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Special features of neuroendocrine interactions between stress and reproduction in teleosts

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Abstract

Stress and reproduction are both essential functions for vertebrate survival, ensuring on one side adaptative responses to environmental changes and potential life threats, and on the other side production of progeny. With more than 25,000 species, teleosts constitute the largest group of extant vertebrates, and exhibit a large diversity of life cycles, environmental conditions and regulatory processes. Interactions between stress and reproduction are a growing concern both for conservation of fish biodiversity in the frame of global changes and for the development of sustainability of aquaculture including fish welfare. In teleosts, as in other vertebrates, adverse effects of stress on reproduction have been largely documented and will be shortly overviewed. Unexpectedly, stress notably *via* cortisol, may also facilitate reproductive function in some teleost species in relation to their peculiar life cyles and this review will provide some examples. Our review will then mainly address the neuroendocrine axes involved in the control of stress and reproduction, namely the corticotropic and gonadotropic axes, as well as their interactions. After reporting some anatomo-functional specificities of the neuroendocrine systems in teleosts, we will describe the major actors of the corticotropic and gonadotropic axes at the brain-pituitary-peripheral glands (interrenals and gonads) levels, with a special focus on the impact of teleost-specific whole genome duplication (3R) on the number of paralogs and their potential differential functions. We will finally review the current knowledge on the neuroendocrine mechanisms of the various interactions between stress and reproduction at different levels of the two axes in teleosts in a comparative and evolutionary perspective.

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 activation of the hypothalamo-pituitary-adrenal (HPA) axis inhibits the hypothalamo-pituitary-gonads (HPG) axis, this paradigm has been established mainly in mammalian species (Chand and Lovejoy, 2011) but also in fish for which numerous reports emphasizing effects of corticosteroids on reproduction have been produced (Fuzzen et al., 2011; Leatherland et al., 2010; Milla et al., 2009; Pankhurst, 2016; Schreck, 2010) . In this paper, we will focus our interest on the relationships between stress and reproductive neuroendocrine axes, trying to decipher direct stress effects and separate them from systemic effects on other biological functions. Thanks to the recent progress brought by genomic studies, we will be able to integrate the most recent informations provided by molecular phylogeny analyses and describe effects of new actors, which appeared *via* different rounds of whole genome duplications. This review will focus on teleost fish but with an evolutionary perspective requiring comparison with other vertebrate species.

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

Many relationships between stress and reproduction, with the influence of environmental conditions, have been documented in natural situation and in aquaculture. In this context, we first consider in this section the effects of stressors on reproduction, which are frequently associated with high cortisol levels.

1.1. Negative interactions between stress and reproduction

Early works in many teleost species reported the deleterious effects of stress and stress-related increase of cortisol on gonadotropic axis and reproductive performance. Chronically-induced stress such as by confinement or captivity and acutely-induced stress such as by predators or by aquaculture practices (handling, frequent netting, tank draining, crowding, noise) result in reduced plasma androgen and oestrogen levels [brown trout *Salmo trutta*: (Pickering et al., 1987); wild spotted seatrout *Cynoscion nebulosus*: (Safford and Thomas, 1987); rainbow trout

Oncorhynchus mykiss: (Pankhurst and Dedual, 1994); red gurnard *Chelidonichthys kumu*: (Clearwater and Pankhurst, 1997); striped trumpeter *Latris lineata*: (Morehead, 1998); roach *Rutilus rutilus*: (Pottinger et al., 1999); black bream *Acanthopagrus butcheri*: (Haddy and Pankhurst, 1999); sockeye salmon *Oncorhynchus nerka*: (Kubokawa et al., 1999); snapper *Pagrus auratus*: (Carragher and Pankhurst, 1991; Cleary et al., 2000); spiny damselfish *Acanthochromis polyacanthus*: (Pankhurst, 2001); striped bass *Morone saxatilis*: (Castranova et al., 2005); jundia *Rhamdia quelen*: (Soso et al., 2008); tilapia *Oreochromis mossambicus*: (Chabbi and Ganesh, 2012)]. Stress is also associated with reduced plasma vitellogenin (Vg) levels [brown and rainbow trout: (Campbell et al., 1994)]. It also decreases plasma luteinizing hormone (LH) levels [white sucker *Catostomus commersoni*: (Van Der Kraak et al., 1992)], suppresses LH secreting cell activity [tilapia: (Chabbi and Ganesh, 2012)], as well as decreases hypothalamic gonadotropin-releasing hormone 1 (GnRH1) mRNA levels [jack mackerel *Trachurus japonicus*: (Imanaga et al., 2014)]. After applied stress, impacts on final stages of reproduction are also observed such as delayed ovulation [rainbow trout: (Campbell et al., 1992; Contreras-Sanchez et al., 1998)], reduced egg size in females [brown and rainbow trout: (Campbell et al., 1994, 1992) ; *Neolamprologus pulcher*: (Mileva et al., 2011)] and reduced sperm counts in males [brown and rainbow trout: (Campbell et al., 1994)], increased gonadal atresia [(pike *Esox lucius*: (De Montalembert et al., 1978); red gurnard: (Clearwater and Pankhurst, 1997); snapper: (Cleary et al., 2000); Atlantic bluefin tuna *Thunnus thynnus*: (Corriero et al., 2011)], and reduced fecundity [rainbow trout : (Contreras-Sanchez et al., 1998)]. Furthermore, impacts on progeny also occur such as reduced length [tropical damselfish *Pomacentrus amboinensis*: (McCormick, 2009, 2006, 1999, 1998)], decreased survival [brown and rainbow trout: (Campbell et al., 1994, 1992)] or occurrence of abnormalities [Atlantic cod *Gadus morhua*: (Morgan et al., 1999)] [for reviews: (Billard, 1981; Pankhurst and Van der Kraak, 1997; Pankhurst, 2016; Pickering, 1989)].

Socially mediated stress response and downregulated reproductive function are observed in some teleosts, such as in cichlids. For example, subordinate (non-territorial) males of *Astatotilapia (Haplochromis) burtoni* display high expression of hypothalamic and pituitary corticotropin-releasing hormone (CRH) receptor as well as high plasma cortisol levels, but low mRNA levels of hypothalamic GnRH1 and of pituitary GnRH receptor, LH and FSH, as well as low plasma levels of LH and FSH, and androgens, compared to dominant (territorial) males [for review: (Maruska, 2014)].

1.2. Positive interactions between cortisol and reproduction related to peculiar life cycles

1.2.1. Cortisol and environmentally-related spawning activity in some teleosts

The catfish, *Heteropneustes fossilis*, awaits the onset of the monsoon rainfall for spawning in order to get favorable environmental conditions. Interestingly, in this species, plasma cortisol levels exhibit a peak at monsoon (Lamba et al., 1983; Sundararaj and Goswami, 1966a, 1966b), and glucocorticoids are effective both *in vivo* and *in vitro* in inducing ovulation (Sundararaj and Goswami, 1977). *In vivo* administration of an ovulatory dose of LH in this species induces an increase in plasma levels of cortisol followed by an increase in sex steroid (T and E2) levels, while ACTH injection only stimulates cortisol levels. The authors suggest that gonadotropin acts at two loci, the interrenal and the ovary (Goswami et al., 1985). All these data indicate a potential positive role of cortisol in the induction of spawning in the catfish. Another striking example is the killifish *Fundulus heteroclitus* which exhibits synchronized spawning with the semilunar cycle of spring tides and a peak of plasma cortisol level coincides with spawning (Bradford and Taylor, 1987).

1.2.2. Cortisol and upstream reproductive migration in salmonids

Upstream migration and spawning require high energy reserve mobilization; in Atlantic salmon *Salmo salar*, for example, between 60% and 70% of the body reserves are spent during upstream migration and spawning (Jonsson et al., 1997). High plasma cortisol levels and interrenal hyperplasia have long been reported during the later stages of the spawning migration and at the time of spawning in various salmonids [Pacific sockeye salmon: (Donaldson and Fagerlund, 1972; Hane and Robertson, 1959; Idler et al., 1959); migratory (steelhead) rainbow trout: (Robertson et al., 1961); Atlantic salmon: (Schmidt and Idler, 1962); kokanee salmon, landlocked form of sockeye salmon: (Carruth et al., 2000)]. However, one study in sockeye salmon reports that sexual maturation is not necessarily accompanied by elevated plasma cortisol levels (Fagerlund, 1967). Increased cortisol level is also described at spawning in non-migratory rainbow trout (Bry, 1985; Robertson et al., 1961). Altogether these studies indicate that high cortisol levels in salmonids are, at least, not deleterious to sexual maturation and spawning.

1.2.3. Cortisol and oceanic reproductive migration in eels

The downstream and oceanic migrations of eels (*Anguilla* species), as well as their whole gonadal development from prepubertal stage to full sexual maturation, require both metabolic energy and metabolites that come exclusively from body stores [for review: (Palstra and van den Thillart, 2010)]. Clevestam and collaborators report that 45% of European eel (*Anguilla Anguilla*) from Baltic sea would be within 90% of complete energy depletion after migration and reproduction and 20% would have completey exhausted their initial fat reserves (Clevestam et al., 2011). Eel, at the silver prepubertal, downstream migratory, stage and during their subsequent reproductive oceanic migration and sexual migration, are fasting and all their metabolic stores, accumulated during the juvenile growth (yellow stage) phase, will be mobilized. In silver eels, an elevation of plasma cortisol levels is observed prior to downstream migration (Van Ginneken et al., 2007). Early studies of hypophysectomy and adrenalectomy report the need of an intact pituitary-interrenal axis for maintenance of liver glycogen levels in eels [*Anguilla anguilla*: (Hatey, 1951); American eel *Anguilla rostrata*: (Butler, 1968)]. Cortisol induces mobilization of lipid and protein stores and stimulates hepatic neoglucogenesis [for review: (Butler, 1973); Japanese eel *Anguilla japonica*: (Chan and Woo, 1978); *Anguilla anguilla*: (Dave et al., 1979); *Anguilla rostrata*: (Butler, 1968; Foster and Moon, 1986)]. Cortisol also induces eel vertebral demineralization, by promoting both osteocytic osteolysis and osteoclastic resorption, allowing mobilization of phospho-calcic stores necessary for vitellogenin synthesis (Sbaihi et al., 2009). Besides these actions on metabolism necessary for the eel migratory and reproductive processes, cortisol may also directly stimulate the gonadotropic axis, as shown by its positive effect on pituitary *lhβ* mRNA and LH protein content *in vivo* and *in vitro* [*Anguilla anguilla*: (Huang et al., 1999)]. Thus, in the eel, cortisol may both coordinate storage mobilization and participate in the induction of sexual maturation during reproductive migration.

