (Bernier et al., 1999);

434 flounder *Platichthys flesus*: (Lu et al., 2004); zebrafish: (Alderman and Bernier, 2007);

435 Japanese eel: (Amano et al., 2014); *Astatotilapia burtoni*: (Carpenter et al., 2014);

436 *Schizothorax prenanti*: (Wang et al., 2014)]. To our knowledge, the expression of the *crha*

437 (*crh1a*) paralog was only investigated in *Astatotilapia burtoni* and zebrafish: in the zebrafish,

438 *crha* expression is restricted to the lateral tuberal nucleus of the ventral hypothalamus, while

439 in *A. burtoni*, no *crha* expression is detected in the brain (Grone and Maruska, 2015). The

440 authors also show that, while both forms are expressed in the retina of *Astatotilapia burtoni*,

441   only *crhb* expression is observed in the retina of zebrafish (Grone and Maruska, 2015). These

442   first data suggest species-specific variations in the respective roles of 3R-duplicated *crh1*

443   paralogs in teleosts.

444   In mammals, CRH binds to G-protein coupled receptors, CRHR1 and CRHR2, which belong

445   to the class 2 subfamily B1 of secretin-like receptor superfamily. *Crhr1* was duplicated *via*

446   teleost-3R into two paralogs (*crhr1a* and *crhr1b*) which were conserved in many extant

447   teleosts, while one of 3R-duplicated *crhr2* paralogs would have been lost [for review:

448   (Cardoso et al., 2014)]. CRHR1s are thought to mediate CRH action along the

449   corticotropic/stress axis, as, like mammalian CRHR1, teleost CRHR1s have similar affinity

450   for CRH and UI/Ucn1 while CRHR2 has higher affinity for UI and urocortins (2 and 3) than

451   for CRH [catfish *Ameirus nebulosus*: (Arai et al., 2001); chum salmon *Oncorhynchus keta*:

452   (Pohl et al., 2001); common carp: (Manuel et al., 2014)].

453   The ACTH-releasing action of CRH has been demonstrated *in vitro* in many teleost species

454   [goldfish : (Fryer et al., 1984); rainbow trout: (Baker et al., 1996; Pierson et al., 1996);

455   gilthead sea bream *Sparus aurata*: (Rotllant et al., 2001, 2000); Mozambique tilapia

456   *Oreochromis mossambicus*: (Van Enckevort et al., 2000); common carp: (Metz et al., 2004)],

457   as in mammals (Rivier et al., 1983; Rivier and Plotsky, 1986), birds (Carsia et al., 1986) and

458   amphibians (Tonon et al., 1986). In the common carp, the release of ACTH is stimulated by

459   CRH but only when ACTH cells are submitted to DA inhibition (Metz et al., 2004).

460   CRH stimulates not only ACTH release, but also α-MSH release, in various teleosts such as

461   in Mozambique tilapia (Lamers et al., 1994; Van Enckevort et al., 2000), gilthead sea bream

462   (Rotllant et al., 2001), red porgy *Pagrus pagrus* (Van Der Salm et al., 2004) and common

463   carp (Van Den Burg et al., 2005). This α-MSH-releasing effect of CRH is also reported in

464   mammals such as rat (Meunier et al., 1982; Proulx-Ferland et al., 1982). In contrast, in an

465   amphibian, the frog *Rana ridibunda*, while CRH is a potent stimulator of ACTH release by

466 anterior pituitary cells, it is ineffective on α-MSH release by neurointermediate lobes *in*

467 *vitro* (Tonon et al., 1986).

468 Other CRH-related peptides such as UI and sauvagine can induce in goldfish the release *in*

469 *vitro* of ACTH (Fryer et al., 1984, 1983), as well as of α-MSH (Tran et al., 1990).

470 Interestingly, UI and SVG are equipotent to CRH in stimulating ACTH release by rat anterior

471 pituitary cells (Rivier et al., 1983), while in the frog *Rana ridibunda*, they are unable to

472 stimulate ACTH release (Tonon et al., 1986). Concerning α-MSH, UI and SVG induce its

473 release by the neurointermediate lobe *in vitro* in *Xenopus laevis* (Verburg-Van Kemenade et

474 al., 1987), but not in *Rana ridibunda* (Tonon et al., 1986). In addition to its action on the

475 pituitary, UI is able to directly stimulate cortisol release, and to potentiate ACTH-stimulatory

476 effect, on interrenals *in vitro* in rainbow trout (Arnold-Reed and Balment, 1994) and

477 European flounder (Kelsall and Balment, 1998). Finally, in maturing masou salmon

478 *Oncorhynchus masou*, UI rather than CRH could be involved in the control of

479 hypercortisolemia, as hypothalamic *uI* expression rises in correlation with enhanced cortisol

480 secretion, while *crh* expression does not (Westring et al., 2008).

481 In the rainbow trout, both *crh* and *uI* expressions in the brain (hypothalamus and preoptic

482 area) increase in response to various stressors: hyperosmotic challenge (Craig et al., 2005),

483 hyperammonemia, isolation (Bernier et al., 2008) as well as hypoxia (Bernier et al., 2008;

484 Bernier and Craig, 2005). Notably*, crh* and *uI* expressions increase also in the caudal

485 neurosecretory system (CNSS) in response to various stressors in the rainbow trout

486 [hyperosmotic challenge: (Craig et al., 2005); hyperammonemia: (Bernier et al., 2008)] and in

487 the olive Japanese flounder, *Paralichthys olivaceus* [acute hypothermal stress: (Yuan et al.,

488 2020)]. In the European flounder, net restraint induces an increase in *crh* expression in the

489 CNSS, but not in the hypothalamus, as well as an increase in CNSS cortisol receptors in

490 addition to an increase in plasma cortisol levels (Lu et al., 2004). In this species,

491   glucocorticoid receptors have been colocalized with UI in the CNSS (Bond et al., 1999). All

492   these data suggest the possible involvement of the CNSS in the stress-specific regulation of

493   cortisol production in teleosts and the existence of an extra-pituitary feedback system on

494   CNSS for the suppression of cortisol secretion. Earlier *in vivo* studies already reported the

495   possible involvement of CNSS in the regulation of the corticotropic axis: injection of

496   urophysis extracts or synthetic *Catostomus commersoni* UI in flounder induces an elevation

497   of cortisol (Arnold-Reed and Balment, 1989); in goldfish, urophysectomy produces marked

498   elevation of hypothalamic UI-like activity, pituitary ACTH and plasma cortisol, which can

499   not be observed in urophysectomized fish receiving dexamethasone (Woo et al., 1985). More

500   functional investigations are needed to assess the possibility of a major contribution of CNSS

501   CRH-related peptides to the regulation of cortisol secretion and stress responses.

502   **2.2.2.2. Dopamine and other neurohormones**

503   **Dopamine*

504   In mammals, different data have been reported concerning the effects of dopamine (DA) on

505   ACTH release between *in vitro* and *in vivo* studies. Treatment of rat anterior pituitary glands

506   (Van Loon and Kragt, 1970) or human corticotroph adenoma cells (Ishibashi and Yamaji,

507   1981) with DA lowers ACTH release. In contrast, administration of DA agonists to rats

508   elevates plasma ACTH concentrations and subsequently plasma corticosterone levels, and this

509   elevation is prevented by pretreatment with DA antagonists (Borowsky and Kuhn, 1992;

510   Ježová et al., 1985). An α-MSH-release inhibitory effect of DA is observed in amphibians

511   [*Rana pipiens*: (Saland et al., 1982); *Rana ridibunda* : (Jenks et al., 1985); *Xenopus laevis* :

512   (Verbug-Van Kemenade et al., 1986)].

513   Possible involvement of DA in the hypothalamic regulation of teleost corticotropes and

514   melanotropes has been suggested by Metz and colleagues. As basal ACTH release increases

515   slowly and steadily over time when pituitary glands of common carp are incubated *in vitro*,

they conclude that ACTH release is under a predominant inhibitory control *in vivo* (Metz et al., 2004). They also show that DA inhibits ACTH release and is necessary for CRH-stimulation of ACTH release (Metz et al., 2004). It was previously reported that DA was able to inhibit *in vitro* α-MSH release by goldfish (Omeljaniuk et al., 1989) and red porgy (Van Der Salm et al., 2004) pituitaries as well as by Mozambique tilapia neurointermediate lobes (Lamers et al., 1991). *In vitro* treatment with DA D2 receptor agonists inhibits α-MSH release, while DA D1 receptor agonists have a stimulatory effect on α-MSH release, in Mozambique tilapia exposed to water with low pH (acid stress) (Lamers et al., 1997). Overall, these results support an involvement of DA in the regulation of ACTH and α-MSH release probably interdependently with CRH pathway [for review: (Gorissen and Flik, 2016)].

*Serotonin

In mammals, serotonin (5-hydroxytryptamine, 5-HT), a monoamine neurotransmitter, is known to stimulate the HPA axis [for review: (Dinan, 1996)] and to control stress coping [for review: (Puglisi-Allegra and Andolina, 2015)]. 5-HT mainly acts on the brain, but it can also act directly on the adrenal and pituitary glands [for review: (Dinan, 1996)]. The brain network involves CRH, GABA and glutamate neurons [for review: (Puglisi-Allegra and Andolina, 2015)].

Similar results have been reported in teleost fish. Injection of a selective agonist for serotonin receptor 5-HT$_{1A}$ (8-OH-DPAT) results in increased plasma cortisol concentrations in some teleosts [rainbow trout: (Winberg et al., 1997); Gulf toadfish *Opsanus beta*: (Medeiros et al., 2010); goldfish: (Lim et al., 2013)]. In the Arctic charr *Salvelinus alpinus*, comparison between stressed and unstressed fish show that this selective agonist has a stimulatory effect on the HPI axis in unstressed fish, while having a suppressive effect on the stress-induced activation of the HPI axis in fish stressed by handling and *ip* injections (Höglund et al., 2002). In the Gulf toadfish, injection of 8-OH-DPAT results in increased hypothalamic *crh* mRNA

541 levels and ACTH release from the pituitary and these effects are inhibited by crowding stress

542 (Medeiros et al., 2014). However in goldfish, injection of this agonist has no effect at the

543 brain level but rather acts at interrenal tissue to stimulate cortisol secretion (Lim et al., 2013).

544 *In vitro*, 5-HT stimulates cortisol release by interrenals in Gulf toadfish [kidney pieces:

545 (Medeiros and McDonald, 2012)] and in goldfish [superfused head kidney tissue: (Lim et al.,

546 2013)]. In goldfish, Lim and colleagues demonstrate the involvement of multiple 5-HT

547 receptor subtypes (5-HT$_{1A}$ and 5-HT$_4$) in the interrenal paracrine effect of 5-HT (Lim et al.,

548 2013), while in Gulf toadfish, Medeiros and McDonald show that 5-HT$_4$ does mediate 5-HT

549 action but 5-HT$_{1A}$ does not (Medeiros and McDonald, 2012).

