Hormones, Gender, And The Aging Brain: The Endocrine Basis Of Geriatric Psychiatry

Physiol Rev 95: 785–807, 2015
Published June 24, 2015; doi:10.1152/physrev.00036.2014

ESTROGEN EFFECTS ON COGNITIVE AND SYNAPTIC HEALTH OVER THE LIFECOURSE

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Fishberg Department of Neuroscience and Kastor Neurobiology of Aging Laboratories, Friedman Brain Institute, Department of Geriatrics and Palliative Medicine, Graduate School of Biomedical Sciences, Icahn School of Medicine at Mount Sinai, New York, New York; and Harold and Margaret Milliken Hatch Laboratory of Neuroendocrinology, The Rockefeller University, New York, New York

Hara Y, Waters EM, McEwen BS, Morrison JH. Estrogen Effects on Cognitive and Synaptic Health Over the Lifecourse. *Physiol Rev* 95: 785–807, 2015; Published June 24, 2015; doi:10.1152/physrev.00036.2014.—Estrogen facilitates higher cognitive functions by exerting effects on brain regions such as the prefrontal cortex and hippocampus. Estrogen induces spinogenesis and synaptogenesis in these two brain regions and also initiates a complex set of signal transduction pathways via estrogen receptors (ERs). Along with the classical genomic effects mediated by activation of ER α and ER β, there are membrane-bound ER α, ER β, and G protein-coupled estrogen receptor 1 (GPER1) that can mediate rapid nongenomic effects. All key ERs present throughout the body are also present in synapses of the hippocampus and prefrontal cortex. This review summarizes estrogen actions in the brain from the standpoint of their effects on synapse structure and function, noting also the synergistic role of progesterone. We first begin with a review of ER subtypes in the brain and how their abundance and distributions are altered with aging and estrogen loss (e.g., ovariectomy or menopause) in the rodent, monkey, and human brain. As there is much evidence that estrogen loss induced by menopause can exacerbate the effects of aging on cognitive functions, we then review the clinical trials of hormone replacement therapies and their effectiveness on cognitive symptoms experienced by women. Finally, we summarize studies carried out in nonhuman primate models of age- and menopause-related cognitive decline that are highly relevant for developing effective interventions for menopausal women. Together, we highlight a new understanding of how estrogen affects higher cognitive functions and synaptic health that go well beyond its effects on reproduction.

I. INTRODUCTION

Estrogen receptors were first identified by radioautography in the rodent hypothalamus after the introduction of tritium-labeled steroid hormones and the discovery of the nuclear receptor mechanism of steroid hormone action (reviewed in Refs. 90, 169, 252). These receptors were tied to the regulation of reproductive behavior and neuroendocrine function. Nuclear estrogen receptors were only sparsely present outside of the hypothalamus, yet there were many actions of estrogens on brain systems and behaviors unrelated to reproduction and neuroendocrine regulation (reviewed in Ref. 133). Resolution of this inconsistency came via the identification of rapid nonnuclear actions of estrogens and identification of membrane-associated estrogen receptors, first in nonneural cells and subsequently in the brain (reviewed in Ref. 101). The hippocampal formation was the first brain region in which these membrane-associated, nonnuclear forms of the classical estrogen receptor were identified along with signaling pathways (reviewed in Ref. 134). These findings were prompted by the discovery that ovarian hormones modulate and mediate the density of spine synapses in the hippocampus of rodents and later of rhesus monkeys. Subsequent investigations revealed the presence of estrogen receptors in many, if not all, brain regions with subcellular localizations in synaptic terminals and dendritic spines, dendritic shafts, axons, mitochondria, and glial cell processes. Cell nuclear labeling in cortical areas is often in inhibitory interneurons. Further investigations of androgen and progestin receptors have revealed both nuclear and nonnuclear forms and locations of classical receptors (reviewed in Ref. 134).

The discovery that ovarian hormones regulate the turnover of a subset of synapses in the hippocampus, along with regulating signaling pathways and neurotransmitter release and actions, has triggered much further investigation showing, among other findings, that the hormonal regulation of synapse turnover is not limited to the hippocampus (re-

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