1.3. Cortisol and gonadal sex differentiation

In some teleost fish species, gonadal sex determination and/or sex change are under the regulation of environmental factors. An increasing number of data proposes cortisol as a key factor integrating environmental cues (such as temperature or social status) to induce male sex determination/sex change [for reviews: (Fernandino et al., 2013; Fernandino and Hattori, 2019; Goikoetxea et al., 2017; Liu et al., 2017; Perry and Grober, 2003; Solomon-Lane et al., 2013; Todd et al., 2016)]. Cortisol administration or stress-induced cortisol release (including high temperature-induced effects) promotes masculinization in a number of teleosts [rainbow trout: (van den Hurk and van Oordt, 1985); pejerrey *Odontesthes bonariensis*: (Hattori et al., 2009); Japanese flounder *Paralichthys olivaceus*: (Yamaguchi et al., 2010); Southern flounder *Paralichthys lethostigma*: (Mankiewicz et al., 2013); three-spot wrasse *Halichoeres trimaculatus*: (Nozu and Nakamura, 2015); black sea bass *Centropristis striata*: (Miller et al., 2019); medaka *Oryzias latipes* (Hayashi et al., 2010); orange spotted grouper *Epinephelus coioides* (Chen et al., 2020)]. Several potential pathways are described for cortisol triggering maleness: cross-talk between glucocorticoid and androgen metabolism (11β-hydroxysteroid dehydrogenase, 11βHSD, and 11β-hydroxylase, Cyp11b, enzymes) promoting the synthesis of 11-ketotestosterone (11KT); inhibition of aromatase (*cyp19a1a*) expression, leading to a shift in steroidogenesis from estrogens to androgens; and upregulation of anti-Müllerian homone (*amh*) expression [for reviews: (Fernandino et al., 2013; Fernandino and Hattori, 2019; Goikoetxea et al., 2017; Liu et al., 2017; Perry and Grober, 2003; Solomon-Lane et al., 2013)]. In the pejerrey, cortisol increases the expression of *hsd11b2*, the gene for 11βHSD, an enzyme which deactivates cortisol to cortisone and catalyzes the final step in 11-KT synthesis (Fernandino et al., 2012). Typical DNA binding sites of glucocorticoid receptor (GR) *i.e.* glucocorticoid response elements (GRE) are identified in the *cyp19a1a* promoter in the goby *Gobiodon histrio* (Gardner et al., 2005) and in the black sea bass (Miller et al., 2019). Interestingly, GR is also shown to directly interact with cAMP-responsive element (CRE) on *cyp19a1a* promoter of Japanese flounder, down-regulating the expression of aromatase (Yamaguchi et al., 2010). Temperature-dependent sex determination (TSD) is shown to involve regulation of DNA methylation of the *cyp19a1a* promoter [European sea bass *Dicentrarchus labrax*: (Navarro-Martín et al., 2011)], and such epigenetic modifications may also be a mechanism by which cortisol regulates aromatase expression.

All these studies highlight the role of cortisol as a mediator between environmental conditions, especially temperature, and male sex determination in various teleost species. This confers to cortisol a key-role in the potential impact of global climatic change on the modification of sex ratio in some teleost species and its consequences on population sustainability.

1.4. Animal welfare, environment, stress and reproduction

Concerns about fish welfare have increased considerably during the recent years owing to the growing public interest for the negative impacts of intensification in aquaculture and for scientific debate about pain in fish. Many authors agree on a definition for which welfare is not only based on physical health but also lack of mental suffering and presence of positive feelings (Huntingford et al., 2006; Segner et al., 2012; Sneddon et al., 2016; Stevens et al., 2017; Toni et al., 2019). In this context, most of the welfare issues are related to stress responses, experience of pains, growth problems, incidence of disease, abnormal behaviors and less frequently to degradated breeding with negative impact on male or female reproduction. These effects observed in aquaculture environment are not only the consequence of exposure of adult fish to stressors (*e.g.* confinement, handling, hypoxia or poor water quality) but also associated with abnormal behavior or impossibility to develop a normal behavior created by captive environment (Sneddon et al., 2016). Thus, one potential consequence of confinement is irregular spawners which suffer from a low fertilisation rate and a broken ovulatory rhythm (Kjesbu, 1989; Patterson et al., 2004). Intense swimming activity during chase and capture can also be sufficient to compromise reproduction (Pankhurst and Van der Kraak, 1997). Repeated acute confinement stress during the spawning season as well as poor body condition or food deprivation have also negative effects on fecundity in cod, all effects which have been suggested to be related to altered energy allocation (Bogevik et al., 2012; Kjesbu et al., 1991; Kjesbu, 1989; Lambert and Dutil, 2000). Behavioral needs can also be a welfare issue, not only by preventing maltreatment but also by providing adult fish resources to perform natural behavioural repertoire necessary for reproduction, accommodations which are species specific (Sneddon et al., 2016). Sometimes also, search for optimal performance in aquaculture can lead to welfare issue in relation to reproduction. In salmon aquaculture, early maturation can be a significant welfare issue. The maturation process is energetically expensive which is reflected in early maturing salmon by decreased growth rate and increased mortality through susceptibility to pathogens (Gjerde, 1984; Thorpe, 1994). Selection for both fast growth and late sexual maturation has been considered problematic as it has been suggested that there is a correlation between the phenotypes fast growth and early sexual maturation (Thorpe et al., 1983). The importance of energy cost for reproduction also appears when considering exercised female sockeye salmon compared to non-exercised fish: they displayed lower lipid content, delayed maturity, lower egg deposition rate and higher egg mortality prior to ovulation (Chellappa and Huntingford, 1989; Hansen et al., 2010). Methods used in aquaculture for egg collection from female is also a crucial procedure for fish reproduction in salmonid aquaculture: comparison between various methods (massage of the fish abdomen versus pressure of gas) in rainbow trout indicated that air stripping led to better quality of eggs and better juvenile survival rate (Kowalski et al., 2018). In recreational fisheries, studies on angling and release of nesting species during the spawning season reported decreased progenity survival and paternal nest abandonment and impaired care (Cooke et al., 2000; Hanson et al., 2007; Philipp et al., 1997). However, specific investigations on gonadal development of final maturation find very few adverse effects (Booth et al., 1995; Hall et al., 2009; Lowerre-Barbieri et al., 2011). Moreover, when testing effects of mild angling and release on golden perch *Macquaria ambigua*, normal gonadal development is observed in angled fish, a result attributed to the flexible reproductive strategy of that species and benigness of the mouth hooking (Hall et al., 2017). These results illustrate the complexity of welfare questions related to reproduction, which certainly need to take into account the specificity of the fish species and/or the characterisitics of the environment and stressors.

2. Overview of neuroendocrine stress and reproductive axes in teleosts

2.1. Teleost specific traits compared to other vertebrates

In mammals, brain-pituitary-peripheral glands axes are a classical schema when describing the endocrine regulation of major physiological functions, such as reproduction with the gonadotropic axis or stress with the corticotropic axis. Similar structures are observed in teleost fish which also present specificities which need to be considered for understanding stress/reproduction relationship in these species.

2.1.1. Anatomo-functional specificities

2.1.1.1. Pituitary regionalisation and direct innervation

The pituitary gland is a vertebrate innovation [for reviews: (Dufour et al., 2020; Sower, 2018)]. In all vertebrates, the pituitary consists of the adenohypophysis and the neurohypophysis. The adenohypophysis has been subdivided by early studies into the *pars distalis* and the *pars intermedia*, with in tetrapods, an additional *pars tuberalis* [for reviews: (De Beer, 1923; Dores, 2017)]. In contrast to tetrapods in which cells of the *pars distalis* seem widely distributed, in teleosts, the different types of cells of the *pars distalis* are regionalised [*Poecilia formosa* and *latipinna* (Olivereau and Ball, 1964); European eel (Olivereau, 1967); Atlantic halibut *Hippoglossus hippoglossus* (Weltzien et al., 2004); zebrafish *Danio rerio* (Pogoda and Hammerschmidt, 2007)*;* for reviews: (Schreibman et al., 1973; Trudeau and Somoza, 2020; Zohar et al., 2010)]. This allowed an anatomical subdivision of the *pars distalis* (PD), in teleosts, into an anterior region, the rostral *pars distalis* (RPD) composed of lactotropes (prolactin cells) and corticotropes (corticotropin, ACTH cells), and a posterior region, the proximal (or caudal) *pars distalis* (PPD) composed of somatotropes (growth hormone cells), thyreotropes (thyrotropin TSH cells) and gonadotropes (luteinizing hormone LH and follicle stimulating hormone FSH cells). Interestingly, in teleosts, the two gonadotropins, LH and FSH, are expressed in different pituitary cells, in contrast to the situation observed in mammals which produce LH and FSH in the same pituitary cell [for 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 the pituitary level. ACTH is the result of tissue-specific post-translational processing of proopiomelanocortin (POMC), together with melanocyte stimulating hormone (MSH), and β-endorphin (β-END). ACTH and MSH, called melanocortins (MC) act *via* MC receptors (MCR), while β-END acts *via* opioid receptors. ACTH from the corticotrophs of the *pars distalis* of the pituitary controls via type 2 MCR (melanocortin-2 receptor, MC2R), glucocorticoid production and release from adrenal cortex cells in amniotes or interrenal cells in amphibians and teleosts. Major glucocorticoids are cortisol in most mammals and ray finned fish and corticosterone in most birds, amphibians and reptiles [for review: (Aerts, 2018)]. MC2R, in teleosts as in tetrapods, is ligand selective as it can only be activated by ACTH and not by MSH, and requires coexpression with an accessory protein, melanocortin-2 receptor accessory protein (MRAP) for trafficking to the cell surface [for reviews: (Dores, 2016; Dores et al., 2016)]. Glucocorticoids negatively feedback on the brain (hypothalamic CRH) / pituitary (ACTH) corticotropic axis [for reviews: (Bernier et al., 2009; Faught et al., 2016; Gorissen and Flik, 2016)]; this negative feedback regulation of the HPI axis involves glucocorticoid receptor (GR) signaling pathway.

2.2.2. Specific features of the corticotropic axis in teleosts

The hypothalamic regulation of corticotropes and melanotropes in teleosts has already been extensively reviewed by Bernier and collaborators (Bernier et al., 2009).

2.2.2.1. CRH and related peptides and their receptors

CRH, first isolated from sheep hypothalamus, together with urotensin I (UI) isolated from the CNSS of the white sucker (Lederis et al., 1982) and the common carp (Ichikawa et al., 1982), and with sauvagine (SVG) isolated from the skin of the amphibian *Phylomedusa sauvagei* (Montecucchi et al., 1980), form a large family of peptides. Later on, urocortins were identified in mammals and also found to be related to CRH: urocortin 1 (Ucn1), ortholog of UI and SVG (Vaughan et al., 1995); urocortin 2 [Ucn2: (Reyes et al., 2001)] and urocortin 3

[Ucn3: (Lewis et al., 2001)] [for review: (Lovejoy and Balment, 1999)]. All these peptides, CRH and urocortins in mammals and CRH and UI/SVG in teleosts and amphibians, represent the CRH/urocortin family.

The complex evolutionary scenario of this family was recently clarified by Cardoso and collaborators (Cardoso et al., 2016). As previously suggested by Hwang and collaborators, two ancestral *crh/ucn1* and *ucn2/ucn3* genes likely arose by specific gene duplication before vertebrate WGD events (Hwang et al., 2013). Both ancestral genes were duplicated twice in ancestral vertebrates *via* 1R and 2R, followed by some paralog losses, leading to up to 5 genes (*crh1, crh2, ucn1* issued from ancestral *crh/ucn1*; *ucn2, ucn3*, issued from ancestral *ucn2/ucn3*) in extant representative species of some vertebrate lineages such as chondrichthyans, holosteans and actinistians (Cardoso et al., 2016). Teleost specific 3R resulted in the duplication of *crh1* into two paralogs *crh1a* and *crh1b* conserved in many species [for review: (Cardoso et al., 2016)]. *Crh2* may have been lost in recent teleosts (Cardoso et al., 2016), while one 3R-*crh2* paralog has been conserved in basal groups of teleosts [(Maugars et al., 2016) and Maugars et al. unpublished data].