550 *** Thyrotropin-releasing hormone**

551 In mammals and in adult amphibians, thyrotropin-releasing hormone (TRH) is the main

552 neurohormone controlling the thyrotropic axis *i.e.* the synthesis and release of thyrotropin

553 (TSH) at the pituitary level, which stimulates the production of thyroid hormones at the

554 thyroid level. This TSH-releasing role seems to be taken on by CRH in larval amphibians,

555 reptiles and birds [for reviews: (De Groef et al., 2006; Galas et al., 2009)]. In teleosts,

556 investigations on the *in vitro* effect of TRH on pituitary TSH production show either no effect

557 [common carp: synthesis, (Kagabu et al., 1998); mRNA levels, (Geven et al., 2009); coho

558 salmon *Oncorhynchus kisutch*, release: (Larsen et al., 1998)] or a stimulatory effect [bighead

559 carp *Aristichthys nobilis*, mRNA levels: (Chatterjee et al., 2001; Chowdhury et al., 2004);

560 Japanese eel, mRNA levels: (Han et al., 2004)]. CRH acts as a TSH-releasing factor on coho

561 salmon pituitary cells (Larsen et al., 1998), but has no effect on *tshβ* mRNA levels in

562 common carp pituitary glands *in vitro* (Geven et al., 2009).

563 Conversely to the effect of CRH on TSH, TRH can exert an ACTH-releasing effect in teleosts

564 as shown by *in vitro* studies [goldfish pituitary dispersed cells: (Tran et al., 1989); gilthead

565 sea bream pituitary: (Rotllant et al., 2000)]. TRH is also a potent stimulator of α-MSH release

566 by the *pars intermedia* in many teleost species [goldfish: (Tran et al., 1989); tilapia: (Lamers

567 et al., 1991); rainbow trout: (Schwartzentruber et al., 1994); gilthead sea bream: (Rotllant et

568 al., 2000); red porgy: (Van Der Salm et al., 2004)]. This α-MSH-releasing effect of TRH is

569 also observed in amphibians [*Rana ridibunda*: (Tonon et al., 1980); *Xenopus laevis*: (B.

570 Verburg-Van Kemenade et al., 1987)].

571 After a stress (prolonged crowding), in the gilthead sea bream, the pituitary presents a

572 differential response of ACTH and α-MSH to TRH and CRH treatments: the stimulation of

573 ACTH by CRH is attenuated, but not the stimulation of ACTH by TRH, while both CRH and

574 TRH stimulation of α-MSH are enhanced (Rotllant et al., 2000). In Mozambique tilapia, a

575 dual organization of the stress axis has been demonstrated, as after exposure to low-pH water,

576 the CRH/ACTH axis is replaced by a TRH/di-acetylated α-MSH axis for the production of

577 cortisol (Lamers et al., 1994). Overall, these results suggest the involvement of TRH in the

578 regulation of corticotropes and melanotropes, notably during exposure to stress.

579 ***Arginine vasotocin, isotocin and arginine vasopressin***

580 Arginine vasotocin (AVT), isotocin (IST) and arginine vasopressin (AVP) are all peptides

581 produced by neurons of the preoptic nucleus and released by the neurohypophysis. AVT and

582 IST are present in non-mammalian vertebrates and closely related to mammalian AVP.

583 As in mammals, these neuropeptides are able to stimulate the release of ACTH *in vitro*

584 [goldfish: (Fryer et al., 1985); trout: (Baker et al., 1996; Bond et al., 2007; Pierson et al.,

585 1996)] and thus increase plasma cortisol levels in teleosts *in vivo* [goldfish: (Fryer and Leung,

586 1982); trout: (Baker et al., 1996; Bond et al., 2007; Pierson et al., 1996)]. In addition, in

587 mammals and birds [for review: (Cornett et al., 2012)], they potentiate the stimulatory action

588 of CRH on ACTH *in vivo* and *in vitro* (Gillies et al., 1982; Rivier and Vale, 1983; Turkelson

589 et al., 1982). In teleosts, contradictory data are available concerning a possible synergy with

590 CRH on ACTH release *in vitro*: they do synergize in trout (Baker et al., 1996), while they do

591   not in goldfish (Fryer et al., 1985)]. In the frog *Rana ridibunda*, no potentiation of CRH-

592   induced ACTH release is observed when anterior pituitary cells are incubated with a

593   combination of AVP and CRH (Tonon et al., 1986).

594   In rainbow trout, a study shows that AVT mRNA levels in neurons of the preoptic nucleus are

595   elevated during acute stress but not chronic stress (Gilchriest et al., 2000).

2.2.2.3. POMC-derived peptides and their receptors

597   **POMC-derived peptides*

598   Pro-opiomelanocortin (POMC), together with proenkephalin (PENK), prodynorphin (PDNY)

599   and proorphanin (PNOC), form the opioid/orphanin gene family [(Sundström et al., 2010); for

600   review: (Dores et al., 2002)]. POMC is post-translationally processed and some of the

601   peptides obtained undergo further modifications such as C-terminal amidation and N-

602   acetylation [for reviews: (Dores and Baron, 2011; Takahashi and Mizusawa, 2013)]. POMC

603   organizational plan varies among vertebrates [for reviews: (Dores and Baron, 2011; Dores

604   and Lecaude, 2005)]. POMC is the precursor for ACTH, melanotropins (α-, β- and γ- MSH),

605   corticotropin-like intermediate peptide (CLIP), lipotropins (β- and γ- LPH) and β-endorphin,

606   in tetrapods and lungfish (Amemiya et al., 1999a; Nakanishi et al., 1979). Chondrichthyans

607   have an additional melanotropin, δ-MSH (Amemiya et al., 1999b). Teleosts lack γ-MSH

608   (Kitahara et al., 1988; Lee et al., 1999), but *pomc-β* of cichlids and pomacentrids encodes a

609   novel melanocortin peptide, ε-MSH, the result of a tandem duplication of the segment

610   encoding ACTH (Harris et al., 2014). In all these vertebrates, the adenohypophysis possesses

611   two cell populations that express POMC: in the *pars distalis* (PD), the corticotropes in which

612   POMC is processed to ACTH (and β-lipotropin), and in the *pars intermedia* (PI), the

613   melanotropes in which POMC is processed to ACTH, which is further cleaved to give α-

614   MSH, corticotropin-like intermediate peptide and β-endorphin [for review: (Takahashi and

615   Mizusawa, 2013)]. Differently, agnathans possess two 'POMC' genes: pro-opiocortin (POC),

616   which encodes ACTH and a different β-endorphin, is expressed in the *pars distalis*; pro-

617   opiomelanotropin (POM), which encodes α-, and β- MSH, and β-endorphin, is expressed in

618   the *pars intermedia* (Takahashi et al., 2012, 1995).

619   Teleost 3R gave rise to *pomc* gene duplicates: *pomc-α* (*a* or *A*) and *pomc-β* (*b* or *B*), with

620   *pomc-β* having lost a functional *β*-endorphin (De Souza et al., 2005). Further independent

621   gene duplications during teleost evolution resulted in duplicates of *pomc-α* such as in halibut

622   and carp [*pomc*-I and –II: (De Souza et al., 2005)], sea bream [*pomc-α1* and -*α2*: (Cardoso et

623   al., 2011)] and *Astatotilapia burtoni* [*pomc-α1* and -*α2*: (Harris et al., 2014)]. In barfin

624   flounder *Verasper moseri*, a third *pomc* gene, named *pomc-C*, was also identified (Takahashi

625   et al., 2006); *pomc-C* belongs to the *pomc-β* clade while *pomc-A* and-*B* belong to the *pomc-α*

626   clade and thus should be renamed -*β, -α1* and -*α2*, respectively, according to Cardoso and

627   collaborators (Cardoso et al., 2011). In rainbow trout, apart from *pomc-B*, *pomc-A1* and -*A2*

628   are likely the result of the salmonid genome duplication (4R) (Leder and Silverstein, 2006).

629   As in other vertebrates [*e.g.* in rodents: (Kraicer et al., 1973)], ACTH is produced in teleosts

630   from POMC by both the *pars distalis* (PD; corticotropes) and the *pars intermedia* (PI;

631   melanotropes) of the pituitary, but ACTH of the *pars intermedia* is further cleaved to produce

632   smaller peptides and cortisol feedbacks only on the *pars distalis* ACTH [for review: (Fryer

633   and Lederis, 1986)]. In tetraodon *Tetraodon nigroviridis*, *pomc-α* and not *pomc-β* is

634   expressed in the PD, while both are expressed in the PI (De Souza et al., 2005). In the sea

635   bream, *pomc-α2* and not *pomc-α1* is expressed in the PD, while only *pomc-α1* is expressed in

636   the PI (Cardoso et al., 2011). In the pituitary of barfin flounder, all three *pomc* genes present

637   in this species are expressed in the PD (Takahashi et al., 2006). In *Astatotilapia burtoni*

638   (Harris et al., 2014) and rainbow trout (Leder and Silverstein, 2006), all three *pomc* are

639   expressed in the pituitary, but no indication of the region is reported. This indicates species-

640   specific variation in the expression of the various *pomc* paralogs by the PD corticotropic cells

641   through teleost radiation.

642   Species-specific variations among teleosts may also concern the *pomc* paralog linked to stress

643   response. In the gilthead sea bream, an enhanced pituitary expression of *pomc-α2* (*pomc-b* in

644   the paper) and a decreased one of *pomc-α1* (*pomc-a* in the paper) are observed after acute

645   stress due to air exposure (Skrzynska et al., 2018)], leading the authors to link *pomc-α2* and

646   not *pomc-α1* to stress response in sea bream. However, in the same species, no change in the

647   expression of both paralogs was previously reported after exposure to other acute stress,

648   chasing and persecution (Toni et al., 2015). In *Rhamdia quelen*, both pituitary *pomc-α2*

649   (*pomcb* in the paper) and *pomc-α1* (*pomca* in the paper) expressions are unchanged after

650   stressful situation (transport) (Saccol et al., 2018). In contrast, in the Senegalese sole, *Solea*

651   *senegalensis*, *pomc-α1* (*pomc-a* in the paper) expression in the pituitary is down-regulated in

652   juveniles chronically stressed by high stocking density, whereas *pomc-α2* (*pomc-b* in the

653   paper) expression levels remain unaffected (Wunderink et al., 2012). All these data in three

654   different species do not lead to clear conclusions concerning a preferential involvement of one

655   or another *pomc* paralog in stress response among teleosts.

656   An *in vitro* corticotropic action (*i.e.* induction of cortisol release from head kidney) of α-MSH

657   (desacetyl and diacetyl forms) has been reported in rainbow trout (Rance and Baker, 1981),

658   Mozambique tilapia (Lamers et al., 1992) and barfin flounder (Kobayashi et al., 2011), but

659   not in common carp (Metz et al., 2005).

660   ****Melanocortin receptors***

661   In tetrapods, five MCRs have been identified. In teleost fish, the number of receptors

662   increases up to six in zebrafish, which has two MC5R paralogs (*mc5ra* and *mc5rb*)

663   (Västermark and Schiöth, 2011), while pufferfish *Fugu* has only four, with no melanocortin

664   *mc3r* and only one copy of melanocortin *mc5r* (Logan et al., 2003). Concerning the ligand

665   selectivity of MCRs, all of the paralogous MCRs can be activated by both ACTH and α-MSH

666 in extant cartilaginous fishes, while in extant teleosts and tetrapods, MC2R can be activated

667 only by ACTH. The appearance of MRAP1 paralleled the emergence of this MC2R ligand

668 selectivity [for reviews: (Dores, 2016; Dores et al., 2016)].

