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Review article

Regulation of astroglia by gonadal steroid hormones under physiological and pathological conditions

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ABSTRACT

In the last years there has been a considerable advance in the knowledge on the regulation of astrocytes by sex steroids under physiological and pathological conditions. By the activation of a variety of nuclear and membrane receptors, sex steroid hormones regulate the functions of astrocytes and their communication with other cell types in the central nervous system. Under physiological conditions astrocytes participate in the neuroendocrine and behavioral actions of gonadal steroids, as well as in the hormonal control of brain tissue homeostasis. Under pathological conditions astrocytes mediate, at least partially, the neuroprotective effects of gonadal steroid hormones; given that sex steroids modulate reactive astrogliosis and reduce the release of pro-inflammatory molecules by these cells. Given the side effects that sex steroids may have when administered systemically, a number of synthetic agonists of the receptors for gonadal steroid hormones in the nervous system have been developed, and may be considered for clinical use after brain injury as potential enhancers of the neuroprotective astrocytic functions.

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Abbreviations: Aldh1L1, aldehyde dehydrogenase 1 family, member L1; ApoE, apolipoprotein E; BBB, blood brain barrier; BLBP, brain lipid binding protein; BDNF, brain derived neurotrophic factor; BrdU, 5-bromo-2′-deoxyuridine; cAMP, cyclic adenosine monophosphate; CB, cannabinoid receptor; CNS, central nervous system; DHEA, dehydroepiandrosterone; DHT, dihydrotestosterone; ER, estrogen receptor; FGF, fibroblast growth factor; GABA, gamma-amino butyric acid; GFAP, glial fibrillary acidic protein; GLAST, glutamate aspartate transporter; GLT-1, glutamate type 1 transporter; GnRH, gonadotropin-releasing hormone; GPER, G protein-coupled estrogen receptor; IL, interleukin; LPS, lipopolysaccharide; MPO, myeloperoxidase; mPR, membrane progesterone receptor; mRNA, messenger ribonucleic acid; N-CAM, neural cell adhesion molecule; Ndrg2, N-myc downstream-regulated gene 2; NG2, neural/glial antigen 2; PDGF, platelet derived growth factor; Pgrmc1, progesterone receptor membrane component-1; PR, progesterone receptor; PSA, polysialic acid; SERM, selective estrogen receptor modulator; StAR, steroidogenic acute regulatory protein; STEAR, selective tissue estrogenic activity regulator; S100B, S100 calcium binding protein B; TGF, transforming growth factor; TNF, tumor necrosis factor; TSPO, translocator protein 18 kDa.

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1. Introduction

The brain and the endocrine glands are in a continuous cross-talk to maintain the homeostatic equilibrium of the organism. Brain function is regulated by multiple hormonal signals emanating from all the endocrine organs of the body. In turn, the central nervous system (CNS) regulates the activity of the peripheral glands through the release of hypothalamic hormones and by the innervation of the endocrine organs. The communication between the brain and the endocrine glands is revealed under both physiological and pathological conditions. Under pathological conditions, endocrine secretions impact on the endogenous neuroprotective and reparative mechanisms activated by brain injury. In turn, brain injury causes alterations in the release of pituitary hormones that result in modifications in the function of endocrine glands (Garcia-Segura, 2009; Powner et al., 2006).

Astrocytes are important players in body-brain communication. Astrocytes participate in the control of endocrine glands, regulating hormonal release by the hypothalamus (Garcia-Segura et al., 2008; Ojeda et al., 2008; Oliet et al., 2001; Rage et al., 1997; Zwain et al., 2002). At the same time, the function of astrocytes and their communication with other cell types within the CNS is regulated by peripheral hormones (Arnold et al., 2008; Fuente-Martín et al., 2012; Garcia-Segura et al., 1996; Micevych et al., 2010; Patel et al., 1989; Sinchak et al., 2003).

Among the multiple hormonal signals that affect the function of astrocytes, gonadal steroid hormones have received special attention in recent years. In addition to regulate reproduction and neuroendocrine events via its actions on the CNS (Micevych and Sinchak, 2008; Micevych et al., 2003), gonadal hormones preserve neural tissue homeostasis and exert trophic and neuroprotective actions. These actions of sex steroids in the CNS include the regulation of a variety of cellular, molecular and functional parameters in astrocytes (Acaz-Fonseca et al., 2014; Karki et al., 2014a,b; Micevych et al., 2010; Tamrakar and Briski, 2015). Here we will review the actions of gonadal steroid hormones on astrocytes under physiological and pathological conditions. Although this review focuses on astrocytes, it is important to consider that the actions of gonadal steroids on astrocytes are exerted in parallel with hormonal actions on other cell types. Gonadal steroid hormones have direct actions on microglia, oligodendrocytes, neurons and endothelial cells that may contribute to alter the function of astrocytes (Chen and Lee, 2013; Habib et al., 2013; Habib et al., 2014b; Hirahara et al., 2013; Lee et al., 2012a,b; Lei et al., 2014; Nevzati et al., 2015; Parkash et al., 2015; Patel et al., 2013; Ruiz-Palmero et al., 2013). In turn, the actions of gonadal hormones on astrocytes may have important consequences for the function of the other cell types in the CNS.

2. Glial cells in the central nervous system

The existence of glial cells in the CNS was first described in 1856 by Rudolph Virchow. He observed the presence of an interstitial component or conjunctive tissue in the CNS, wrapping neuronal processes and he named it as *Nervenkitt* or neuroglia. Later, in 1865, Otto Deiters was the first researcher to discover non-neuronal cells in the white matter. Camillo Golgi was able to observe the detailed morphology of distinct cell types, including glial cells, in the CNS by using his silver nitrate impregnation method (1885–1886). He described glial cells as arachnoid or stellate conjunctive cells. Later, in 1893, Michael Van Lenhossek used the term “astrocytes” to define stellate-like neuroglial cells, and William Lloyd Adriezen classified glia as fibrous, those cells present in white matter, and protoplasmic, present throughout the grey matter. Fibrous glia are characterized by their stellate morphology with thin, large and poorly ramified processes, while protoplasmic glia present numerous and short prolongations. Later, Santiago Ramón y Cajal named these two cell types as astrocytes and later described the presence of a third cellular element in the CNS (1913), besides astrocytes and neurons. In 1921, Pío del Río Hortega, a Cajal’s fellow, discovered that this “third element” was composed by two different cell types: microglia and oligodendrocytes. He initially defined these cells as interfascicular glia. In parallel, Penfield (1924) published a report about oligodendroglia. At the beginning of 20th century, it was finally defined that these three cell types would be named as astrocytes, microglia, and oligodendrocytes, and it was observed that the relative proportion of each cell type varied between species, brain regions and age. More recently a fourth type of glial cells has been described, known as NG2 cells or polydendrocytes (Levine et al., 1993; Stallcup et al., 1983; Wilson et al., 1981). These cells are widely distributed throughout the brain parenchyma and are characterized by the expression of the NG2 antigen and the alpha receptor for platelet-derived growth factor (Pdgfra) (Nishiyama, 2007; Nishiyama et al., 1996). NG2 cells are precursors for myelinating oligodendrocytes (Polito and Reynolds, 2005; Raff et al., 2016; Watanabe et al., 2002; Zhu et al., 2008), but they are also involved in maintaining brain homeostasis through different mechanisms that are still being investigated (Birey et al., 2015; Dimou and Gallo, 2015; Hill and Nishiyama, 2014; Nishiyama et al., 2015).

Finally, tanycytes constitute a small population of glial cells located around the third ventricle and in the cicumventricular

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