The involvement of CRH in the stress response in teleosts is well-documented [for reviews: (Flik et al., 2006; Gorissen and Flik, 2016)]. Teleost *crhb* (*crh1b*) paralog is widely expressed in the brain of various teleost species [goldfish *Carassius auratus*: (Bernier et al., 1999); flounder *Platichthys flesus*: (Lu et al., 2004); zebrafish: (Alderman and Bernier, 2007); Japanese eel: (Amano et al., 2014); *Astatotilapia burtoni*: (Carpenter et al., 2014); *Schizothorax prenanti*: (Wang et al., 2014)]. To our knowledge, the expression of the *crha* (*crh1a*) paralog was only investigated in *Astatotilapia burtoni* and zebrafish: in the zebrafish, *crha* expression is restricted to the lateral tuberal nucleus of the ventral hypothalamus, while in *A. burtoni*, no *crha* expression is detected in the brain (Grone and Maruska, 2015). The authors also show that, while both forms are expressed in the retina of *Astatotilapia burtoni*, only *crhb* expression is observed in the retina of zebrafish (Grone and Maruska, 2015). These first data suggest species-specific variations in the respective roles of 3R-duplicated *crh1* paralogs in teleosts.

In mammals, CRH binds to G-protein coupled receptors, CRHR1 and CRHR2, which belong to the class 2 subfamily B1 of secretin-like receptor superfamily. *Crhr1* was duplicated *via* teleost-3R into two paralogs (*crhr1a* and *crhr1b*) which were conserved in many extant teleosts, while one of 3R-duplicated *crhr2* paralogs would have been lost [for review: (Cardoso et al., 2014)]. CRHR1s are thought to mediate CRH action along the corticotropic/stress axis, as, like mammalian CRHR1, teleost CRHR1s have similar affinity for CRH and UI/Ucn1 while CRHR2 has higher affinity for UI and urocortins (2 and 3) than for CRH [catfish *Ameirus nebulosus*: (Arai et al., 2001); chum salmon *Oncorhynchus keta*: (Pohl et al., 2001); common carp: (Manuel et al., 2014)].

The ACTH-releasing action of CRH has been demonstrated *in vitro* in many teleost species [goldfish : (Fryer et al., 1984); rainbow trout: (Baker et al., 1996; Pierson et al., 1996); gilthead sea bream *Sparus aurata*: (Rotllant et al., 2001, 2000); Mozambique tilapia *Oreochromis mossambicus*: (Van Enckevort et al., 2000); common carp: (Metz et al., 2004)], as in mammals (Rivier et al., 1983; Rivier and Plotsky, 1986), birds (Carsia et al., 1986) and amphibians (Tonon et al., 1986). In the common carp, the release of ACTH is stimulated by CRH but only when ACTH cells are submitted to DA inhibition (Metz et al., 2004).

CRH stimulates not only ACTH release, but also α-MSH release, in various teleosts such as in Mozambique tilapia (Lamers et al., 1994; Van Enckevort et al., 2000), gilthead sea bream (Rotllant et al., 2001), red porgy *Pagrus pagrus* (Van Der Salm et al., 2004) and common carp (Van Den Burg et al., 2005). This α-MSH-releasing effect of CRH is also reported in mammals such as rat (Meunier et al., 1982; Proulx-Ferland et al., 1982). In contrast, in an amphibian, the frog *Rana ridibunda*, while CRH is a potent stimulator of ACTH release by anterior pituitary cells, it is ineffective on α-MSH release by neurointermediate lobes *in vitro* (Tonon et al., 1986).

Other CRH-related peptides such as UI and sauvagine can induce in goldfish the release *in vitro* of ACTH (Fryer et al., 1984, 1983), as well as of α-MSH (Tran et al., 1990). Interestingly, UI and SVG are equipotent to CRH in stimulating ACTH release by rat anterior pituitary cells (Rivier et al., 1983), while in the frog *Rana ridibunda*, they are unable to stimulate ACTH release (Tonon et al., 1986). Concerning α-MSH, UI and SVG induce its release by the neurointermediate lobe *in vitro* in *Xenopus laevis* (Verburg-Van Kemenade et al., 1987), but not in *Rana ridibunda* (Tonon et al., 1986). In addition to its action on the pituitary, UI is able to directly stimulate cortisol release, and to potentiate ACTH-stimulatory effect, on interrenals *in vitro* in rainbow trout (Arnold-Reed and Balment, 1994) and European flounder (Kelsall and Balment, 1998). Finally, in maturing masou salmon *Oncorhynchus masou*, UI rather than CRH could be involved in the control of hypercortisolemia, as hypothalamic *uI* expression rises in correlation with enhanced cortisol secretion, while *crh* expression does not (Westring et al., 2008).

In the rainbow trout, both *crh* and *uI* expressions in the brain (hypothalamus and preoptic area) increase in response to various stressors: hyperosmotic challenge (Craig et al., 2005), hyperammonemia, isolation (Bernier et al., 2008) as well as hypoxia (Bernier et al., 2008; Bernier and Craig, 2005). Notably, *crh* and *uI* expressions increase also in the caudal neurosecretory system (CNSS) in response to various stressors in the rainbow trout [hyperosmotic challenge: (Craig et al., 2005); hyperammonemia: (Bernier et al., 2008)] and in the olive Japanese flounder, *Paralichthys olivaceus* [acute hypothermal stress: (Yuan et al., 2020)]. In the European flounder, net restraint induces an increase in *crh* expression in the CNSS, but not in the hypothalamus, as well as an increase in CNSS cortisol receptors in addition to an increase in plasma cortisol levels (Lu et al., 2004). In this species, glucocorticoid receptors have been colocalized with UI in the CNSS (Bond et al., 1999). All these data suggest the possible involvement of the CNSS in the stress-specific regulation of cortisol production in teleosts and the existence of an extra-pituitary feedback system on CNSS for the suppression of cortisol secretion. Earlier *in vivo* studies already reported the possible involvement of CNSS in the regulation of the corticotropic axis: injection of urophysis extracts or synthetic *Catostomus commersoni* UI in flounder induces an elevation of cortisol (Arnold-Reed and Balment, 1989); in goldfish, urophysectomy produces marked elevation of hypothalamic UI-like activity, pituitary ACTH and plasma cortisol, which can not be observed in urophysectomized fish receiving dexamethasone (Woo et al., 1985). More functional investigations are needed to assess the possibility of a major contribution of CNSS CRH-related peptides to the regulation of cortisol secretion and stress responses.

2.2.2.2. Dopamine and other neurohormones

Dopamine

In mammals, different data have been reported concerning the effects of dopamine (DA) on ACTH release between *in vitro* and *in vivo* studies. Treatment of rat anterior pituitary glands (Van Loon and Kragt, 1970) or human corticotroph adenoma cells (Ishibashi and Yamaji, 1981) with DA lowers ACTH release. In contrast, administration of DA agonists to rats elevates plasma ACTH concentrations and subsequently plasma corticosterone levels, and this elevation is prevented by pretreatment with DA antagonists (Borowsky and Kuhn, 1992; Ježová et al., 1985). An α-MSH-release inhibitory effect of DA is observed in amphibians [*Rana pipiens*: (Saland et al., 1982); *Rana ridibunda* : (Jenks et al., 1985); *Xenopus laevis* : (Verbug-Van Kemenade et al., 1986)].

Possible involvement of DA in the hypothalamic regulation of teleost corticotropes and melanotropes has been suggested by Metz and colleagues. As basal ACTH release increases 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 levels and ACTH release from the pituitary and these effects are inhibited by crowding stress (Medeiros et al., 2014). However in goldfish, injection of this agonist has no effect at the brain level but rather acts at interrenal tissue to stimulate cortisol secretion (Lim et al., 2013). *In vitro*, 5-HT stimulates cortisol release by interrenals in Gulf toadfish [kidney pieces: (Medeiros and McDonald, 2012)] and in goldfish [superfused head kidney tissue: (Lim et al., 2013)]. In goldfish, Lim and colleagues demonstrate the involvement of multiple 5-HT receptor subtypes (5-HT_{1A} and 5-HT_4) in the interrenal paracrine effect of 5-HT (Lim et al., 2013), while in Gulf toadfish, Medeiros and McDonald show that 5-HT_4 does mediate 5-HT action but 5-HT_{1A} does not (Medeiros and McDonald, 2012).

**** Thyrotropin-releasing hormone***

In mammals and in adult amphibians, thyrotropin-releasing hormone (TRH) is the main neurohormone controlling the thyrotropic axis *i.e.* the synthesis and release of thyrotropin (TSH) at the pituitary level, which stimulates the production of thyroid hormones at the thyroid level. This TSH-releasing role seems to be taken on by CRH in larval amphibians, reptiles and birds [for reviews: (De Groef et al., 2006; Galas et al., 2009)]. In teleosts, investigations on the *in vitro* effect of TRH on pituitary TSH production show either no effect [common carp: synthesis, (Kagabu et al., 1998); mRNA levels, (Geven et al., 2009); coho salmon *Oncorhynchus kisutch*, release: (Larsen et al., 1998)] or a stimulatory effect [bighead carp *Aristichthys nobilis*, mRNA levels: (Chatterjee et al., 2001; Chowdhury et al., 2004); Japanese eel, mRNA levels: (Han et al., 2004)]. CRH acts as a TSH-releasing factor on coho salmon pituitary cells (Larsen et al., 1998), but has no effect on *tshβ* mRNA levels in common carp pituitary glands *in vitro* (Geven et al., 2009).

Conversely to the effect of CRH on TSH, TRH can exert an ACTH-releasing effect in teleosts as shown by *in vitro* studies [goldfish pituitary dispersed cells: (Tran et al., 1989); gilthead sea bream pituitary: (Rotllant et al., 2000)]. TRH is also a potent stimulator of α-MSH release by the *pars intermedia* in many teleost species [goldfish: (Tran et al., 1989); tilapia: (Lamers et al., 1991); rainbow trout: (Schwartzentruber et al., 1994); gilthead sea bream: (Rotllant et al., 2000); red porgy: (Van Der Salm et al., 2004)]. This α-MSH-releasing effect of TRH is also observed in amphibians [*Rana ridibunda*: (Tonon et al., 1980); *Xenopus laevis*: (B. Verburg-Van Kemenade et al., 1987)].

After a stress (prolonged crowding), in the gilthead sea bream, the pituitary presents a differential response of ACTH and α-MSH to TRH and CRH treatments: the stimulation of ACTH by CRH is attenuated, but not the stimulation of ACTH by TRH, while both CRH and TRH stimulation of α-MSH are enhanced (Rotllant et al., 2000). In Mozambique tilapia, a dual organization of the stress axis has been demonstrated, as after exposure to low-pH water, the CRH/ACTH axis is replaced by a TRH/di-acetylated α-MSH axis for the production of cortisol (Lamers et al., 1994). Overall, these results suggest the involvement of TRH in the regulation of corticotropes and melanotropes, notably during exposure to stress.

Arginine vasotocin, isotocin and arginine vasopressin

Arginine vasotocin (AVT), isotocin (IST) and arginine vasopressin (AVP) are all peptides produced by neurons of the preoptic nucleus and released by the neurohypophysis. AVT and IST are present in non-mammalian vertebrates and closely related to mammalian AVP.