669 In mammals, the MCRs have distinct expression site and functions [for reviews: (Cone, 2006;

670 Dores et al., 2014)]: MC1R, expressed in melanocytes, is involved in skin and hair

671 pigmentation; MC2R, expressed in adrenal cortex, is involved in adrenal steroidogenesis and

672 stress response; MC3R and MC4R, expressed in the brain, are involved in the control of

673 energy homeostasis; MC5R, expressed in a variety of exocrine glands, such as sebaceous,

674 lacrimal and preputial glands, is involved in exocrine gland secretion. These features can be

675 also found in teleosts but some peculiarities can be noted. Of particuliar interest, *mc5r* is co-

676 expressed with *mc2r* in the interrenal of several teleosts [rainbow trout: (Aluru and Vijayan,

677 2008; Haitina et al., 2004); common carp *Cyprinus carpio*: (Metz et al., 2005); barfin

678 flounder: (Kobayashi et al., 2011)], as in the chicken adrenal (Takeuchi and Takahashi, 1998)

679 and *Xenopus tropicalis* interrenal/kidney (Dores and Garcia, 2015), suggesting a possible role

680 of MC5R in the regulation of HPI/HPA axis in these non-mammalian vertebrates.

681 <div align="center">**2.2.2.4. Corticosteroids and their receptors**</div>

682 ***Glucocorticoids***

683 In fish, corticosteroids are synthetized by the interrenal tissue, a tissue embedded inside the

684 anterior part of the kidney and homologous to the adrenal cortex in mammals. Corticosteroids

685 are steroid hormones divided into glucocorticoids and mineralocorticoids. Even if cortisol is

686 the major corticosteroid in teleosts [for review: (Mommsen et al., 1999)], others such as 11-

687 deoxycortisol (17, 21 dihydroxy-4-pregnene-3,20 dione), 11-deoxycorticosterone (DOC) and

688 corticosterone are also detected in plasma of teleosts [for review: (Butler, 1973); winter

689 flounder *Pseudopleuronectes americanus*: (Campbell et al., 1976); rainbow trout *Salmo*

690 *gairdneri*: (Campbell et al., 1980)]. All teleosts so far studied lack aldosterone, which is the

691 principal mineralocorticoid in mammals (Gilmour, 2005), and it is generally accepted that

692 cortisol exerts both glucocorticoid and mineralocorticoid actions in teleosts (McCormick,

693 2001; McCormick et al., 2008). DOC is shown to be a potent agonist of mineralocorticoid

694 receptor (MR) (Sturm et al., 2005). Study in rainbow trout has shown a sustained up-

695 regulation of plasma DOC levels during a confinement stress time-course. However, the low

696 DOC levels compared to cortisol measured in the plasma do not favour an activity of DOC

697 through MR receptors (Kiilerich et al., 2018) and physiological relevance of this hormone

698 action is still unclear in fish (Prunet et al., 2006).

699 ***Glucocorticoid and mineralocorticoid receptors***

700 Glucocorticoid and mineralocorticoid receptors (GR and MR respectively) are corticosteroid

701 receptors which belong to the nuclear receptor superfamily [for review: (Bury, 2017)]. In

702 teleosts, 3R gave rise to duplicated *gr* (*gr1* and *gr2*) with one receptor (GR1) retaining a 9

703 aminoacid insert which does not exist in GR2 [for review: (Bury, 2017)]. Zebrafish is an

704 exception as this species conserved only one of the two *gr* paralogs (Schaaf et al., 2008). In

705 some teleosts, GR1 has two splice variants, GR1a and GR1b [rainbow trout: (Takeo et al.,

706 1996); *Haplochromis burtoni*: (Greenwood et al., 2003); Tetraodon and Takifugu species:

707 (Stolte et al., 2006); marine medaka *Oryzias dancena*: (M. Kim et al., 2011)]. 3R gave also

708 rise to duplicated *mr* (*mr1* and *mr2*) which have been both conserved in a basal teleost, the

709 European eel [(Lafont et al., 2014) and Lafont et al. unpublished data], while only the *mr1*

710 paralog would have been conserved in extant teleosts so far studied [for review: (Baker and

711 Katsu, 2019)]. As they are issued from the 3R, these two *mr* paralogs in the eel should rather

712 be named *mra* and *mrb*, according to the commonly used nomenclature for teleost 3R-

713 paralogs. However, they must be distinguished from the two *mr* forms previously found in the

714 rainbow trout, named rt*mra* and rt*mrb* (Sturm et al., 2005), which may represent allelic

715 variants or paralogs issued from salmonid-4R of *mr1*.

716 GR1 and GR2 present differential affinities (sensitivities) and show distinct functionality with

717 GR2 having a higher hormonal transcriptional activity at equimolar concentration and higher

718 sensitivity (Bury et al., 2003). This difference in sensitivity is not restricted to the

719 salmoniformes and have been also observed with the two GRs in *Pantodon buchholzi* (Li et

720 al., 2012), carp (Stolte et al., 2008), marine medaka (*Oryzias dacena*) (M. Kim et al., 2011),

721 and the Japanese medaka (*Oryzias latipes*) (Miyagawa et al., 2015). From such *in vitro*

722 differences in functionality, one can hypothetize that the two teleost GRs may have different

723 roles: the hypersensitive GR2 could play a prominent role during basal circulatory cortisol

724 concentrations (unstressed) whereas the less sensitive GR1 may become prominent during

725 stressful situations when cortisol levels are high [(Bury et al., 2003); for review: (Bury,

726 2017)]. So far, such functionally distinct roles have not been established in fish. However, a

727 recent study of stress effects in salmonids shows differential contribution of the corticosteroid

728 receptors in the regulation of HPI axis activity (Kiilerich et al., 2018) and suggests a negative

729 feedback regulation of cortisol release at the pituitary level *via* MR, while a short loop

730 regulation occurs at the interrenal level *via* GR in rainbow trout exposed to 7 day-

731 confinement. The authors also observe the presence of the 2 GR and the MR in hypophysial

732 ACTH cells confirming the regulation of the HPI axis at the pituitary level by both GRs and

733 MR. Similar conclusions have been also suggested when studying in the Atlantic salmon

734 effects of unpredictable chronic stress or to repeated chasing stress (Madaro et al., 2016,

735 2015). In the common carp, Stolte and collaborators report that, in fish exposed to prolonged

736 and strong stressors, mRNA levels of all three corticosteroid receptors (*gr1*, *gr2* and *mr*) are

737 down-regulated in some brain regions, but not in CRH neurons or pituitary ACTH cells

738 (Stolte et al., 2008), suggesting a role of all three receptors in stress regulation in this species.

739 In zebrafish (Schaaf et al., 2008), the single *gr* (*gr2*) gene has two splice variants, *grα* and

740 *grβ* (Hollenberg et al., 1985), with a variant lacking the C-terminal portion of the GR as

described in human (Hollenberg et al., 1985). In human, *grβ* may act as a dominant-repressor of the wildtype variant (Bamberger et al., 1995). These splicing variants are co-expressed in a number of zebrafish tissues (brain, spleen, liver, intestine, heart, gills and muscle), *grα* mRNA levels being significantly higher than those of *grβ* (Schaaf et al., 2008). Despite initial data suggesting that *grβ* has a key role in the negative regulation of *grα* (Chatzopoulou et al., 2015), a recent study by the same group using transgenic zebrafish with inducible expression of *grβ* suggests that this isoform does not have a functional role in transcription regulation (Chatzopoulou et al., 2017). Functional roles of corticosteroid receptors during stress have been studied in this fish species using mutant fish. Thus, GR knockout zebrafish show an inability to cope with stressor such as placement into an unfamiliar environment, even after repeated exposure (Ziv et al., 2013). These fish also show hypercortisolemia and fail to exihibit a cortisol stress response, while KO zebrafish for MR have a delayed but sustained cortisol response (Faught and Vijayan, 2018). Both KO mutants do not show the hyperactivity in response to light observed in wild type zebrafish (Faught and Vijayan, 2018). These recent data suggest distinct but complementary roles for GR and MR in the development and regulation of the stress axis in zebrafish: MR represses HPI axis during development while GR regulates basal cortisol levels in the context of negative feedback regulation during stress. Both receptors are also involved in the control of stress-related behaviour in zebrafish (Faught and Vijayan, 2018). Such a role in the regulation of stress-related behaviour is suggested in medaka as well (Sakamoto et al., 2016).

2.3. The gonadotropic axis

2.3.1. Main actors of the gonadotropic axis in vertebrates

The brain-pituitary-gonadal axis is responsible for the control of the reproductive function in all vertebrates. It regulates gamete production, sexual secondary characters and behaviors, as

766 well as key-steps of the life cycle such as puberty, seasonal reproduction or sex change in

767 some hermaphrodic species including teleost representatives.

768 The brain integrates various environmental and social cues, such as temperature, photoperiod,

769 habitat conditions, presence of partners, as well as internal cues such as developmental stage,

770 size, nutritional status and energy stores, *via* various neuronal networks which converge into

771 the positive or negative regulation of the activity of gonadotropin-releasing hormone (GnRH)

772 hypophysiotropic neurons considered as the master control of reproduction (Gore, 2002).

773 GnRH binds to its cognate membrane receptor (GnRH-R) expressed by the pituitary

774 gonadotrope cells, and which belongs to the rhodopsin-like, class A, G-protein coupled

775 receptor (GPCR) superfamily [for reviews: (Flanagan and Manilall, 2017; Millar et al.,

776 2004)]. GnRH stimulates the synthesis and release of the gonadotropins, LH and FSH.

777 The two pituitary gonadotropins, LH and FSH are glycoprotein hormones, composed of two

778 subunits alpha and beta. The alpha subunit, named glycoprotein hormone alpha subunit

779 (Gpα), is common to both gonadotropins, LH, FSH and to the thyrotropin, TSH, while the

780 beta subunit is specific to each hormone [for reviews: (Cahoreau et al., 2015; Pierce and

781 Parsons, 1981)]. LH and FSH bind to their respective GPCR membrane receptors LHR and

782 FSHR expressed by the gonads. The gonadotropins activate gonadal functions, gametogenesis

783 and steroidogenesis. The enzymatic pathway of the biosynthesis of sex steroids is largely

784 conserved among vertebrates. Sex steroids, androgens, estrogens, progestagens, bind to their

785 respective nuclear receptors, AR, ER, PR, belonging to the nuclear receptor superfamily [for

786 review: (Mangelsdorf et al., 1995)]. As more recently discovered, steroid may also act *via*

787 binding to GPCR membrane receptors, such as estradiol-membrane receptor and progesterone

788 membrane receptor [for review: (Thomas, 2012)]. Sex steroids act on multiple targets,

789 including the gonads themselves, a variety of peripheral tissues as well as the brain and

790 pituitary, where they exert positive and negative feedback controls on the gonadotropic axis.

