

Research Report

The expression of brain sexual dimorphism in artificial selection of rat strains

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Abstract

Central nervous system sex differences have two morphological patterns. In one pattern, males show larger measurements (volume, number of neurons) than females (male > female; m > f) and, in the other, the opposite is true (female > male; f > m). The bed nucleus of the stria terminalis (BST) is a unique model for the study of sex differences because it has dimorphic and isomorphic subdivisions, with the former showing the two sexually differentiated morphological patterns. Meanwhile, other CNS structures, like the locus coeruleus (LC), present the f > m pattern. The phylogenetic maintenance of the two patterns of sexual differentiation can help to disentangle the functional meaning of sex differences. Laboratory rat strains, whether albino or pigmented, descend from the Wistar strain through artificial selection. The present work compares the BST and LC of Wistar and Long–Evans rats. The medial posterior subdivision of the BST (BSTMP) is sexually dimorphic (m > f pattern) in the original (Wistar) and derived (Long–Evans) strains, while the lateral anterior and medial anterior subdivisions of the BST and the LC only present sex differences (f > m pattern) in the ancestor Wistar strain. Isomorphic BST regions are the same in both strains. The fact that the BSTMP, which is implicated in male copulatory behavior, is sexually dimorphic in both strains, as well as in other species, including humans, indicates the relevance of this structure in male sexual behavior in mammals.

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1. Introduction

A relevant aspect of any theory on the physiological and behavioral functions of brain sexual dimorphism has to do with its continuance in strains and species. Sex differences in rats have been described with respect to different morphological parameters such as volume, number of cells, shape, and anatomical asymmetry [18–20,24,25,28,29] whether the same (or the homologous) brain nucleus or structure presents sexual dimorphism in several strains or

along the phylogenetic line is very important to help disentangle the functional meaning of sex differences. In this sense, there are brain nuclei, like the sexually dimorphic nucleus of the preoptic area (SDN-POA), that present sexual dimorphism in several species like quails [5,78] and doves [71], or sheep [62], or hamsters [26], and polygamous montane voles [68] and rats [24,25,40], or rhesus monkeys [8], and human beings [38,73].

Comparing brain sexual dimorphism in different strains and species is also important for testing general hypotheses related to sexual dimorphism. For instance, it has been proposed that the Accessory Olfactory (or Vomeronasal) System (VNS), which is related to reproductive behavior

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[33,34], is sexually dimorphic in mammals [27,65–67]. The SDN-POA is contained in the medial preoptic area (MPA), which in turn is a tertiary projection of the vomeronasal organ. To a much lesser extent, sex differences have been demonstrated with respect to the medial posterior division of the bed nucleus of the stria terminalis (BSTMP), a region that has been related to male rat copulatory behavior [9,22]. The BST, a secondary projection structure of the VNS [69], can be a unique model for the study of sex differences and their evolution because it has dimorphic and isomorphic subdivisions in rats and the former present both different morphological patterns, $m > f$ and $f > m$. In the medial posterior subdivision (BSTMP), male Wistar rats show a larger subdivision volume and a higher number of neurons than do females [16,29]. These results have also been reported in the Sprague–Dawley strain [10]. On the contrary, in the lateral and medial anterior subdivisions (BSTLA and BSTMA), females show a larger subdivision volume and/or higher number of neurons than do males [16,29]. The BST also presents several isomorphic regions in the lateral subdivision: the BST lateral posterior region (BSTLP) and the BST lateral juxtacapsular region (BSTLjx). With regards to the BST, and as far as we know, sex differences have been shown in the Wistar [16,29,60] and Sprague–Dawley [10] strains, in guinea pigs [37], in chickens [44], and in human beings [3,46,83].

Another structure, the locus coeruleus (LC), sends rich noradrenergic projections to the VNS [12,76], and it, also, has been demonstrated to be sexually dimorphic in the Wistar strain [28] but not in Sprague–Dawley rats [4]. Moreover, sex differences in the LC have also been reported in humans [7]. In the LC, which is implicated in a variety of physiological and behavioral functions, including reproduction [2,52], Nissl [28,58] and dopamine- β -hydroxylase [49] studies have shown that females have a larger volume and a higher number of neurons than do males. The origin and maintenance of these differences seem to depend on the action of estradiol [14,28].

Laboratory rat strains, whether albino or pigmented, descend from the Wistar strain as a consequence of artificial selection [56,84], a selection process that helped Darwin to understand and then define sexual selection [13]. In the present study, in order to test the consistency of sex differences for structures related to sexual behavior and reproductive physiology, we compare the BST and the LC between Wistar rats and their descendants, the pigmented Long–Evans rat strain.

2. Materials and methods

2.1. Subjects

Adult male and female Wistar rats (Charles River, Criffa; Saint-Aubin-Les-Elbeuf, France) and adult male and female Long–Evans rats (Janvier, Madrid, Spain), weighing 250–300 g, were divided into 4 groups (7 rats each) according to strain (Wistar and Long–Evans) and sex (male and female).

They were housed in standard cages in same-sex and strain groups and maintained in 12:12 light:dark cycle (lights off at 8:00 PM). Food and water were provided ad libitum. The stock room was kept at 22 ± 2 °C. Animal care and handling throughout the experimental procedures were in accordance with the European Community Council Directive of 24 November 1986 (86/609/EEC).

2.2. Histology

At the age of 90 days, the animals were deeply anesthetized with an intraperitoneal injection (250 mg/kg) of tribromoethanol and perfused intracardially with saline (0.9%) followed by 4% paraformaldehyde. The brains were removed and stored in paraformaldehyde for 2 days followed by 3–5 days in 30% sucrose at 4 °C. The brains were frozen and coronally sectioned at a thickness of 50 μ m (fore and midbrain) or 40 μ m (pons and cerebellum). All sections were stained with a 0.1% solution of cresyl violet (Merck) brought to pH 4 with glacial acetic acid.

2.3. Stereology

Stereological methods were used to determine the volume and neuron number of the BST subdivisions and the LC. The Cavalieri principle was used to estimate volume [51] and the total number of neurons was estimated using the disector and fractionator techniques [30,31,72]. To measure these morphological parameters, we used a Diaplan Leitz microscope with a computer-controlled stage (MultiControl 2000; Mörzhäuser Wetzlar, Germany) allowing randomly chosen steps to be generated on the x and y axes. This specially fitted rotating stage allows the slices to be shifted by 360°, independently of the x – y movements. The stereological software package (GRID; Interactivision, Denmark) makes it possible to superimpose the required grid patterns over the microscope image. Finally, an electronic microcator (Heidenhain, Germany) with a resolution of 0.5 μ m is attached to the microscope so the z axis measurements of the stage can be taken.

The BSTMA, BSTLA, BSTMP, BSTLP, BSTLjx, and LC volumes were estimated using the classic Cavalieri principle [51]. On each coronal section (only every other section, with first one being randomly selected), a set of points (generated by the GRID system) was systematically placed and the points that coincided within the area studied were counted. The total volume was obtained by multiplying the number of points by the area associated with each point and by the distance between two sections counted. This distance was obtained from the product of the cut thickness (50 μ m BST, 40 μ m LC) multiplied by the sampling interval.

The number of neurons in the BSTMA, BSTLA, BSTMP, BSTLP, BSTLjx, and LC was estimated using the optical fractionator, which combines the optical disector and fractionator techniques [30,31,72]. The sections were cut with a cryostat to a thickness of 50 μ m (BST) and 40 μ m (LC), but their actual width after using the microcator was

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