As in mammals, these neuropeptides are able to stimulate the release of ACTH *in vitro* [goldfish: (Fryer et al., 1985); trout: (Baker et al., 1996; Bond et al., 2007; Pierson et al., 1996)] and thus increase plasma cortisol levels in teleosts *in vivo* [goldfish: (Fryer and Leung, 1982); trout: (Baker et al., 1996; Bond et al., 2007; Pierson et al., 1996)]. In addition, in mammals and birds [for review: (Cornett et al., 2012)], they potentiate the stimulatory action of CRH on ACTH *in vivo* and *in vitro* (Gillies et al., 1982; Rivier and Vale, 1983; Turkelson et al., 1982). In teleosts, contradictory data are available concerning a possible synergy with CRH on ACTH release *in vitro*: they do synergize in trout (Baker et al., 1996), while they do not in goldfish (Fryer et al., 1985)]. In the frog *Rana ridibunda*, no potentiation of CRH-induced ACTH release is observed when anterior pituitary cells are incubated with a combination of AVP and CRH (Tonon et al., 1986).

In rainbow trout, a study shows that AVT mRNA levels in neurons of the preoptic nucleus are elevated during acute stress but not chronic stress (Gilchriest et al., 2000).

2.2.2.3. POMC-derived peptides and their receptors

POMC-derived peptides

Pro-opiomelanocortin (POMC), together with proenkephalin (PENK), prodynorphin (PDNY) and proorphanin (PNOC), form the opioid/orphanin gene family [(Sundström et al., 2010); for review: (Dores et al., 2002)]. POMC is post-translationally processed and some of the peptides obtained undergo further modifications such as C-terminal amidation and N-acetylation [for reviews: (Dores and Baron, 2011; Takahashi and Mizusawa, 2013)]. POMC organizational plan varies among vertebrates [for reviews: (Dores and Baron, 2011; Dores and Lecaude, 2005)]. POMC is the precursor for ACTH, melanotropins (α-, β- and γ- MSH), corticotropin-like intermediate peptide (CLIP), lipotropins (β- and γ- LPH) and β-endorphin, in tetrapods and lungfish (Amemiya et al., 1999a; Nakanishi et al., 1979). Chondrichthyans have an additional melanotropin, δ-MSH (Amemiya et al., 1999b). Teleosts lack γ-MSH (Kitahara et al., 1988; Lee et al., 1999), but *pomc-β* of cichlids and pomacentrids encodes a novel melanocortin peptide, ε-MSH, the result of a tandem duplication of the segment encoding ACTH (Harris et al., 2014). In all these vertebrates, the adenohypophysis possesses two cell populations that express POMC: in the *pars distalis* (PD), the corticotropes in which POMC is processed to ACTH (and β-lipotropin), and in the *pars intermedia* (PI), the melanotropes in which POMC is processed to ACTH, which is further cleaved to give α-MSH, corticotropin-like intermediate peptide and β-endorphin [for review: (Takahashi and Mizusawa, 2013)]. Differently, agnathans possess two 'POMC' genes: pro-opiocortin (POC), which encodes ACTH and a different β-endorphin, is expressed in the *pars distalis*; pro-opiomelanotropin (POM), which encodes α-, and β- MSH, and β-endorphin, is expressed in the *pars intermedia* (Takahashi et al., 2012, 1995).

Teleost 3R gave rise to *pomc* gene duplicates: *pomc-α* (*a* or *A*) and *pomc-β* (*b* or *B*), with *pomc-β* having lost a functional *β*-endorphin (De Souza et al., 2005). Further independent gene duplications during teleost evolution resulted in duplicates of *pomc-α* such as in halibut and carp [*pomc*-I and –II: (De Souza et al., 2005)], sea bream [*pomc-α1* and -*α2*: (Cardoso et al., 2011)] and *Astatotilapia burtoni* [*pomc-α1* and -*α2*: (Harris et al., 2014)]. In barfin flounder *Verasper moseri*, a third *pomc* gene, named *pomc-C*, was also identified (Takahashi et al., 2006); *pomc-C* belongs to the *pomc-β* clade while *pomc-A* and-*B* belong to the *pomc-α* clade and thus should be renamed -*β, -α1* and -*α2*, respectively, according to Cardoso and collaborators (Cardoso et al., 2011). In rainbow trout, apart from *pomc-B*, *pomc-A1* and -*A2* are likely the result of the salmonid genome duplication (4R) (Leder and Silverstein, 2006).

As in other vertebrates [*e.g.* in rodents: (Kraicer et al., 1973)], ACTH is produced in teleosts from POMC by both the *pars distalis* (PD; corticotropes) and the *pars intermedia* (PI; melanotropes) of the pituitary, but ACTH of the *pars intermedia* is further cleaved to produce smaller peptides and cortisol feedbacks only on the *pars distalis* ACTH [for review: (Fryer and Lederis, 1986)]. In tetraodon *Tetraodon nigroviridis*, *pomc-α* and not *pomc-β* is expressed in the PD, while both are expressed in the PI (De Souza et al., 2005). In the sea bream, *pomc-α2* and not *pomc-α1* is expressed in the PD, while only *pomc-α1* is expressed in the PI (Cardoso et al., 2011). In the pituitary of barfin flounder, all three *pomc* genes present in this species are expressed in the PD (Takahashi et al., 2006). In *Astatotilapia burtoni* (Harris et al., 2014) and rainbow trout (Leder and Silverstein, 2006), all three *pomc* are expressed in the pituitary, but no indication of the region is reported. This indicates species-specific variation in the expression of the various *pomc* paralogs by the PD corticotropic cells through teleost radiation.

Species-specific variations among teleosts may also concern the *pomc* paralog linked to stress response. In the gilthead sea bream, an enhanced pituitary expression of *pomc-α2* (*pomc-b* in the paper) and a decreased one of *pomc-α1* (*pomc-a* in the paper) are observed after acute stress due to air exposure (Skrzynska et al., 2018)], leading the authors to link *pomc-α2* and not *pomc-α1* to stress response in sea bream. However, in the same species, no change in the expression of both paralogs was previously reported after exposure to other acute stress, chasing and persecution (Toni et al., 2015). In *Rhamdia quelen*, both pituitary *pomc-α2* (*pomcb* in the paper) and *pomc-α1* (*pomca* in the paper) expressions are unchanged after stressful situation (transport) (Saccol et al., 2018). In contrast, in the Senegalese sole, *Solea senegalensis*, *pomc-α1* (*pomc-a* in the paper) expression in the pituitary is down-regulated in juveniles chronically stressed by high stocking density, whereas *pomc-α2* (*pomc-b* in the paper) expression levels remain unaffected (Wunderink et al., 2012). All these data in three different species do not lead to clear conclusions concerning a preferential involvement of one or another *pomc* paralog in stress response among teleosts.

An *in vitro* corticotropic action (*i.e.* induction of cortisol release from head kidney) of α-MSH (desacetyl and diacetyl forms) has been reported in rainbow trout (Rance and Baker, 1981), Mozambique tilapia (Lamers et al., 1992) and barfin flounder (Kobayashi et al., 2011), but not in common carp (Metz et al., 2005).

*Melanocortin receptors

In tetrapods, five MCRs have been identified. In teleost fish, the number of receptors increases up to six in zebrafish, which has two MC5R paralogs (*mc5ra* and *mc5rb*) (Västermark and Schiöth, 2011), while pufferfish *Fugu* has only four, with no melanocortin *mc3r* and only one copy of melanocortin *mc5r* (Logan et al., 2003). Concerning the ligand selectivity of MCRs, all of the paralogous MCRs can be activated by both ACTH and α-MSH in extant cartilaginous fishes, while in extant teleosts and tetrapods, MC2R can be activated only by ACTH. The appearance of MRAP1 paralleled the emergence of this MC2R ligand selectivity [for reviews: (Dores, 2016; Dores et al., 2016)].

In mammals, the MCRs have distinct expression site and functions [for reviews: (Cone, 2006; Dores et al., 2014)]: MC1R, expressed in melanocytes, is involved in skin and hair pigmentation; MC2R, expressed in adrenal cortex, is involved in adrenal steroidogenesis and stress response; MC3R and MC4R, expressed in the brain, are involved in the control of energy homeostasis; MC5R, expressed in a variety of exocrine glands, such as sebaceous, lacrimal and preputial glands, is involved in exocrine gland secretion. These features can be also found in teleosts but some peculiarities can be noted. Of particuliar interest, *mc5r* is co-expressed with *mc2r* in the interrenal of several teleosts [rainbow trout: (Aluru and Vijayan, 2008; Haitina et al., 2004); common carp *Cyprinus carpio*: (Metz et al., 2005); barfin flounder: (Kobayashi et al., 2011)], as in the chicken adrenal (Takeuchi and Takahashi, 1998) and *Xenopus tropicalis* interrenal/kidney (Dores and Garcia, 2015), suggesting a possible role of MC5R in the regulation of HPI/HPA axis in these non-mammalian vertebrates.

2.2.2.4. Corticosteroids and their receptors

***Glucocorticoids**

In fish, corticosteroids are synthetized by the interrenal tissue, a tissue embedded inside the anterior part of the kidney and homologous to the adrenal cortex in mammals. Corticosteroids are steroid hormones divided into glucocorticoids and mineralocorticoids. Even if cortisol is the major corticosteroid in teleosts [for review: (Mommsen et al., 1999)], others such as 11-deoxycortisol (17, 21 dihydroxy-4-pregnene-3,20 dione), 11-deoxycorticosterone (DOC) and corticosterone are also detected in plasma of teleosts [for review: (Butler, 1973); winter flounder *Pseudopleuronectes americanus*: (Campbell et al., 1976); rainbow trout *Salmo gairdneri*: (Campbell et al., 1980)]. All teleosts so far studied lack aldosterone, which is the principal mineralocorticoid in mammals (Gilmour, 2005), and it is generally accepted that cortisol exerts both glucocorticoid and mineralocorticoid actions in teleosts (McCormick, 2001; McCormick et al., 2008). DOC is shown to be a potent agonist of mineralocorticoid receptor (MR) (Sturm et al., 2005). Study in rainbow trout has shown a sustained up-regulation of plasma DOC levels during a confinement stress time-course. However, the low DOC levels compared to cortisol measured in the plasma do not favour an activity of DOC through MR receptors (Kiilerich et al., 2018) and physiological relevance of this hormone action is still unclear in fish (Prunet et al., 2006).

****Glucocorticoid and mineralocorticoid receptors***

Glucocorticoid and mineralocorticoid receptors (GR and MR respectively) are corticosteroid receptors which belong to the nuclear receptor superfamily [for review: (Bury, 2017)]. In teleosts, 3R gave rise to duplicated *gr* (*gr1* and *gr2*) with one receptor (GR1) retaining a 9 aminoacid insert which does not exist in GR2 [for review: (Bury, 2017)]. Zebrafish is an exception as this species conserved only one of the two *gr* paralogs (Schaaf et al., 2008). In some teleosts, GR1 has two splice variants, GR1a and GR1b [rainbow trout: (Takeo et al., 1996); *Haplochromis burtoni*: (Greenwood et al., 2003); Tetraodon and Takifugu species: (Stolte et al., 2006); marine medaka *Oryzias dancena*: (M. Kim et al., 2011)]. 3R gave also rise to duplicated *mr* (*mr1* and *mr2*) which have been both conserved in a basal teleost, the European eel [(Lafont et al., 2014) and Lafont et al. unpublished data], while only the *mr1* paralog would have been conserved in extant teleosts so far studied [for review: (Baker and Katsu, 2019)]. As they are issued from the 3R, these two *mr* paralogs in the eel should rather be named *mra* and *mrb*, according to the commonly used nomenclature for teleost 3R-paralogs. However, they must be distinguished from the two *mr* forms previously found in the rainbow trout, named rt*mra* and rt*mrb* (Sturm et al., 2005), which may represent allelic variants or paralogs issued from salmonid-4R of *mr1*.