2.3.2. Specific features of the gonadotropic axis in teleosts

2.3.2.1. GnRHs and their receptors

793 Up to three *gnrh* genes are present in extant teleosts, a larger number than in mammals (up to

794 two genes), which had been initially attributed to the 3R. However, subsequent comparative

795 studies revealed the presence of three *gnrh* genes also in basal vertebrate representatives such

796 as a chondrichthyan, the catshark, *Scyliorhynus canicula* and a basal sarcopterygian, the

797 coelacanth, *Latimeria chalumnae*. Phylogeny and synteny studies support the 1R/2R origin of

798 the three vertebrate *gnrh* and their inheritance by the teleost lineage. In contrast, 3R had no

799 impact on the *gnrh* gene number in extant teleosts, indicating an early loss of 3R-paralogs in

800 this lineage [for reviews: (D. K. Kim et al., 2011; Roch et al., 2011; Tostivint, 2011)]. A

801 maximum of three *gnrh* (1, 2, 3) genes are thus present in teleosts, such as in medaka, while

802 additional, independent and species-specific losses led to the presence of only two *gnrh* genes

803 in some species, *e.g. gnrh1* and *2* in the eel, or *gnrh2* and *3* in the zebrafish. The situation is

804 more complex concerning GnRH receptors. Recent studies indicate that a large number of

805 GnRH receptors resulted from 1R/2R as well as from local gene duplications in ancestral

806 vertebrates; subsequently, several independent gene loss events led to a variable number of

807 *gnrhr* genes throughout vertebrate evolution. In teleosts, 3R-duplicated paralogs as well as

808 additional duplications in some lineages increased the number of GnRH-R [up to 5 in

809 acanthopterygians and 6 in salmonids: (Ciani et al., 2020)] as compared to other

810 actinopterygians, with species-specific variations among teleosts due to independent gene

811 losses [(Ciani et al., 2020); for reviews: (Roch et al., 2014; Sefideh et al., 2014; Williams et

812 al., 2014)].

813 **2.3.2.2. Dopamine and other neurohormones**

814 ***Dopamine***

815   A crucial control is exerted by dopaminergic neurons which directly inhibit the gonadotrope

816   cell activity and counteract the effect of GnRH, as first discovered in cyprinids by Peter and

817   collaborators and retrieved in many other teleosts species including basal representatives such

818   as the eel [for reviews: (Dufour et al., 2010, 2005)]. In relation with environmental and

819   internal cues, and in a species-specifc manner, this dopaminergic control of gonadotropic cells

820   plays key roles in various reproductive steps in teleosts such as puberty, final oocyte

821   maturation and ovulation, spermiation, or sex change [for reviews: (Dufour et al., 2010,

822   2005)]. A major inhibitory role of DA in regulating reproduction is also reported in

823   amphibians, especially in the control of spawning [for review: (Vu and Trudeau, 2016)].

824   Beside GnRH and DA, a variety of other neurohomones can also directly regulate the activity

825   of teleost gonadotrophs, with species-specific variations, such as kisspeptin (Kiss),

826   gonadotropin-inhibitory hormone (GnIH), neurokinin, gamma-aminobutyric acid (GABA),

827   noradrenaline, serotonin *etc* [for reviews: (Dufour et al., 2020; Zohar et al., 2010)]. As

828   proposed by Trudeau, these multiple independent controls of gonadotropic cells may provide

829   compensatory regulatory mechanisms, possibly explaining the low or no impact of KO of

830   major genes such as *kiss* or *gnrh* observed in recent studies (Trudeau, 2018). Species-specific

831   variations in the multiple controls of gonadotrophs highlight the evolutionary plasticity of the

832   brain-pituitary anatomo-functional relationships in the teleost lineage, which may have

833   favored the remarkable diversity of their reproductive cycles.

834   **GnIH*

835   Gonadotropin-inhibitory hormone (GnIH or RFRP-3 in mammals), a RFamide peptide, was

836   discovered from quail brain by Tsutsui and collaborators and found to be involved in the

837   direct inhibitory pituitary regulation of LH (Tsutsui et al., 2000). Shortly after, the GnIH

838   precursor was shown to encode two other peptides (Satake et al., 2001). Since then, *gnih* gene

839   homologs, encoding multiple peptides, have been identified in other vertebrates [for reviews:

840   (Muñoz-Cueto et al., 2017; Tsutsui et al., 2018)]. These peptides, in mammals, also possess

841   an inhibitory action on gonadotropins, while in amphibians they have GH-releasing effects

842   [for review: (Dufour et al., 2020)]. Recently, it was demonstrated that only a single *gnih* gene

843   was present in representative species of elopomorphs (*Anguilla* species), the most basal group

844   of teleosts, as well as in the other teleosts (Maugars et al., 2020). This result indicates a loss

845   of one of the two 3R-duplicated *gnih* paralogs shortly after the 3R (Maugars et al., 2020).

846   Depending on teleost species, inhibitory [*e.g.* European eel (Pasquier et al., 2018); common

847   carp (Peng et al., 2016); zebrafish (Spicer et al., 2017)], stimulatory [*e.g.* sockeye salmon

848   (Amano et al., 2006); grass puffer *Takifugu niphobles* (Shahjahan et al., 2011); tilapia

849   *Oreochromis niloticus* (Biran et al., 2014); catla *Catla catla* (Kumar et al., 2019); half-smooth

850   tongue sole *Cynoglossus semilaevis* (Wang et al., 2019)] or a lack of effect [*e.g.* goldfish (Qi

851   et al., 2013); *Astyanax altiparanae* (Branco et al., 2019)] of GnIH have been described for

852   gonadotropins *in vitro* [for review: (Muñoz-Cueto et al., 2017; Tsutsui et al., 2018; Ubuka

853   and Parhar, 2018)], suggesting a large variability of GnIH function in reproduction across

854   teleosts.

855   ** Kisspeptin*

856   Kisspeptin, another RF-amide peptide, is encoded by the *Kiss-1* gene, a metastasis suppressor

857   gene, isolated in 1996 from melanoma cells (Lee et al., 1996). This 54 amino-acid peptide,

858   also called metastin, is processed into shorter peptides which all bind to kisspeptin receptor,

859   KissR (or GPR54) (Ohtaki et al., 2001). In 2003, three research groups discovered the key

860   role of the kisspeptin system in the activation of gonadotropic axis and the control of

861   reproduction in human and mice (de Roux et al., 2003; Funes et al., 2003; Seminara et al.,

862   2004). *In vivo* and *in vitro* studies further demonstrate the stimulatory role of kisspeptin at

863   different levels of the gonadotropic axis: hypothalamus (GnRH neurons), pituitary (LH cells)

864   and gonads [for reviews: (Pinilla et al., 2012; Putteeraj et al., 2016)]. The few available

865   studies in amphibians and reptiles also suggest a stimulatory role of kisspeptin on the HPG

866   axis, while this system might have been lost in some birds [for review: (Dufour et al., 2020)].

867   However, data in teleosts report stimulatory, no or inhibitory effects of kisspeptin peptides on

868   GnRH or gonadotropins, suggesting a large variabilty of the role of Kiss system in eleost

869   reproduction according to species [for reviews: (Dufour et al., 2020; Tena-Sempere et al.,

870   2012)]. Up to four paralogs of *Kiss* and *KissR* resulted from 1R and 2R in early vertebrates,

871   but subsequent gene losses led to the presence of only a single *Kiss* gene and a single *KissR*

872   gene in human. In teleosts, due to paralog losses, no impact of 3R on the number of both *Kiss*

873   and *KissR* genes has been found, leading to a maximum of two *Kiss* and three *KissR* genes,

874   which is no more than in a non-teleost actinopterygian such as the gar, *Lepisosteus oculatus*

875   [for reviews: (Pasquier et al., 2014, 2012)].

876   **2.3.2.3. Gonadotropins and their receptors**

877   As in mammals, only two gonadotropins, LH and FSH, are present in all extant teleosts,

878   including basal representative species such as the eel (elopomorphs) (Yoshiura et al., 1999),

879   indicating an early loss after 3R of the putative additional 3R-paralogs [for review: (Dufour et

880   al., 2020)]. In tetrapods, LH and FSH bind to their respective receptors, LHR and FSHR. As

881   recently shown, an additional *lhr* paralog arose from a local gene duplication in ancestral

882   actinopterygians, and the two *lhr* (*lhr1* and *lhr2*) where inherited by the teleost lineage

883   (Maugars and Dufour, 2015). Due to gene losses after 3R, the number of gonadotropin

884   receptors did not further increase in teleosts with a single *fshr* and up to two *lhr*. Additional

885   independent and species-specific gene losses led to the presence of a single *lhr* in some

886   teleosts, such as only *lhr1* in medaka and *lhr2* in zebrafish (Maugars and Dufour, 2015).

887   **2.3.2.4. Sex steroids and their receptors**

888   Gonadal sex steroids are produced from cholesterol by a succession of enzymatic activities. In

889   teleosts, 3R duplication of a key-enzyme, the aromatase (*Cyp19a1a* and *b*), has been largely

890   documented [for review: (Zhang et al., 2014)].

891   Sex steroid nuclear receptors have been duplicated by 3R and the conservation of most of the

892   paralogs led to the presence of a larger number of nuclear receptors in teleosts as compared to

893   mammals [for review: (Ogino et al., 2018)]. This is also the case for the steroid membrane

894   receptors. Concerning estradiol receptors, tetrapods possess two nuclear receptors (ESR1 also

895   named ERα, and ESR2 also named ERß) and a single membrane receptor (GPER) while

896   teleosts, as a result of 3R, possess three nuclear receptors (*esr1* and duplicated *esr2a* and

897   *esr2b*) and two membrane receptors (*gpera* and *gperb*) (Lafont et al., 2016). One of the

898   duplicated *esr1* paralog would have been lost shortly after 3R. A species-specific gene loss

899   occurred in zebrafish, which possesses a single *gper* paralog, while both *gpera* and *b* paralogs

900   have been conserved in the other teleosts investigated so far (Lafont et al., 2016). For

901   androgen receptors, 3R also generated two *ar* paralogs (*ara* and *arb*) in teleosts (Ogino et al.,

902   2009). Recently, Morini and colleagues revealed the presence of duplicated progesterone

903   nuclear receptors (*pgra* or *pgr1*, and *pgrb* or *pgr2*) in the eel, which originated from 3R. In

904   other teleosts however only a single *pgr* (orthologous to eel *pgrb/pgr2*) has been found, and

905   synteny analysis indicates the loss of *pgra* (*pgr1)* paralog in the teleost lineage after the

906   emergence of the basal teleost group of elopomorphs (Morini et al., 2017). Two *pgr* paralogs

907   are reported in the goldfish, likely resulting from 4R. The evolutionary history of membrane

908   progestin receptors is even more complex as five isoforms have been characterized in

909   vertebrates (Morini et al., 2017). The conservation of multiple steroid receptor genes in

910   teleosts likely reflects subfonctionalization and neofunctionalization processes, which may

911   have contributed to species-specific diversification of sexual chararacters, regulatory

912   processes and reproductive cycles throughout teleost radiation.

913

3. Neuroendocrine mechanisms of the interactions between corticotropic and gonadotropic axes in teleosts

    3.1. Regulatory effects of actors of the corticotropic axis on the gonadotropic axis

        3.1.1. Roles of corticosteroids and their receptors

            3.1.1.1. Expression and role along the gonadotropic axis

In the rainbow trout, GR are expressed in GnRH- and dopaminergic neurons as well as on gonadotrope cells [(Teitsma et al., 1999); for review: (Teitsma et al., 1998)]. In addition, GR and ER colocalize in the same neurons and pituitary cells [for review: (Teitsma et al., 1998)]. In *Astatotilapia burtoni*, both GR1 and GR2 are expressed in GnRH1 neurons in the preoptic area (Korzan et al., 2014). A direct action of cortisol on GnIH neurons and targets is suggested in teleosts by the presence of several GR responsive elements (GRE) in the promoters of zebrafish *gnih* and *gnih* receptor (Ogawa and Parhar, 2014). GRs are also expressed in gonads in various teleosts [midshipman *Porichthys notatus*: (Arterbery et al., 2010) ; *Astatotilapia burtoni*: (Maruska and Fernald, 2011)].

MR is expressed in brain, especially in GnRH1 neurons [*Astatotilapia burtoni*: (Korzan et al., 2014)], and in gonads of various teleosts [*Haplochromis burtoni*: (Greenwood et al., 2003); rainbow trout: (Milla et al., 2008; Sturm et al., 2005); midshipman *Porichthys notatus*: (Arterbery et al., 2010); *Astatotilapia burtoni*: (Maruska and Fernald, 2011); for review: (Takahashi and Sakamoto, 2013)].

These expression patterns of GR and MR along the gonadotropic axis suggest potential major actions of glucocorticoids on reproductive functions at different levels, involving endocrine loops and/or paracrine/autocrine regulations.

Corticosteroids themselves are produced by gonads in teleosts [for review: (Kime, 1993)]. Cortisol is present in sperm and seminal fluid [Pacific herring *Clupea harengus* and North sea

plaice *Pleuronectes platessa*: (Scott et al., 1991b, 1991a)]. 11-deoxycortisol is produced by the ovary [*Gillichthys mirabilis* and *Microgadus proximus*: (Colombo et al., 1973); sea bass: (Colombo et al., 1978); *Jenynsia lineata*: (Tesone and Charreau, 1980); goldfish: (Kime et al., 1992)] and testis [*Jenynsia lineata*: (Tesone and Charreau, 1980)]. Like 11-deoxycortisol, 11-deoxycorticosterone (DOC) is an important product of ovarian [*Leptocottus armatus*, *Gillichthys mirabilis* and *Microgadus proximus*: (Colombo et al., 1973); sea bass: (Colombo et al., 1978)] and/or testicular [*Jenynsia lineata*: (Tesone and Charreau, 1980)] steroidogenesis. Future studies should investigate whether ACTH, gonadotropins or both, associated or not to other factors are regulating such corticosteroid production by gonads in fish.

3.1.1.2. *In vivo effects of corticosteroids*

Pioneer works in loach *Misgurnus fossilis* (Kirshenblatt, 1952), conger *Conger conger* (Mousset, 1957) and European eel (Fontaine et al., 1964) show that injection of glucocorticoids (desoxycorticosterone acetate) has positive effects on reproduction as it is able to induce oocyte maturation and spawning. In the catfish *Heteropneustes fossilis* also, adrenal corticosteroids (cortisol, cortisone and desoxycorticosterone acetate) are shown to be effective in inducing ovulation and spawning in hypophysectomized gravid fish, suggesting a direct positive action on the ovary independently of the pituitary (Sundararaj and Goswami, 1966a). Use of metopiron, an adrenocortical inhibitor which can induce « chemical interrenalectomy », allows to show that LH-induced effect on ovulation and spawning in catfish was interrenal-dependent (Sundararaj and Goswami, 1966b). Treatment with cortisol increases pituitary gonadotropin in juvenile rainbow trout [implant: (Crim et al., 1981)] and prepubertal European eel [injection: (Dufour et al., 1983; Huang et al., 1999)]. Altogether, these data suggest positive interactions of glucocorticoids on the HPG axis at both juvenile and adult stages in some teleost species.

In contrast, a lot of studies report negative effects of glucocorticoids on the reproductive axis. Most of them are conducted in salmonids. In the brown trout, implantation of cortisol to sexually maturing male and female fishes result in smaller gonads, lower plasma levels of sex steroids and pituitary gonadotropin content (Carragher et al., 1989). Differently, in the maturing male rainbow trout, a cortisol implant decreases plasma gonadotropin levels while having no effects on other parameters (plasma sex steroids, pituitary gonadotropin content and gonad size) (Carragher et al., 1989). In the rainbow trout, intraperitoneal implant of cortisol decreases hepatic E2-binding site concentration, but increases plasma E2-binding capacity in immature females (Pottinger and Pickering, 1990) and decreases ER and Vg expression in maturating females (Lethimonier et al., 2000). Cortisol injection depresses plasma E2 and T levels, without affecting plasma gonadotropin levels in vitellogenic rainbow trout (Pankhurst and Van Der Kraak, 2000). In the male rainbow trout, testicular *mr* expression and plasma DOC increase around the time of spermiation, and the co-administration of DOC with 17α, 20β-dihydroprogesterone decreases the spermatocrit value and therefore increases the sperm fluidity (Milla et al., 2008). In Atlantic salmon, Eriksen and collaborators report impact on progeny of maternal exposure to cortisol (implant), including increased mortality and prevalence of deformities, reduced development and yolk-sac volume (Eriksen et al., 2007, 2006). During a field study on spawning grounds, use in female pink Pacific salmon *Oncorhynchus gorbuscha* of cortisol implant which further increases endogenous cortisol levels, impairs reproductive success (fewer eggs) and survival (McConnachie et al., 2012). The use of metyrapone, which prevents the synthesis of cortisol from 11-deoxycortisol by inhibiting 11β-hydroxylase, does not change reproductive success (McConnachie et al., 2012). Altogether, these studies indicate that endogenous physiological cortisol levels, which raise at the time of upstream migration and spawning in salmonids (cf §1.2.2), do not impair reproduction, although higher levels may have a negative effect

988 (McConnachie et al., 2012).

989 Deleterious reproductive *in vivo* effects of corticosteroids have also been shown in other

990 teleost species. In immature male common carp fed with cortisol-containing food pellets over

991 pubertal period, brain sGnRH content, pituitary *lh* and *fsh* mRNA levels, plasma LH levels

992 and testicular androgen (T and 11KT) secretion are decreased (Consten et al., 2001a).

993 Testicular development in this species is retarded by this long-term cortisol treatment

994 (Consten et al., 2001a, 2001b). In contrast, dietary administered cortisol to channel catfish

995 *Ictalurus punctatus* does not modify reproduction (Small, 2004). In the Arctic char, co-

996 exposure to cortisol and E2 results in reduced plasma Vg levels and no change in *Vg* mRNA

997 levels, suggesting a post-transcriptional action of cortisol (Berg et al., 2004). Implantation of

998 cortisol causes retardation of the ovarian growth and depression of plasma sex steroid levels

999 in tilapia *Oreochromis mossambicus* [female: (Foo and Lam, 1993a); male: (Foo and Lam,

1000 1993b)]. Later, Gennotte and collaborators show that cortisol treatment induces both positive

1001 (reduction of the time before ovulation) and negative (reduction of fecundity) effects on the

1002 reproduction in other tilapia species, *Oreochromis niloticus* (Gennotte et al., 2012).

1003 In the cinnamon clownfish, *Amphiprion melanopus*, injection of cortisol increases *gnih*

1004 *mRNA,* and reduces *sbGnRH* mRNA and plasma levels of LH and FSH (Choi et al., 2017).

1005 As, in this teleost species, GnIH inhibits gonadotropin expression (Choi et al., 2016), cortisol

1006 treatment leads to a dual negative effect on gonadotropin *via* an increase in GnIH and

1007 decrease in GnRH. A similar upregulation of hypothalamic *gnih* (*rfrp3*) mRNA levels is

1008 observed in rats after acute or chronic immobilization/restraint stress (Kirby et al., 2009;

1009 Yang et al., 2017), upregulation which is abolished by adrenalectomy (Kirby et al., 2009) .

1010 Concerning the effect of stress or corticosteroid treatment on the kisspeptin system, all the

1011 available data have been obtained in rodents [for reviews: (Acevedo-Rodriguez et al., 2018;

1012 Iwasa et al., 2018)] and show a reduction of hypothalamic *Kiss1* and *KissR1* mRNA levels

1013　[rat, restraint stress or subcutaneous injection of corticosterone: (Kinsey-Jones et al., 2009);

1014　mice, implant containing corticosterone: (Luo et al., 2016); mice, restraint stress: (Yang et al.,

1015　2017)]. It would be relevant to investigate the regulation of the kisspeptin system by stress

1016　and corticosteroids in teleosts, which show different effects of kisspeptin on the control of

1017　gonadotropins according to the species.

3.1.1.3. *In vitro effects of corticosteroids*

1019　*In vitro* investigations pin-point the direct actions of cortisol at the different levels of the HPG

1020　axis. In the rat hypothalamic rfrp-expressing cell line (rHypoE-23) (Gingerich et al., 2009),

1021　treatment with corticosterone increases *gnih(rfrp)* mRNA levels and the application of a GR

1022　antagonist blocks this increase (Gojska and Belsham, 2014; Son et al., 2014). *In vitro*

1023　investigations should be developed in teleosts, using hypothalamic neurons, to study possible

1024　direct effects of corticosteroids on the various neuronal populations (GnRH, DA, GnIH and

1025　kisspeptin) involved in the gonadotropic axis.

1026　At the pituitary level, cortisol affects reproduction-related gene expression in Atlantic cod

1027　pituitary cultures (von Krogh et al., 2019). In this species, cortisol has dual effects on *fshβ*

1028　expression, stimulating expression in cells from mature fish, while inhibiting expression in

1029　cells from spent fish (von Krogh et al., 2019). In contrast, cortisol has no direct effect on *lhβ*

1030　expression (von Krogh et al., 2019). While *gnrhr2a* transcript levels largely increase

1031　following cortisol treatment, *gnrhr1b* expression decreases in cells from spent fish and was

1032　unaffected at other maturity stages (von Krogh et al., 2019). In the prepubertal European eel,

1033　cortisol increases LH cellular content and *lhβ* mRNA levels by pituitary cells in culture

1034　(Huang et al., 1999). Future studies should investigate the effects of corticosteroids on the

1035　levels of other pituitary targets such as GnIH and kisspeptin receptors in different teleost

1036　species, considering that, in teleosts, GnIH and kisspeptin possess direct inhibitory or

1037　stimulatory effects on the pituitary depending on the species.

1038   At the liver level, dexamethasone inhibits both basal and E2-stimulated ER expression and

1039   subsequent Vg expression in trout hepatocyte aggregates (Lethimonier et al., 2000). This is

1040   achieved *via* an inhibition by GR of the transcriptional factor CCAAT/enhancer-binding

1041   protein (C/EPBβ) binding to the ER promoter region (Lethimonier et al., 2002).

1042   At the gonadal level, different data are available on the direct effect of cortisol on female

1043   gonadal steroidogenesis depending on species [(Pankhurst, 1998); for review: (Pankhurst,

1044   2016)]. A decrease in E2 and T release by cultured ovarian follicles after cortisol treatment

1045   has been observed in rainbow trout (Carragher and Sumpter, 1990), while no such effect has

1046   been reported in goldfish, common carp and *Pagrus auratus* (Pankhurst et al., 1995). In the

1047   rainbow trout*,* cortisol is shown to have suppressive effects on basal and LH- or cAMP-

1048   stimulated T and E2 production and secretion, but no effect on basal or LH-stimulated

1049   17,20β-dihydroxy-4-pregnene-3-one (17,20β-P) (Barkataki et al., 2011; Reddy et al., 1999)*.*

1050   In the same species, cortisol is reported to enhance the efficiency of gonadotropin to induce

1051   intrafollicular oocyte maturation (Jalabert, 1975) and to positively regulate the secretion of

1052   follicular 17α-hydroxy-20β-dihydroprogesterone (DHP) induced by gonadotropin *in vitro*

1053   (Jalabert and Fostier, 1984). All these data suggest that, in the rainbow trout, cortisol has a

1054   positive (or no) effect on the synthesis of progestagen (Maturation Inducing Steroid, MIS)

1055   during final oocyte maturation, while being inhibitor at earlier stages of oogenesis, on the

1056   production of T and E2 during vitellogenesis. In the zebrafish, cortisol does not inhibit hCG-

1057   stimulated E2 production, while ACTH did (Alsop et al., 2009). In other teleost species,

1058   glucocorticoids are also able to act on final oocyte maturation. Glucocorticoids have been

1059   shown to induce *in vitro* oocyte maturation in the goldfish [desoxycorticosterone: (Jalabert et

1060   al., 1973)] and ovulation in the medaka [cortisol: (Hirose, 1976)]. In the amago salmon

1061   (*Oncorhynchus rhodurus*), DOC can enhance oocyte maturation induced by gonadotropin or

1062   by DHP *in vitro* (Young et al., 1982). Cortisol treatment induces DNA damage on zebrafish

stage I and II follicles, and increases *mc2r* expression in stage II follicles *in vitro* (Sousa et al., 2015).