GR1 and GR2 present differential affinities (sensitivities) and show distinct functionality with GR2 having a higher hormonal transcriptional activity at equimolar concentration and higher sensitivity (Bury et al., 2003). This difference in sensitivity is not restricted to the salmoniformes and have been also observed with the two GRs in *Pantodon buchholzi* (Li et al., 2012), carp (Stolte et al., 2008), marine medaka (*Oryzias dacena*) (M. Kim et al., 2011), and the Japanese medaka (*Oryzias latipes*) (Miyagawa et al., 2015). From such *in vitro* differences in functionality, one can hypothetize that the two teleost GRs may have different roles: the hypersensitive GR2 could play a prominent role during basal circulatory cortisol concentrations (unstressed) whereas the less sensitive GR1 may become prominent during stressful situations when cortisol levels are high [(Bury et al., 2003); for review: (Bury, 2017)]. So far, such functionally distinct roles have not been established in fish. However, a recent study of stress effects in salmonids shows differential contribution of the corticosteroid receptors in the regulation of HPI axis activity (Kiilerich et al., 2018) and suggests a negative feedback regulation of cortisol release at the pituitary level *via* MR, while a short loop regulation occurs at the interrenal level *via* GR in rainbow trout exposed to 7 day-confinement. The authors also observe the presence of the 2 GR and the MR in hypophysial ACTH cells confirming the regulation of the HPI axis at the pituitary level by both GRs and MR. Similar conclusions have been also suggested when studying in the Atlantic salmon effects of unpredictable chronic stress or to repeated chasing stress (Madaro et al., 2016, 2015). In the common carp, Stolte and collaborators report that, in fish exposed to prolonged and strong stressors, mRNA levels of all three corticosteroid receptors (*gr1*, *gr2* and *mr*) are down-regulated in some brain regions, but not in CRH neurons or pituitary ACTH cells (Stolte et al., 2008), suggesting a role of all three receptors in stress regulation in this species.

In zebrafish (Schaaf et al., 2008), the single *gr* (*gr2*) gene has two splice variants, *grα* and *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 well as key-steps of the life cycle such as puberty, seasonal reproduction or sex change in some hermaphrodic species including teleost representatives.

The brain integrates various environmental and social cues, such as temperature, photoperiod, habitat conditions, presence of partners, as well as internal cues such as developmental stage, size, nutritional status and energy stores, *via* various neuronal networks which converge into the positive or negative regulation of the activity of gonadotropin-releasing hormone (GnRH) hypophysiotropic neurons considered as the master control of reproduction (Gore, 2002). GnRH binds to its cognate membrane receptor (GnRH-R) expressed by the pituitary gonadotrope cells, and which belongs to the rhodopsin-like, class A, G-protein coupled receptor (GPCR) superfamily [for reviews: (Flanagan and Manilall, 2017; Millar et al., 2004)]. GnRH stimulates the synthesis and release of the gonadotropins, LH and FSH.

The two pituitary gonadotropins, LH and FSH are glycoprotein hormones, composed of two subunits alpha and beta. The alpha subunit, named glycoprotein hormone alpha subunit (Gpα), is common to both gonadotropins, LH, FSH and to the thyrotropin, TSH, while the beta subunit is specific to each hormone [for reviews: (Cahoreau et al., 2015; Pierce and Parsons, 1981)]. LH and FSH bind to their respective GPCR membrane receptors LHR and FSHR expressed by the gonads. The gonadotropins activate gonadal functions, gametogenesis and steroidogenesis. The enzymatic pathway of the biosynthesis of sex steroids is largely conserved among vertebrates. Sex steroids, androgens, estrogens, progestagens, bind to their respective nuclear receptors, AR, ER, PR, belonging to the nuclear receptor superfamily [for review: (Mangelsdorf et al., 1995)]. As more recently discovered, steroid may also act *via* binding to GPCR membrane receptors, such as estradiol-membrane receptor and progesterone membrane receptor [for review: (Thomas, 2012)]. Sex steroids act on multiple targets, including the gonads themselves, a variety of peripheral tissues as well as the brain and 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

Up to three *gnrh* genes are present in extant teleosts, a larger number than in mammals (up to two genes), which had been initially attributed to the 3R. However, subsequent comparative studies revealed the presence of three *gnrh* genes also in basal vertebrate representatives such as a chondrichthyan, the catshark, *Scyliorhynus canicula* and a basal sarcopterygian, the coelacanth, *Latimeria chalumnae*. Phylogeny and synteny studies support the 1R/2R origin of the three vertebrate *gnrh* and their inheritance by the teleost lineage. In contrast, 3R had no impact on the *gnrh* gene number in extant teleosts, indicating an early loss of 3R-paralogs in this lineage [for reviews: (D. K. Kim et al., 2011; Roch et al., 2011; Tostivint, 2011)]. A maximum of three *gnrh* (1, 2, 3) genes are thus present in teleosts, such as in medaka, while additional, independent and species-specific losses led to the presence of only two *gnrh* genes in some species, *e.g. gnrh1* and *2* in the eel, or *gnrh2* and *3* in the zebrafish. The situation is more complex concerning GnRH receptors. Recent studies indicate that a large number of GnRH receptors resulted from 1R/2R as well as from local gene duplications in ancestral vertebrates; subsequently, several independent gene loss events led to a variable number of *gnrhr* genes throughout vertebrate evolution. In teleosts, 3R-duplicated paralogs as well as additional duplications in some lineages increased the number of GnRH-R [up to 5 in acanthopterygians and 6 in salmonids: (Ciani et al., 2020)] as compared to other actinopterygians, with species-specific variations among teleosts due to independent gene losses [(Ciani et al., 2020); for reviews: (Roch et al., 2014; Sefideh et al., 2014; Williams et al., 2014)].

2.3.2.2. Dopamine and other neurohormones

Dopamine

A crucial control is exerted by dopaminergic neurons which directly inhibit the gonadotrope cell activity and counteract the effect of GnRH, as first discovered in cyprinids by Peter and collaborators and retrieved in many other teleosts species including basal representatives such as the eel [for reviews: (Dufour et al., 2010, 2005)]. In relation with environmental and internal cues, and in a species-specifc manner, this dopaminergic control of gonadotropic cells plays key roles in various reproductive steps in teleosts such as puberty, final oocyte maturation and ovulation, spermiation, or sex change [for reviews: (Dufour et al., 2010, 2005)]. A major inhibitory role of DA in regulating reproduction is also reported in amphibians, especially in the control of spawning [for review: (Vu and Trudeau, 2016)].

Beside GnRH and DA, a variety of other neurohomones can also directly regulate the activity of teleost gonadotrophs, with species-specific variations, such as kisspeptin (Kiss), gonadotropin-inhibitory hormone (GnIH), neurokinin, gamma-aminobutyric acid (GABA), noradrenaline, serotonin *etc* [for reviews: (Dufour et al., 2020; Zohar et al., 2010)]. As proposed by Trudeau, these multiple independent controls of gonadotropic cells may provide compensatory regulatory mechanisms, possibly explaining the low or no impact of KO of major genes such as *kiss* or *gnrh* observed in recent studies (Trudeau, 2018). Species-specific variations in the multiple controls of gonadotrophs highlight the evolutionary plasticity of the brain-pituitary anatomo-functional relationships in the teleost lineage, which may have favored the remarkable diversity of their reproductive cycles.

GnIH

Gonadotropin-inhibitory hormone (GnIH or RFRP-3 in mammals), a RFamide peptide, was discovered from quail brain by Tsutsui and collaborators and found to be involved in the direct inhibitory pituitary regulation of LH (Tsutsui et al., 2000). Shortly after, the GnIH precursor was shown to encode two other peptides (Satake et al., 2001). Since then, *gnih* gene homologs, encoding multiple peptides, have been identified in other vertebrates [for reviews:

(Muñoz-Cueto et al., 2017; Tsutsui et al., 2018)]. These peptides, in mammals, also possess an inhibitory action on gonadotropins, while in amphibians they have GH-releasing effects [for review: (Dufour et al., 2020)]. Recently, it was demonstrated that only a single *gnih* gene was present in representative species of elopomorphs (*Anguilla* species), the most basal group of teleosts, as well as in the other teleosts (Maugars et al., 2020). This result indicates a loss of one of the two 3R-duplicated *gnih* paralogs shortly after the 3R (Maugars et al., 2020). Depending on teleost species, inhibitory [*e.g.* European eel (Pasquier et al., 2018); common carp (Peng et al., 2016); zebrafish (Spicer et al., 2017)], stimulatory [*e.g.* sockeye salmon (Amano et al., 2006); grass puffer *Takifugu niphobles* (Shahjahan et al., 2011); tilapia *Oreochromis niloticus* (Biran et al., 2014); catla *Catla catla* (Kumar et al., 2019); half-smooth tongue sole *Cynoglossus semilaevis* (Wang et al., 2019)] or a lack of effect [*e.g.* goldfish (Qi et al., 2013); *Astyanax altiparanae* (Branco et al., 2019)] of GnIH have been described for gonadotropins *in vitro* [for review: (Muñoz-Cueto et al., 2017; Tsutsui et al., 2018; Ubuka and Parhar, 2018)], suggesting a large variability of GnIH function in reproduction across teleosts.

**** Kisspeptin***

Kisspeptin, another RF-amide peptide, is encoded by the *Kiss-1* gene, a metastasis suppressor gene, isolated in 1996 from melanoma cells (Lee et al., 1996). This 54 amino-acid peptide, also called metastin, is processed into shorter peptides which all bind to kisspeptin receptor, KissR (or GPR54) (Ohtaki et al., 2001). In 2003, three research groups discovered the key role of the kisspeptin system in the activation of gonadotropic axis and the control of reproduction in human and mice (de Roux et al., 2003; Funes et al., 2003; Seminara et al., 2004). *In vivo* and *in vitro* studies further demonstrate the stimulatory role of kisspeptin at different levels of the gonadotropic axis: hypothalamus (GnRH neurons), pituitary (LH cells) and gonads [for reviews: (Pinilla et al., 2012; Putteeraj et al., 2016)]. The few available studies in amphibians and reptiles also suggest a stimulatory role of kisspeptin on the HPG axis, while this system might have been lost in some birds [for review: (Dufour et al., 2020)]. However, data in teleosts report stimulatory, no or inhibitory effects of kisspeptin peptides on GnRH or gonadotropins, suggesting a large variabilty of the role of Kiss system in eleost reproduction according to species [for reviews: (Dufour et al., 2020; Tena-Sempere et al., 2012)]. Up to four paralogs of *Kiss* and *KissR* resulted from 1R and 2R in early vertebrates, but subsequent gene losses led to the presence of only a single *Kiss* gene and a single *KissR* gene in human. In teleosts, due to paralog losses, no impact of 3R on the number of both *Kiss* and *KissR* genes has been found, leading to a maximum of two *Kiss* and three *KissR* genes, which is no more than in a non-teleost actinopterygian such as the gar, *Lepisosteus oculatus* [for reviews: (Pasquier et al., 2014, 2012)].

2.3.2.3. Gonadotropins and their receptors

As in mammals, only two gonadotropins, LH and FSH, are present in all extant teleosts, including basal representative species such as the eel (elopomorphs) (Yoshiura et al., 1999), indicating an early loss after 3R of the putative additional 3R-paralogs [for review: (Dufour et al., 2020)]. In tetrapods, LH and FSH bind to their respective receptors, LHR and FSHR. As recently shown, an additional *lhr* paralog arose from a local gene duplication in ancestral actinopterygians, and the two *lhr* (*lhr1* and *lhr2*) where inherited by the teleost lineage (Maugars and Dufour, 2015). Due to gene losses after 3R, the number of gonadotropin receptors did not further increase in teleosts with a single *fshr* and up to two *lhr*. Additional independent and species-specific gene losses led to the presence of a single *lhr* in some teleosts, such as only *lhr1* in medaka and *lhr2* in zebrafish (Maugars and Dufour, 2015).

2.3.2.4. Sex steroids and their receptors

Gonadal sex steroids are produced from cholesterol by a succession of enzymatic activities. In teleosts, 3R duplication of a key-enzyme, the aromatase (*Cyp19a1a* and *b*), has been largely documented [for review: (Zhang et al., 2014)].

Sex steroid nuclear receptors have been duplicated by 3R and the conservation of most of the paralogs led to the presence of a larger number of nuclear receptors in teleosts as compared to mammals [for review: (Ogino et al., 2018)]. This is also the case for the steroid membrane receptors. Concerning estradiol receptors, tetrapods possess two nuclear receptors (ESR1 also named ERα, and ESR2 also named ERß) and a single membrane receptor (GPER) while teleosts, as a result of 3R, possess three nuclear receptors (*esr1* and duplicated *esr2a* and *esr2b*) and two membrane receptors (*gpera* and *gperb*) (Lafont et al., 2016). One of the duplicated *esr1* paralog would have been lost shortly after 3R. A species-specific gene loss occurred in zebrafish, which possesses a single *gper* paralog, while both *gpera* and *b* paralogs have been conserved in the other teleosts investigated so far (Lafont et al., 2016). For androgen receptors, 3R also generated two *ar* paralogs (*ara* and *arb*) in teleosts (Ogino et al., 2009). Recently, Morini and colleagues revealed the presence of duplicated progesterone nuclear receptors (*pgra* or *pgr1*, and *pgrb* or *pgr2*) in the eel, which originated from 3R. In other teleosts however only a single *pgr* (orthologous to eel *pgrb/pgr2*) has been found, and synteny analysis indicates the loss of *pgra* (*pgr1)* paralog in the teleost lineage after the emergence of the basal teleost group of elopomorphs (Morini et al., 2017). Two *pgr* paralogs are reported in the goldfish, likely resulting from 4R. The evolutionary history of membrane progestin receptors is even more complex as five isoforms have been characterized in vertebrates (Morini et al., 2017). The conservation of multiple steroid receptor genes in teleosts likely reflects subfonctionalization and neofunctionalization processes, which may have contributed to species-specific diversification of sexual chararacters, regulatory processes and reproductive cycles throughout teleost radiation.

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

(McConnachie et al., 2012).

Deleterious reproductive *in vivo* effects of corticosteroids have also been shown in other teleost species. In immature male common carp fed with cortisol-containing food pellets over pubertal period, brain sGnRH content, pituitary *lh* and *fsh* mRNA levels, plasma LH levels and testicular androgen (T and 11KT) secretion are decreased (Consten et al., 2001a). Testicular development in this species is retarded by this long-term cortisol treatment (Consten et al., 2001a, 2001b). In contrast, dietary administered cortisol to channel catfish *Ictalurus punctatus* does not modify reproduction (Small, 2004). In the Arctic char, co-exposure to cortisol and E2 results in reduced plasma Vg levels and no change in *Vg* mRNA levels, suggesting a post-transcriptional action of cortisol (Berg et al., 2004). Implantation of cortisol causes retardation of the ovarian growth and depression of plasma sex steroid levels in tilapia *Oreochromis mossambicus* [female: (Foo and Lam, 1993a); male: (Foo and Lam, 1993b)]. Later, Gennotte and collaborators show that cortisol treatment induces both positive (reduction of the time before ovulation) and negative (reduction of fecundity) effects on the reproduction in other tilapia species, *Oreochromis niloticus* (Gennotte et al., 2012).

In the cinnamon clownfish, *Amphiprion melanopus*, injection of cortisol increases *gnih* mRNA, and reduces *sbGnRH* mRNA and plasma levels of LH and FSH (Choi et al., 2017). As, in this teleost species, GnIH inhibits gonadotropin expression (Choi et al., 2016), cortisol treatment leads to a dual negative effect on gonadotropin *via* an increase in GnIH and decrease in GnRH. A similar upregulation of hypothalamic *gnih* (*rfrp3*) mRNA levels is observed in rats after acute or chronic immobilization/restraint stress (Kirby et al., 2009; Yang et al., 2017), upregulation which is abolished by adrenalectomy (Kirby et al., 2009) . Concerning the effect of stress or corticosteroid treatment on the kisspeptin system, all the available data have been obtained in rodents [for reviews: (Acevedo-Rodriguez et al., 2018; Iwasa et al., 2018)] and show a reduction of hypothalamic *Kiss1* and *KissR1* mRNA levels [rat, restraint stress or subcutaneous injection of corticosterone: (Kinsey-Jones et al., 2009); mice, implant containing corticosterone: (Luo et al., 2016); mice, restraint stress: (Yang et al., 2017)]. It would be relevant to investigate the regulation of the kisspeptin system by stress and corticosteroids in teleosts, which show different effects of kisspeptin on the control of gonadotropins according to the species.

3.1.1.3. *In vitro effects of corticosteroids*

In vitro investigations pin-point the direct actions of cortisol at the different levels of the HPG axis. In the rat hypothalamic rfrp-expressing cell line (rHypoE-23) (Gingerich et al., 2009), treatment with corticosterone increases *gnih(rfrp)* mRNA levels and the application of a GR antagonist blocks this increase (Gojska and Belsham, 2014; Son et al., 2014). *In vitro* investigations should be developed in teleosts, using hypothalamic neurons, to study possible direct effects of corticosteroids on the various neuronal populations (GnRH, DA, GnIH and kisspeptin) involved in the gonadotropic axis.

At the pituitary level, cortisol affects reproduction-related gene expression in Atlantic cod pituitary cultures (von Krogh et al., 2019). In this species, cortisol has dual effects on *fshβ* expression, stimulating expression in cells from mature fish, while inhibiting expression in cells from spent fish (von Krogh et al., 2019). In contrast, cortisol has no direct effect on *lhβ* expression (von Krogh et al., 2019). While *gnrhr2a* transcript levels largely increase following cortisol treatment, *gnrhr1b* expression decreases in cells from spent fish and was unaffected at other maturity stages (von Krogh et al., 2019). In the prepubertal European eel, cortisol increases LH cellular content and *lhβ* mRNA levels by pituitary cells in culture (Huang et al., 1999). Future studies should investigate the effects of corticosteroids on the levels of other pituitary targets such as GnIH and kisspeptin receptors in different teleost species, considering that, in teleosts, GnIH and kisspeptin possess direct inhibitory or stimulatory effects on the pituitary depending on the species.

At the liver level, dexamethasone inhibits both basal and E2-stimulated ER expression and subsequent Vg expression in trout hepatocyte aggregates (Lethimonier et al., 2000). This is achieved *via* an inhibition by GR of the transcriptional factor CCAAT/enhancer-binding protein (C/EPBβ) binding to the ER promoter region (Lethimonier et al., 2002).

At the gonadal level, different data are available on the direct effect of cortisol on female gonadal steroidogenesis depending on species [(Pankhurst, 1998); for review: (Pankhurst, 2016)]. A decrease in E2 and T release by cultured ovarian follicles after cortisol treatment has been observed in rainbow trout (Carragher and Sumpter, 1990), while no such effect has been reported in goldfish, common carp and *Pagrus auratus* (Pankhurst et al., 1995). In the rainbow trout, cortisol is shown to have suppressive effects on basal and LH- or cAMP-stimulated T and E2 production and secretion, but no effect on basal or LH-stimulated 17,20β-dihydroxy-4-pregnene-3-one (17,20β-P) (Barkataki et al., 2011; Reddy et al., 1999). In the same species, cortisol is reported to enhance the efficiency of gonadotropin to induce intrafollicular oocyte maturation (Jalabert, 1975) and to positively regulate the secretion of follicular 17α-hydroxy-20β-dihydroprogesterone (DHP) induced by gonadotropin *in vitro* (Jalabert and Fostier, 1984). All these data suggest that, in the rainbow trout, cortisol has a positive (or no) effect on the synthesis of progestagen (Maturation Inducing Steroid, MIS) during final oocyte maturation, while being inhibitor at earlier stages of oogenesis, on the production of T and E2 during vitellogenesis. In the zebrafish, cortisol does not inhibit hCG-stimulated E2 production, while ACTH did (Alsop et al., 2009). In other teleost species, glucocorticoids are also able to act on final oocyte maturation. Glucocorticoids have been shown to induce *in vitro* oocyte maturation in the goldfish [desoxycorticosterone: (Jalabert et al., 1973)] and ovulation in the medaka [cortisol: (Hirose, 1976)]. In the amago salmon (*Oncorhynchus rhodurus*), DOC can enhance oocyte maturation induced by gonadotropin or 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 rat hypothalamic slices and this inhibition is suppressed by α-helical CRH (Nikolarakis et al., 1986). In parallel to its central inhibitory effect, CRH is also able to act at the pituitary level through CRH-R2 to inhibit LH release in mice (Raftogianni et al., 2018). Previous data in rat failed to show any effect of CRH on LH release *in vitro* (Ono et al., 1984).

In teleosts, there are very few investigations regarding CRH action on the gonadotropic axis. Injection of CRH to stripped tilapia *Oreochromis mossambicus* resulted in diminished immunoreactive LH content in the pituitary, lower GSI and absence of vitellogenic follicles in the ovary (Chabbi and Ganesh, 2014). The glucocorticoid synthesis inhibitor, metyrapone, abolishes the inhibitory effects of CRH treatment on LH secretion and follicle growth, demonstrating an action *via* cortisol (Chabbi and Ganesh, 2014). Direct pituitary or gonadal effect of CRH needs to be investigated through *in vitro* studies. CRH-R mRNAs have already been detected in the pituitary [catfish *Ameiurus nebulosus*: (Arai et al., 2001); common carp: (Huising et al., 2004); *Astatotilapia burtoni*: (Chen and Fernald, 2008); tilapia *Oreochromis mossambicus*: (Aruna et al., 2015, 2012)], but future investigations should aim at determining whether these receptors are expressed in other cell types than corticotrophs, notably in gonadotrophs. CRH-R are also expressed in the ovary [*Astatotilapia burtoni*: (Chen and Fernald, 2008); olive flounder *Paralichthys olivaceus*: (Zhou et al., 2019)], which suggests a direct action of CRH on the gonads.

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

Conversely, some studies reveal a role of actors of the gonadotropic axis on the corticotropic axis in teleosts.