Data on male gonadal steroidogenesis, even if fewer, seem more consistent than those on female steroidogenesis. In the common carp, treatment of male testes *in vitro* with dexamethasone reduces the induction of androgen secretion by carp pituitary extract (Consten et al., 2002). Consten and collaborators have previously reported a decreased *in vitro* production of testicular androgen during early stages of puberty in the common carp fed with cortisol (Consten et al., 2000). In male rainbow trout, DOC possesses an inhibitory effect on the testicular production of DHP *in vitro* (Milla et al., 2008). In the Japanese eel, *in vitro* cortisol treatment induces DNA replication in spermatogonia and enhances the spermatogonial proliferation stimulated by 11KT, revealing a stimulatory effect of cortisol on spermatogenesis (Ozaki et al., 2006).

3.1.2. Roles of POMC-derived peptides

Other stress-related endocrine factors have also been studied for their involvement in the regulation of the HPG axis.

Pomca-deficient zebrafish, obtained with a TALENs approach, have enhanced somatic growth, reduced anxiety-related behavioral responses, and exhibit hypocortisolism associated with hyperandrogenism (Shi et al., 2019). The authors suggest that the hypocortisolemia and hyperandrogenism are probably due to the changes in expression of interrenal steroidogenic enzymes involved in the synthesis of cortisol (downregulation of *hsd3* expression) and androgens (upregulation of *cyp17a1a* and *cyp19a1a* expression), respectively (Shi et al., 2019).

In vitro experiments show a direct role of ACTH on zebrafish ovaries: ACTH treatment suppresses hCG-stimulated E2 release from ovarian follicles (Alsop et al., 2009), and induces a high level of oocyte vacuolization, as well as DNA damage on stage I and II follicles (Sousa

et al., 2015). In agreement with the direct action of ACTH on the gonads, the ACTH receptor MC2R is highly expressed in gonads of various teleosts [rainbow trout: (Aluru and Vijayan, 2008); zebrafish: (Agulleiro et al., 2010; Alsop et al., 2009); barfin flounder: (Kobayashi et al., 2011); sea bass: (Agulleiro et al., 2013)].

Another POMC-related peptides, the opioid peptide β-endorphin, is also produced and released in response to stressors in teleosts [gilthead sea bream: (Arends et al., 1999; Mosconi et al., 1998); tilapia: (Chabbi and Ganesh, 2012)]. This peptide may be involved in the reproductive response to stress as a suppression of LH secretion, an inhibition of vitellogenic follicular growth and a reduction of gonado-somatic index (GSI) are observed in tilapia injected with β-endorphin (Chabbi and Ganesh, 2013; Ganesh and Chabbi, 2013). Treatment with naltrexone, an opioid receptor antagonist, attenuates these inhibitory effects of β-endorphin in tilapia (Chabbi and Ganesh, 2013; Ganesh and Chabbi, 2013). In common carp, naltrexone stimulates the *in vitro* LH release from whole pituitary gland as well as from dispersed pituitary cells, revealing direct paracrine pituitary effects of opioids (Socha et al., 2003).

3.1.3. Roles of CRH

The direct and indirect effects of CRH on the gonadotropic axis have been well-documented in mammals [for reviews: (Chand and Lovejoy, 2011; Kageyama, 2013)]. CRH, injected centrally [ovariectomized female rat: (Ono et al., 1984; Rivier and Vale, 1984); intact and castrated male rat: (Frias et al., 1999)], but not peripherally [human: (D'Agata et al., 1984); rat: (Ono et al., 1984; Rivier and Vale, 1984)], inhibits LH release. Centrally administered CRH also down-regulates *Kiss1* and *Kiss1r* mRNA levels in ovariectomized E2 replaced female rats (Kinsey-Jones et al., 2009). Central administration of α-helical CRH, a non-selective CRH-R antagonist, reverses the inhibitory effect of stress on pulsatile release of LH in castrated male rat (Rivier et al., 1986). *In vitro*, CRH down-regulates GnRH release from

1113   rat hypothalamic slices and this inhibition is suppressed by α-helical CRH (Nikolarakis et al.,

1114   1986). In parallel to its central inhibitory effect, CRH is also able to act at the pituitary level

1115   through CRH-R2 to inhibit LH release in mice (Raftogianni et al., 2018). Previous data in rat

1116   failed to show any effect of CRH on LH release *in vitro* (Ono et al., 1984).

1117   In teleosts, there are very few investigations regarding CRH action on the gonadotropic axis.

1118   Injection of CRH to stripped tilapia *Oreochromis mossambicus* resulted in diminished

1119   immunoreactive LH content in the pituitary, lower GSI and absence of vitellogenic follicles in

1120   the ovary (Chabbi and Ganesh, 2014). The glucocorticoid synthesis inhibitor, metyrapone,

1121   abolishes the inhibitory effects of CRH treatment on LH secretion and follicle growth,

1122   demonstrating an action *via* cortisol (Chabbi and Ganesh, 2014). Direct pituitary or gonadal

1123   effect of CRH needs to be investigated through *in vitro* studies. CRH-R mRNAs have already

1124   been detected in the pituitary [catfish *Ameiurus nebulosus*: (Arai et al., 2001); common carp:

1125   (Huising et al., 2004); *Astatotilapia burtoni*: (Chen and Fernald, 2008); tilapia *Oreochromis*

1126   *mossambicus*: (Aruna et al., 2015, 2012)], but future investigations should aim at determining

1127   whether these receptors are expressed in other cell types than corticotrophs, notably in

1128   gonadotrophs. CRH-R are also expressed in the ovary [*Astatotilapia burtoni*: (Chen and

1129   Fernald, 2008); olive flounder *Paralichthys olivaceus*: (Zhou et al., 2019)], which suggests a

1130   direct action of CRH on the gonads.

1131

1132   **3.2. Regulatory effects of actors of the gonadotropic axis on the corticotropic axis**

1133   Conversely, some studies reveal a role of actors of the gonadotropic axis on the corticotropic

1134   axis in teleosts.

1135   **3.2.1. Roles of sex steroids**

1136   In the sockeye salmon, gonadectomy blocks the cortisol prespawning rise (Donaldson and

1137   Fagerlund, 1970; Robertson, 1961) and sex steroids, estrogens and androgens, can induce

1138   interrenal hyperplasia as well as increase in plasma cortisol levels in both intact and

1139   gonadectomized fish [(Donaldson and Fagerlund, 1969; Fagerlund and Donaldson, 1969); for

1140   review: (Dickhoff, 1989)]. The situation is different in the rainbow and brown trout in which

1141   implantation of T and 11-KT attenuates ACTH and cortisol-elevation after confinement stress,

1142   while E2 implantation increases stress-induced ACTH and cortisol levels (Pottinger et al.,

1143   1996). In the rainbow trout, *in vivo* treatment with 11KT suppresses interrenal responsiveness

1144   to ACTH *in vitro* (Young et al., 1996), while DHP stimulates cortisol production by interrenal

1145   tissue cultured *in vitro* (Barry et al., 1997). McQuillan and collaborators compared the *in vitro*

1146   effect of E2 on cortisol synthesis by interrenals of the chinook salmon, *Oncorhynchus*

1147   *tshawytscha* and rainbow trout: they show that E2 suppresses the ability of juvenile and

1148   mature chinook salmon interrenals to produce cortisol, whereas it has no effect in the rainbow

1149   trout (McQuillan et al., 2003). These data reveal potential differences among species and

1150   reproductive stage concerning the role of sexual steroids in the induction of hypercortisolemia

1151   in salmonids.

1152   Interestingly, the interrenal in fish has been reported to produce androgen [rainbow trout:

1153   (Arai et al., 1969); coho salmon: (Schreck et al., 1989); tilapia *Oreochromis mossambicus*:

1154   (Balm et al., 1989); African catfish, *Clarias gariepinus*: (Vermeulen et al., 1995)], as in

1155   mammals [for review: (Rainey and Nakamura, 2008)]. In human, the production and secretion

1156   of adrenal androgens (dehydroepiandrosterone, DHEA and its sulfate ester, DHEAS) in the

1157   midchildhood, termed adrenarche, has been involved in the timing of puberty (Remer et al.,

1158   2010). Such a role of interrenal androgens could be also envisioned in teleosts.

1159   A potential remarkable interaction between reproductive and stress actors is illustrated by the

1160   recent finding of the ability of progesterone to bind to the mineralocorticoid receptor MR.

1161   Recent *in vitro* studies indicate that progesterone can activate MR in the elephant shark

1162   *Callorhinchus milii*, in ray-finned fishes including trout (Sturm et al., 2005) and zebrafish

(Fuller et al., 2019; Katsu and Baker, 2018) and in chickens, with an EC50 of less than 1 nM for these MRs, which makes this steroid a potential physiological activator of these MRs [for review: (Baker and Katsu, 2020)]. Moreover, in the elephant shark and ray-finned fish, MR are expressed in several tissues, including ovaries and testis (Katsu et al., 2019; Milla et al., 2008; Sturm et al., 2005). This led Baker and Katsu to suggest that progesterone may have multifaceted physiological roles through MR in these species [for review: (Baker and Katsu, 2020)].

3.2.2. Roles of other actors

Injection of salmon gonadotropin to sockeye salmon has no impact on plasma cortisol or cortisone levels nor on interrenal activity (Donaldson and McBride, 1974). However, in catfish *Heteropneustes fossilis*, *in vitro* studies suggest that gonadotropin (LH) stimulates the interrenal to produce corticosteroids which in turn act on the oocytes to induce maturation (Sundararaj and Goswami, 1977). Such studies in *Heteropneustes fossilis* highlight the complex synergy between gonadotropic and corticotropic axes in the induction of oocyte final maturation, ovulation and spawning in response to monsoon-related environmental cues (cf §1.2.1).

Other actors of the gonadotropic axis, such as GnRH, might act on the corticotropic axis in teleosts as evidenced in mammals. GnRH is shown to stimulate ACTH release from the rat pituitary (Gambacciani et al., 1988) and also to regulate the expression of pituitary corticotropin-releasing hormone binding protein (CRH-BP) by gonadotrope-like cell line (Westphal and Seasholtz, 2005), highlighting the potential importance of GnRH/CRH interactions at the pituitary level in the interface between stress and reproductive axes. To our knowledge such investigations have not yet been performed in teleosts.

Recent cyto-anatomical studies suggest a potential role of GnIH not only in the gonadotropic axis but also in the corticotropic axis in teleosts. In tilapia, GnIH (LPXRFa) axons are closely

1188 associated with various pituitary cell types including gonadotrophs, corticotrophs and

1189 melanotrophs, and GnIH receptors (LPXRFa-Receptor) are expressed in LH, ACTH and

1190 alpha MSH cells [(Ogawa et al., 2016); for review: (Muñoz-Cueto et al., 2017)]. It would be

1191 very interesting now to clarify whether GnIH is involved in the regulation of these cell types

1192 and in the production of ACTH and MSH.

1193

1194 **Conclusion and perspectives**

1195 Stress impact on reproduction has long been studied in teleosts, especially in the frame of

1196 aquaculture. However, most of the accumulated data come from studies on the possible action

1197 of peripheral hormone, cortisol, on sexual maturation. Emerging data in mammals show that

1198 actors of higher levels (especially brain) should catch researcher attention. The teleost specific

1199 whole genome duplication (3R) had made such studies perhaps more difficult, multiplicating

1200 the number of genes, but thanks to the recent publications of an increasing number of teleost

1201 genomes and the development of molecular and genome editing technology tools, it is now

1202 possible to investigate their respective functions across teleost species diversity. Thus future

1203 directions should aim, for example, at dissecting mechanisms of action of the different

1204 paralogs of genes involved in the corticotropic axis and in the caudal neurosecretory system in

1205 the regulation of various levels of the gonadotropic axis. Such studies are all the more

1206 important that the present review gives multiple examples of species-specific regulatory

1207 mechanisms which probably reflect the wide species-specific plasticity of fish reproductive

1208 responses when fish are exposed to stressful situations.

1209

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2745

2747   **Figure legends**

2748

2749   **Figure 1: Stress and reproduction neuroendocrine axes in teleosts.**

2750   The figure displays the main actors and regulatory pathways of the stress neuroendocrine axis

2751   (corticotropic axis: brain-pituitary-interrenals; green arrows) and of the reproduction

2752   neuroendocrine axis (gonadotropic axis: brain-pituitary-gonads; blue arrows). The Caudal

2753   Neurosecretory System (CNSS) which may be involved in the stress axis in teleost is

2754   indicated in relation to the corticotropic axis. The liver, which plays a key role in reproduction

2755   in teleosts as in other oviparous vertebrates by producing vitellogenin, is indicated in relation

2756   to the gonadotropic axis. Abbreviations: AVP, arginine vasopressin; AR, androgen receptor;

2757   CNSS, caudal neurosecretory system; CRH, corticotropin-releasing hormone; CRH-R,

2758   corticotropin-releasing hormone receptor; DA, dopamine; DHP, 17-hydroxy-20-

2759   dihydroprogesterone; DOC, 11-deoxycorticosterone; E2, estradiol; ER, estrogen receptor;

2760   FSH, follicle stimulating hormone; FSH-R, follicle stimulating hormone receptor; GnIH,

2761   gonadotropin inhibitory hormone; GnRH, gonadotropin-releasing hormone; GnRH-R,

2762   gonadotropin-releasing hormone receptor; GR, glucocorticoid receptor; kiss, kisspeptin; kiss-

2763   R, kisspeptin receptor; LH, luteinising hormone; LH-R, luteinising hormone receptor; MC2R,

2764   melanocortin receptor 2; other P, other progestins; POMC, proopiomelanocortin; PR,

2765   progestin receptor; T, testosterone; TRH, thyrotropin releasing hormone; UI, urotensin I; Vg,

2766   vitellogenin; 5-HT, 5 hydroxytryptamine, or serotonin; 11-KT, 11-ketotestosterone.

2767
2768   **Figure 2: Effects of corticotropic axis on gonadotropic axis in vertebrates**.

2769   The figure illustrates current knowledge on the regulatory actions (green arrows) exerted by

2770   typical actors of the corticotropic axis (brain-pituitary-interrenal) on the gonadotropic and

2771   liver axis (brain-pituitary-gonad-liver). Abbreviations: ACTH, adrenocorticotropin; β-end, β-

2772   endorphin; CRH, corticotropin-releasing hormone; E2, estradiol; FSH, follicle stimulating

2773   hormone; GnIH, gonadotropin inhibitory hormone; GnRH, gonadotropin-releasing hormone;

2774   GR, glucocorticoid receptor; kiss, kisspeptin; LH, luteinising hormone; MC2R, melanocortin

2775   receptor 2; MR, mineralocorticoid receptor; T, testosterone; 11-KT, 11-ketotestosterone;.

2776

2777   **Figure 3: Effects of gonadotropic axis on corticotropic axis in vertebrates**.

2778   The figure illustrates current knowledge on the regulatory actions (blue arrows) exerted by

2779   typical actors of the gonadotropic axis (brain-pituitary-gonad) on the corticotropic axis (brain-

2780   pituitary-interrenal). Abbreviations: ACTH, adrenocorticotropin; AR, androgen receptor;

2781   CRH, corticotropin-releasing hormone; CRH-BP, corticotropin-releasing hormone binding

2782   protein; DHP, 17-hydroxy-20-dihydroprogesterone; E2, estradiol; ER, estrogen receptor;

2783   FSH, follicle stimulating hormone; GnIH, gonadotropin inhibitory hormone; GnRH,

2784   gonadotropin-releasing hormone; LH, luteinising hormone; LH-R, luteinising hormone

2785   receptor; other P, other progestins; PR, progestin receptor; T, testosterone; Vg, vitellogenin;

2786   11-KT, 11-ketotestosterone.

2787

2788   **Table Legends**

2789

2790   **Table 1**: **Major actors of the corticotropic axis in human and teleosts**.

2791   This table underlines the expansion of gene numbers in teleosts due to teleost-specific whole

2792   genome duplication (3R). In teleosts, some of the paralogs have been lost in some species.

2793   Supplemental paralogs issued from additional whole genome duplication (4R, which occurred

2794   in salmonids and carps) are not indicated. Abbreviations: CRH, corticotropin-releasing

2795   hormone; CRH-R, corticotropin-releasing hormone receptor; POMC, proopiomelanocortin;

2796 MCR, melanocortin receptor; GR, glucocorticoid receptor; MR, mineralocorticoid receptor;

2797 UI, urotensin I.

2798

2799 **Table 2**: **Major actors of the gonadotropic axis in human and teleosts**.
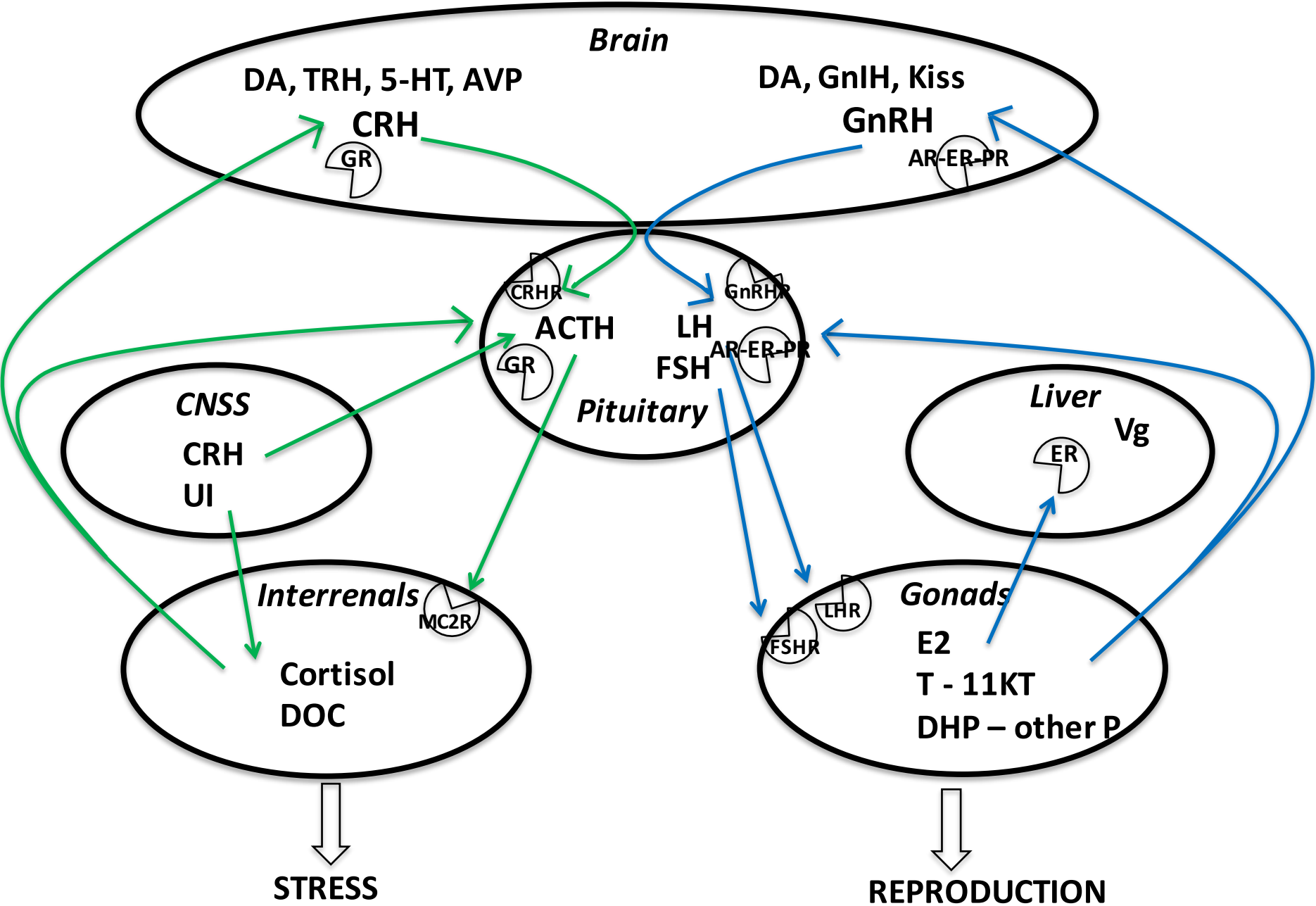
2800 This table underlines the larger gene numbers in teleosts due to teleost-specific whole genome

2801 duplication (3R) but also to the conservation of paralogs resulting from early vertebrate whole

2802 genome duplications (1R and 2R), or from local gene duplication (see the text for details). In

2803 teleosts, some of the paralogs have been lost in some species. Supplemental paralogs issued

2804 from additional whole genome duplication (4R, which occurred in salmonids and carps) are

2805 not indicated. Abbreviations: GnRH, gonadotropin-releasing hormone; GnRH-R,

2806 gonadotropin-releasing hormone receptor; GnIH, gonadotropin inhibitory hormone; kiss,

2807 kisspeptin; kiss-R, kisspeptin receptor; LHβ, luteinising hormone; FSHβ, follicle stimulating

2808 hormone; LH-R, luteinising hormone receptor; FSH-R, follicle stimulating hormone receptor;

2809 ER, estrogen receptor; esr, nuclear estrogen receptor; gper, membrane estrogen receptor; AR,

2810 androgen receptor; PR, progestin receptor; pgr, nuclear progestin receptor; mpgr, membrane