3.2.1. Roles of sex steroids

In the sockeye salmon, gonadectomy blocks the cortisol prespawning rise (Donaldson and Fagerlund, 1970; Robertson, 1961) and sex steroids, estrogens and androgens, can induce interrenal hyperplasia as well as increase in plasma cortisol levels in both intact and gonadectomized fish [(Donaldson and Fagerlund, 1969; Fagerlund and Donaldson, 1969); for review: (Dickhoff, 1989)]. The situation is different in the rainbow and brown trout in which implantation of T and 11-KT attenuates ACTH and cortisol-elevation after confinement stress, while E2 implantation increases stress-induced ACTH and cortisol levels (Pottinger et al., 1996). In the rainbow trout, *in vivo* treatment with 11KT suppresses interrenal responsiveness to ACTH *in vitro* (Young et al., 1996), while DHP stimulates cortisol production by interrenal tissue cultured *in vitro* (Barry et al., 1997). McQuillan and collaborators compared the *in vitro* effect of E2 on cortisol synthesis by interrenals of the chinook salmon, *Oncorhynchus tshawytscha* and rainbow trout: they show that E2 suppresses the ability of juvenile and mature chinook salmon interrenals to produce cortisol, whereas it has no effect in the rainbow trout (McQuillan et al., 2003). These data reveal potential differences among species and reproductive stage concerning the role of sexual steroids in the induction of hypercortisolemia in salmonids.

Interestingly, the interrenal in fish has been reported to produce androgen [rainbow trout: (Arai et al., 1969); coho salmon: (Schreck et al., 1989); tilapia *Oreochromis mossambicus*: (Balm et al., 1989); African catfish, *Clarias gariepinus*: (Vermeulen et al., 1995)], as in mammals [for review: (Rainey and Nakamura, 2008)]. In human, the production and secretion of adrenal androgens (dehydroepiandrosterone, DHEA and its sulfate ester, DHEAS) in the midchildhood, termed adrenarche, has been involved in the timing of puberty (Remer et al., 2010). Such a role of interrenal androgens could be also envisioned in teleosts.

A potential remarkable interaction between reproductive and stress actors is illustrated by the recent finding of the ability of progesterone to bind to the mineralocorticoid receptor MR. Recent *in vitro* studies indicate that progesterone can activate MR in the elephant shark *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 associated with various pituitary cell types including gonadotrophs, corticotrophs and melanotrophs, and GnIH receptors (LPXRFa-Receptor) are expressed in LH, ACTH and alpha MSH cells [(Ogawa et al., 2016); for review: (Muñoz-Cueto et al., 2017)]. It would be very interesting now to clarify whether GnIH is involved in the regulation of these cell types and in the production of ACTH and MSH.

Conclusion and perspectives

Stress impact on reproduction has long been studied in teleosts, especially in the frame of aquaculture. However, most of the accumulated data come from studies on the possible action of peripheral hormone, cortisol, on sexual maturation. Emerging data in mammals show that actors of higher levels (especially brain) should catch researcher attention. The teleost specific whole genome duplication (3R) had made such studies perhaps more difficult, multiplicating the number of genes, but thanks to the recent publications of an increasing number of teleost genomes and the development of molecular and genome editing technology tools, it is now possible to investigate their respective functions across teleost species diversity. Thus future directions should aim, for example, at dissecting mechanisms of action of the different paralogs of genes involved in the corticotropic axis and in the caudal neurosecretory system in the regulation of various levels of the gonadotropic axis. Such studies are all the more important that the present review gives multiple examples of species-specific regulatory mechanisms which probably reflect the wide species-specific plasticity of fish reproductive responses when fish are exposed to stressful situations.

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Figure legends

Figure 1: Stress and reproduction neuroendocrine axes in teleosts.

The figure displays the main actors and regulatory pathways of the stress neuroendocrine axis (corticotropic axis: brain-pituitary-interrenals; green arrows) and of the reproduction neuroendocrine axis (gonadotropic axis: brain-pituitary-gonads; blue arrows). The Caudal Neurosecretory System (CNSS) which may be involved in the stress axis in teleost is indicated in relation to the corticotropic axis. The liver, which plays a key role in reproduction in teleosts as in other oviparous vertebrates by producing vitellogenin, is indicated in relation to the gonadotropic axis. Abbreviations: AVP, arginine vasopressin; AR, androgen receptor; CNSS, caudal neurosecretory system; CRH, corticotropin-releasing hormone; CRH-R, corticotropin-releasing hormone receptor; DA, dopamine; DHP, 17-hydroxy-20-dihydroprogesterone; DOC, 11-deoxycorticosterone; E2, estradiol; ER, estrogen receptor; FSH, follicle stimulating hormone; FSH-R, follicle stimulating hormone receptor; GnIH, gonadotropin inhibitory hormone; GnRH, gonadotropin-releasing hormone; GnRH-R, gonadotropin-releasing hormone receptor; GR, glucocorticoid receptor; kiss, kisspeptin; kiss-R, kisspeptin receptor; LH, luteinising hormone; LH-R, luteinising hormone receptor; MC2R, melanocortin receptor 2; other P, other progestins; POMC, proopiomelanocortin; PR, progestin receptor; T, testosterone; TRH, thyrotropin releasing hormone; UI, urotensin I; Vg, vitellogenin; 5-HT, 5 hydroxytryptamine, or serotonin; 11-KT, 11-ketotestosterone.

Figure 2: Effects of corticotropic axis on gonadotropic axis in vertebrates.

The figure illustrates current knowledge on the regulatory actions (green arrows) exerted by typical actors of the corticotropic axis (brain-pituitary-interrenal) on the gonadotropic and liver axis (brain-pituitary-gonad-liver). Abbreviations: ACTH, adrenocorticotropin; β-end, β-endorphin; CRH, corticotropin-releasing hormone; E2, estradiol; FSH, follicle stimulating hormone; GnIH, gonadotropin inhibitory hormone; GnRH, gonadotropin-releasing hormone; GR, glucocorticoid receptor; kiss, kisspeptin; LH, luteinising hormone; MC2R, melanocortin receptor 2; MR, mineralocorticoid receptor; T, testosterone; 11-KT, 11-ketotestosterone;.

Figure 3: Effects of gonadotropic axis on corticotropic axis in vertebrates.

The figure illustrates current knowledge on the regulatory actions (blue arrows) exerted by typical actors of the gonadotropic axis (brain-pituitary-gonad) on the corticotropic axis (brain-pituitary-interrenal). Abbreviations: ACTH, adrenocorticotropin; AR, androgen receptor; CRH, corticotropin-releasing hormone; CRH-BP, corticotropin-releasing hormone binding protein; DHP, 17-hydroxy-20-dihydroprogesterone; E2, estradiol; ER, estrogen receptor; FSH, follicle stimulating hormone; GnIH, gonadotropin inhibitory hormone; GnRH, gonadotropin-releasing hormone; LH, luteinising hormone; LH-R, luteinising hormone receptor; other P, other progestins; PR, progestin receptor; T, testosterone; Vg, vitellogenin; 11-KT, 11-ketotestosterone.

Table Legends

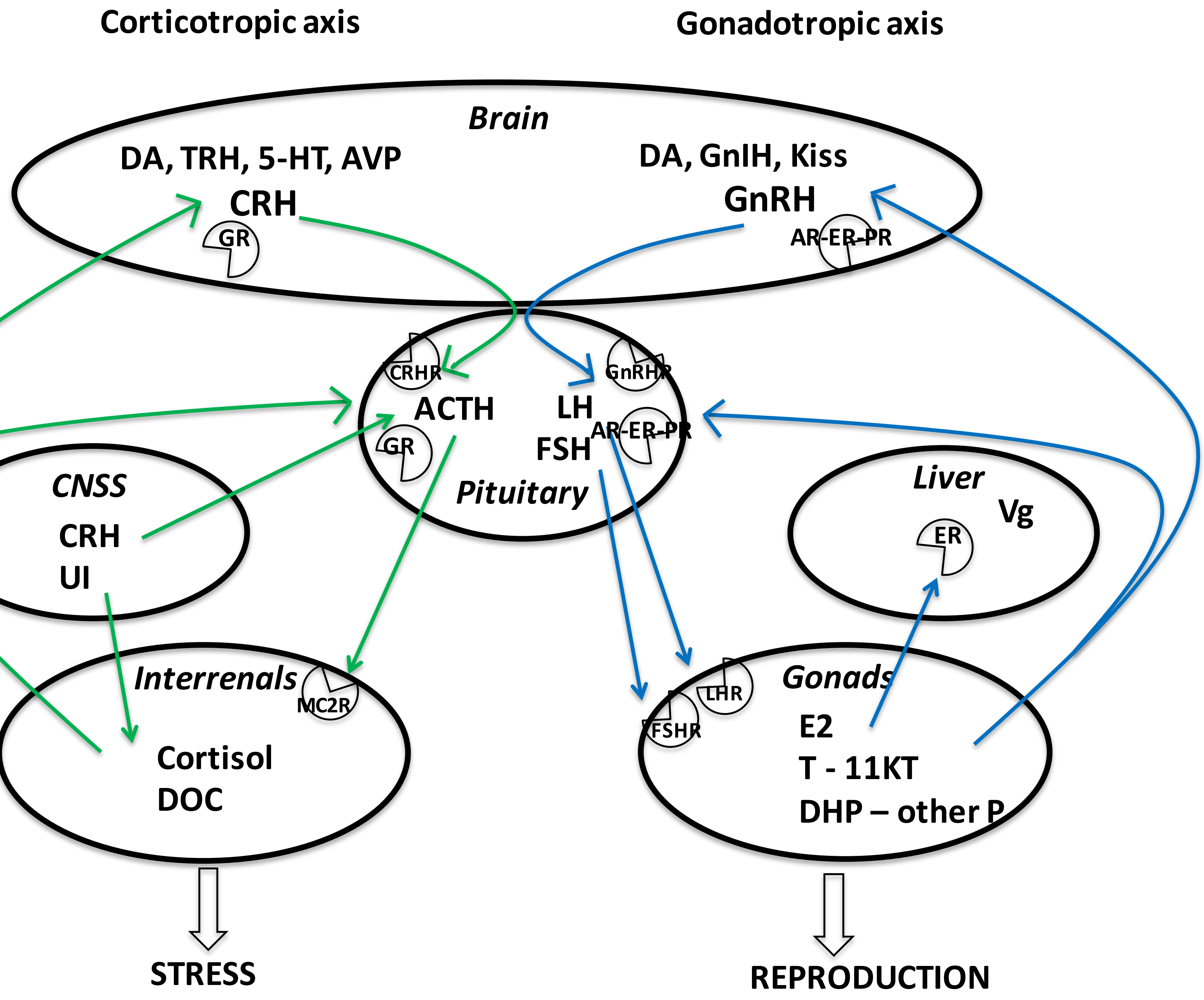
Table 1: **Major actors of the corticotropic axis in human and teleosts**.