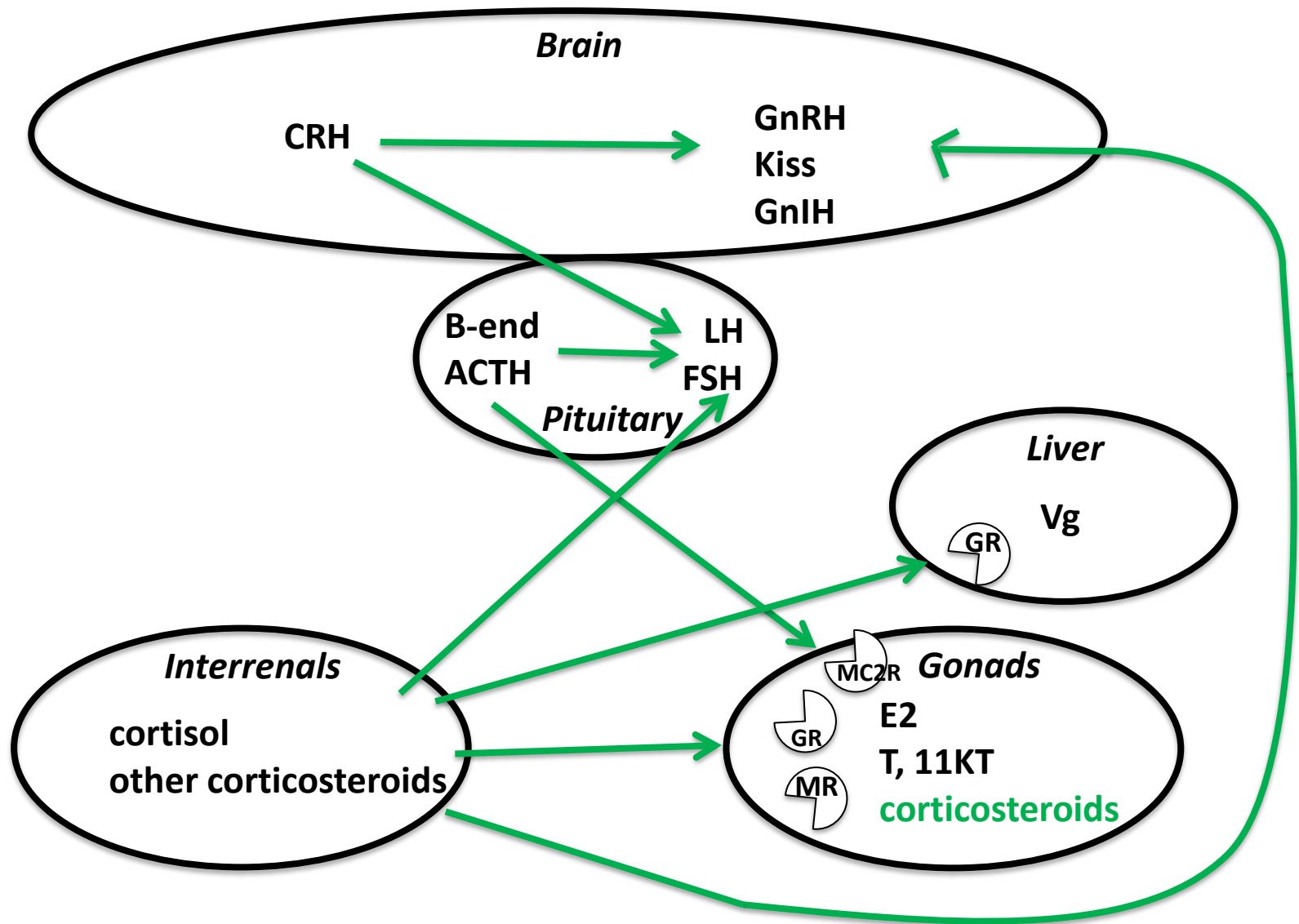2811 progestin receptor.

2812
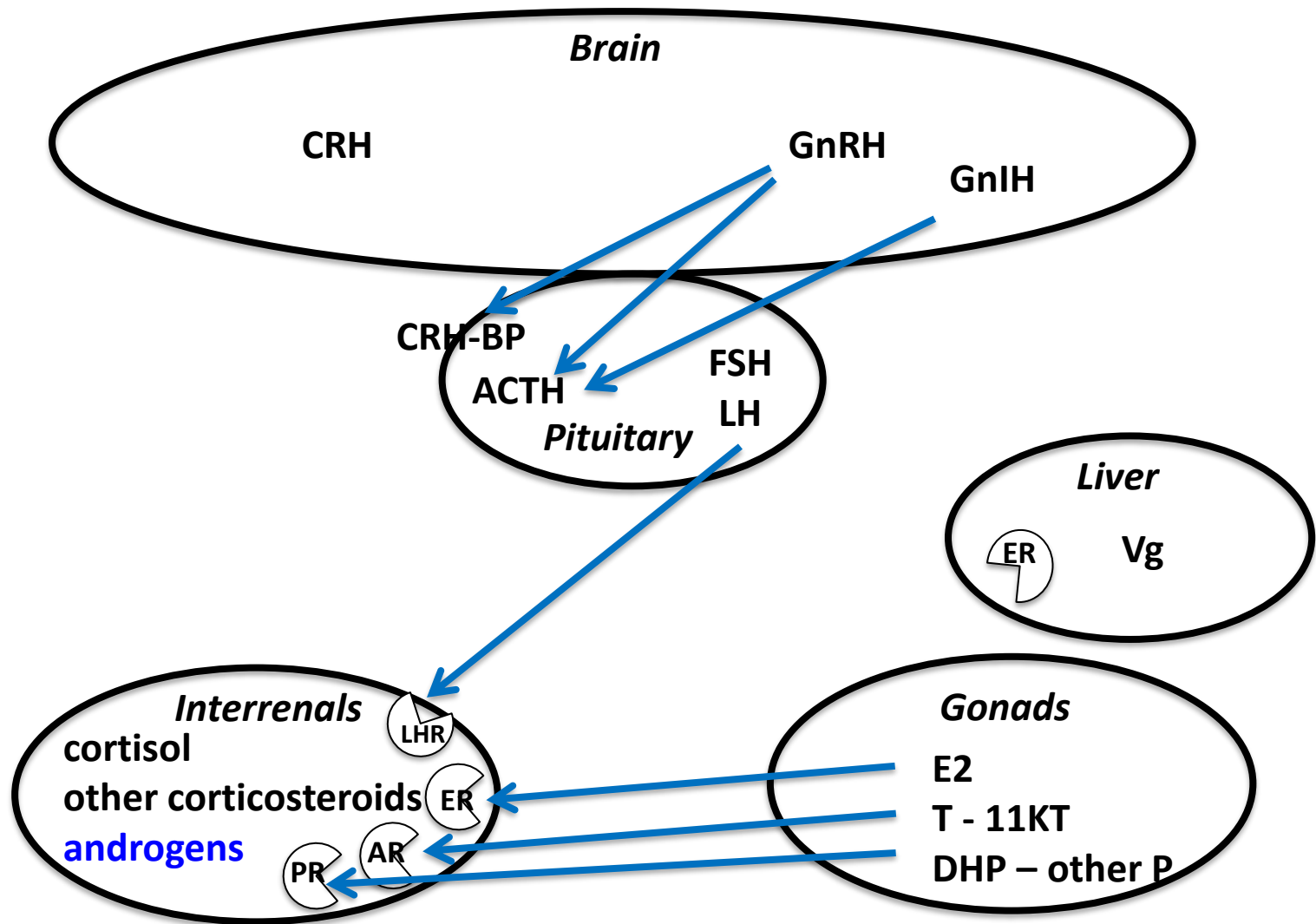
2813

Corticotropic axis

Gonadotropic axis

Brain

DA, TRH, 5-HT, AVP
CRH
GR

DA, GnIH, Kiss
GnRH
AR-ER-PR

CRHR

GnRHR

ACTH
GR

LH
FSH
AR-ER-PR

Pituitary

CNSS
CRH
UI

Liver
ER
Vg

Interrenals
MC2R

Cortisol
DOC

FSHR
LHR
Gonads
E2
T - 11KT
DHP – other P

STRESS

REPRODUCTION

Corticotropic axis **Gonadotropic axis**

Brain

CRH GnRH
Kiss
GnIH

B-end LH
ACTH FSH
Pituitary

Liver

Vg

GR

Interrenals MC2R *Gonads*

cortisol E2
other corticosteroids GR T, 11KT

MR corticosteroids

Table 1: **Major actors of the corticotropic axis in human and teleosts**.

Protein	Gene	Human	Teleosts	References / Review articles
CRH	*crh*	*crh1* *crh2*	*crh1a* *crh1b* *crh2*	Lovejoy et al 2014; Cardoso et al 2016 Maugars et al 2016
CRH-R	*crhr*	*crhr1* *crhr2*	*crhr1a* *crhr1b* *crhr2*	Cardoso et al 2014; Lovejoy et al 2014
POMC	*pomc*	*pomc*	*pomc-α1* *pomc-α2* *pomc-β*	Dores and Lecaude 2005; Cardoso et al 2011; Dores and Baron 2011
MC1R MC2R MC3R MC4R MC5R	*mc1r* *mc2r* *mc3r* *mc4r* *mc5r*	*mc1r* *mc2r* *mc3r* *mc4r* *mc5r*	*mc1r* *mc2r* *mc3r* *mc4r* *mc5ra* *mc5rb*	Vastermark and Schioth 2011; Dores et al 2014, 2016
GR	*gr*	*gr*	*gr1* *gr2*	Bury 2017
MR	*mr*	*mr*	*mr1* *mr2*	Lafont et al 2014; Baker and Katsu 2019
UI	*uI*		*uI*	Lovejoy et al 2014

Table 2: **Major actors of the gonadotropic axis in human and teleosts**.

Protein	Gene	Human	Teleosts	References / Review articles
GnRH	*gnrh*	*gnrh1* *gnrh2*	*gnrh1* *gnrh2* *gnrh3*	Kim et al 2011; Roch et al 2011; Tostivint 2011
GnRH-R	*gnrhr*	*gnrhr-1*	Up to 5 *gnrhr*	Roch et al 2014; Sefideh et al 2014; William et al 2014; Ciani et al 2020
GnIH	*gnih*	*gnih/rfrp*	*gnih*	Tsutsui et al 2018; Maugars et al 2020
Kiss	*kiss*	*kiss1*	*kiss1* *kiss2*	Pasquier et al 2012, 2014
Kiss-R	*kissR*	*kiss1R*	*kiss1R* *kiss2R* *kiss3R*	Pasquier et al 2012, 2014
LHβ	*lhβ*	*lhβ*	*lhβ*	Dufour et al 2020
FSHβ	*fshβ*	*fshβ*	*fshβ*	Dufour et al 2020
LH-R	*lhr*	*lhcgr*	*lhr1* *lhr2*	Maugars and Dufour 2015
FSH-R	*fshr*	*fshr*	*fshr*	Maugars and Dufour 2015
ER	*esr* *gper*	*esr1* *esr2* *gper*	*esr1* *esr2a* *esr2b* *gpera* *gperb*	Lafont et al 2016; Ogino et al 2018 Lafont et al 2016
AR	*ar*	*ar*	*ara* *arb*	Ogino et al 2009
PR	*pgr* *mpgr*	*pgr* multiple	*pgra* *pgrb* multiple	Morini et al 2019 Morini et al 2019