This table underlines the expansion of gene numbers in teleosts due to teleost-specific whole genome duplication (3R). In teleosts, some of the paralogs have been lost in some species. Supplemental paralogs issued from additional whole genome duplication (4R, which occurred in salmonids and carps) are not indicated. Abbreviations: CRH, corticotropin-releasing hormone; CRH-R, corticotropin-releasing hormone receptor; POMC, proopiomelanocortin;

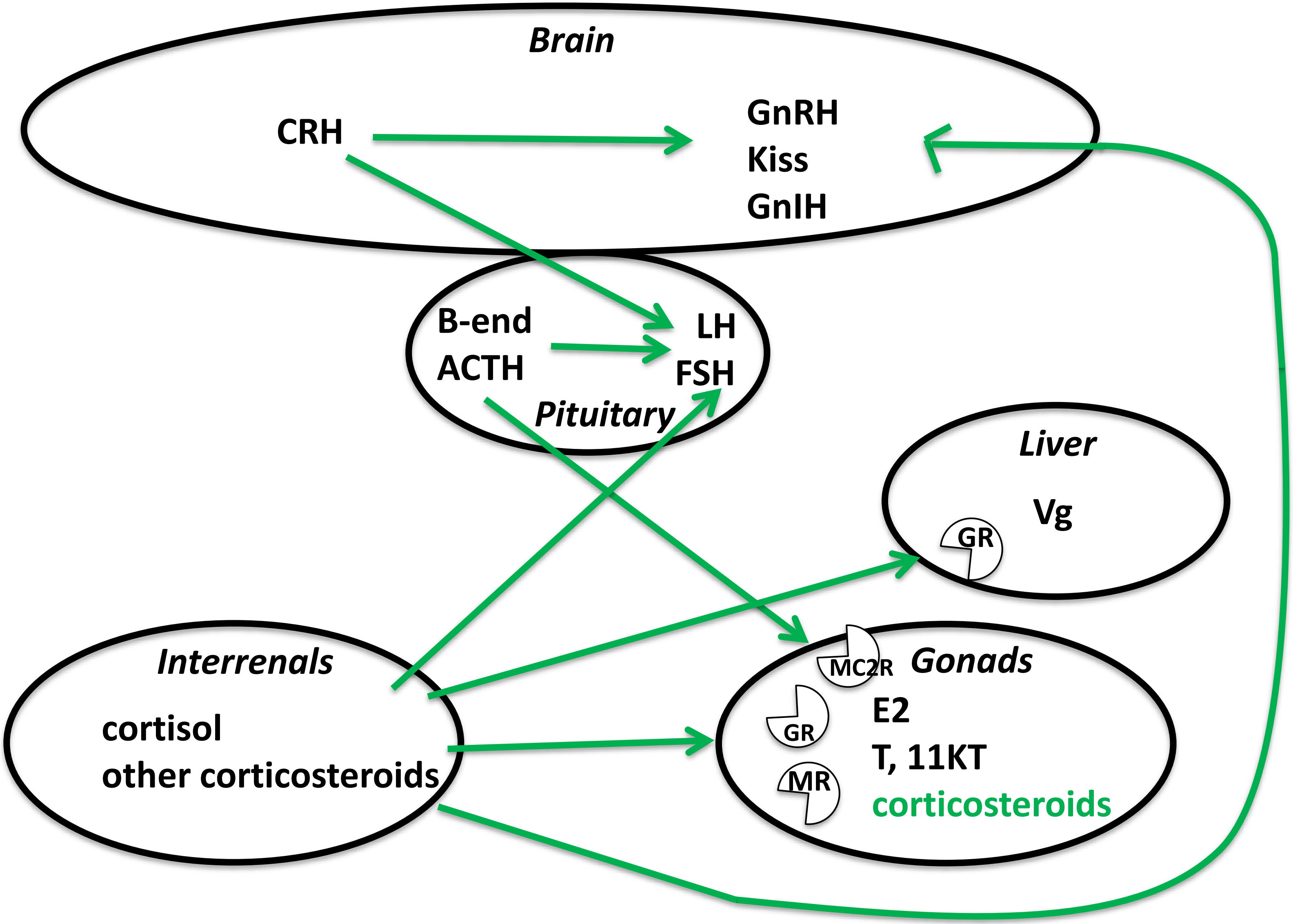
MCR, melanocortin receptor; GR, glucocorticoid receptor; MR, mineralocorticoid receptor; UI, urotensin I.

Table 2: **Major actors of the gonadotropic axis in human and teleosts**.

This table underlines the larger gene numbers in teleosts due to teleost-specific whole genome duplication (3R) but also to the conservation of paralogs resulting from early vertebrate whole genome duplications (1R and 2R), or from local gene duplication (see the text for details). In teleosts, some of the paralogs have been lost in some species. Supplemental paralogs issued from additional whole genome duplication (4R, which occurred in salmonids and carps) are not indicated. Abbreviations: GnRH, gonadotropin-releasing hormone; GnRH-R, gonadotropin-releasing hormone receptor; GnIH, gonadotropin inhibitory hormone; kiss, kisspeptin; kiss-R, kisspeptin receptor; LHβ, luteinising hormone; FSHβ, follicle stimulating hormone; LH-R, luteinising hormone receptor; FSH-R, follicle stimulating hormone receptor; ER, estrogen receptor; esr, nuclear estrogen receptor; gper, membrane estrogen receptor; AR, androgen receptor; PR, progestin receptor; pgr, nuclear progestin receptor; mpgr, membrane progestin receptor.


Corticotropic axis
Gonadotropic axis
Brain
DA, TRH, 5-HT, AVP
CRH
GR
DA, GnIH, Kiss
GnRH
AR-ER-PR
CRHR
ACTH
GR
GnRHR
LH
FSH
AR-ER-PR
Pituitary
CNSS
CRH
UI
Liver
Vg
ER
Interrenals
MC2R
Cortisol
DOC
Gonads
LHR
FSHR
E2
T - 11KT
DHP – other P
STRESS
REPRODUCTION

Corticotropic axis **Gonadotropic axis**



Brain

CRH

GnRH
Kiss
GnIH

B-end
ACTH

LH
FSH

Pituitary

Liver

Vg

GR

MC2R

Gonads

GR

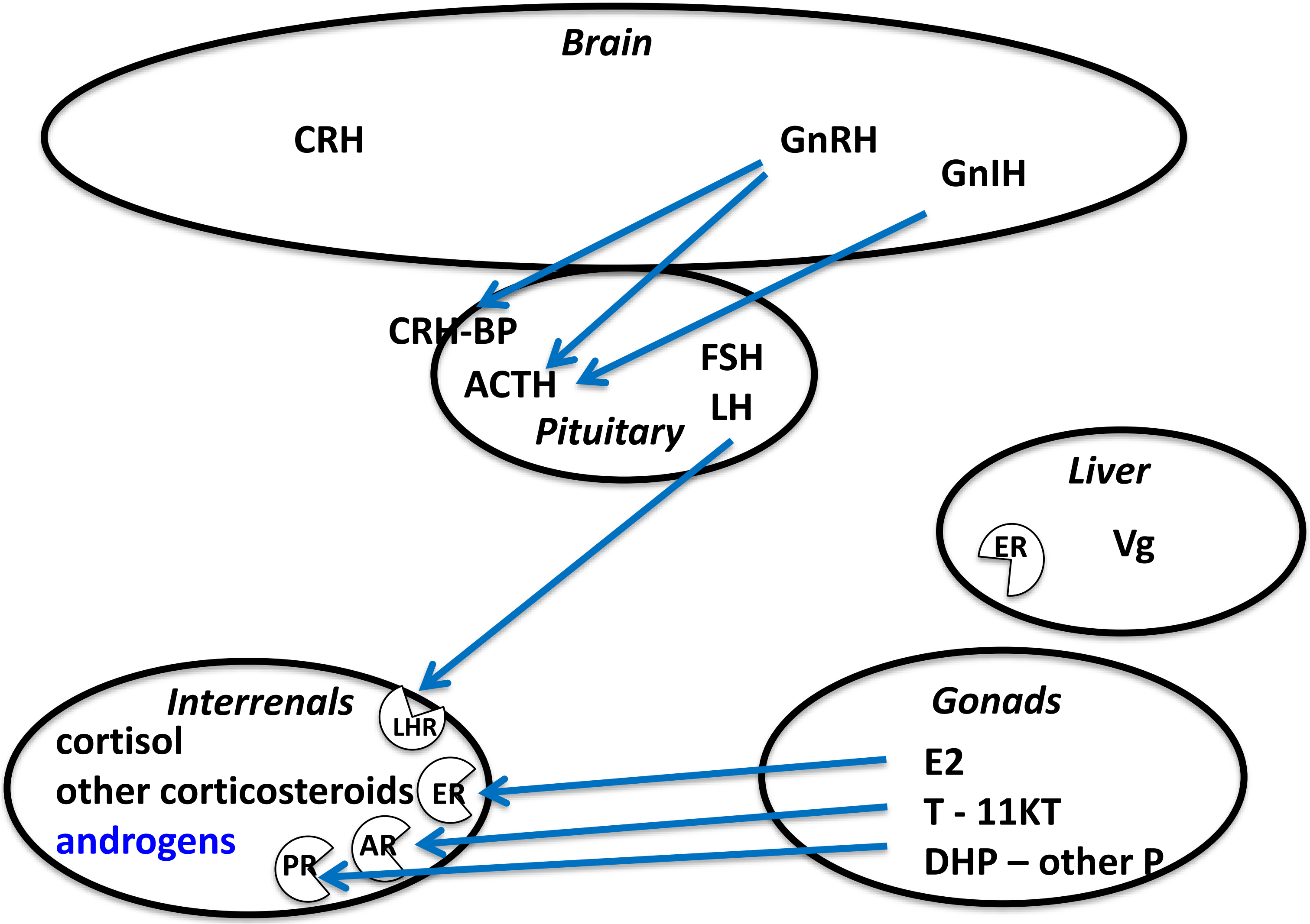
MR

E2
T, 11KT
corticosteroids

Interrenals

cortisol
other corticosteroids

Corticotropic axis **Gonadotropic axis**



Brain

CRH

GnRH

GnIH

CRH-BP

ACTH

Pituitary

FSH

LH

Liver

ER

Vg

Interrenals

LHR

cortisol

other corticosteroids

ER

androgens

AR

PR

Gonads

E2

T - 11KT

DHP – other P

Table 1: **Major actors of the corticotropic axis in human and teleosts**.

Protein	**Gene**	**Human**	**Teleosts**	**References / Review articles**
CRH	*crh*	*crh1*	*crh1a*	Lovejoy et al 2014; Cardoso et al 2016 Maugars et al 2016
			crh1b	
		crh2	*crh2*	
CRH-R	*crhr*	*crhr1*	*crhr1a*	Cardoso et al 2014; Lovejoy et al 2014
			crhr1b	
		crhr2	*crhr2*	
POMC	*pomc*	*pomc*	*pomc-α1* *pomc-α2* *pomc-β*	Dores and Lecaude 2005; Cardoso et al 2011; Dores and Baron 2011
MC1R	*mc1r*	*mc1r*	*mc1r*	Vastermark and Schioth 2011; Dores et al 2014, 2016
MC2R	*mc2r*	*mc2r*	*mc2r*	
MC3R	*mc3r*	*mc3r*	*mc3r*	
MC4R	*mc4r*	*mc4r*	*mc4r*	
MC5R	*mc5r*	*mc5r*	*mc5ra*	
			mc5rb	
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-I*	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*	*esr1* *esr2*	*esr1* *esr2a* *esr2b*	Lafont et al 2016; Ogino et al 2018
	gper	*gper*	*gpera* *gperb*	Lafont et al 2016
AR	*ar*	*ar*	*ara* *arb*	Ogino et al 2009
PR	*pgr*	*pgr*	*pgra* *pgrb*	Morini et al 2019
	mpgr	multiple	multiple	Morini et al 2019