Anatomical and Neurochemical Definition of the Nucleus of the Stria Terminalis in Japanese Quail (Coturnix japonica)


Department of Anatomy, Pharmacology, and Forensic Medicine, University of Torino, 10126 Torino, Italy
Laboratory of Biochemistry, University of Liège, 4020 Liège, Belgium
Institute for Small Animal Research, Federal Research Center of Agriculture, 29223 Celle, Germany

ABSTRACT

This study in birds provides anatomical, immunohistochemical, and hodological data on a prosencephalic region in which the nomenclature is still a matter of discussion. In quail, this region is located just dorsal to the anterior commissure and extends from the level of the medial part of the preoptic area at its most rostral end to the caudal aspects of the nucleus preopticus medialis. At this caudal level, it reaches its maximal elongation and extends from the ventral tip of the lateral ventricles to the dorsolateral aspects of the paraventricular nucleus. This area contains aromatase-immunoreactive cells and a sexually dimorphic population of small, vasotocinergic neurons. The Nissl staining of adjacent sections revealed the presence of a cluster of intensely stained cells outlining the same region delineated by the vasotocin-immunoreactive structures. Cytoarchitectonic, immunohistochemical, and in situ hybridization data support the notion that this area is similar and is probably homologous to the medial part of the nucleus of the stria terminalis of the mammalian brain. The present data provide a clear definition of this nucleus in quail: They show for the first time the presence of sexually dimorphic vasotocinergic neurons in this region of the quail brain and provide the first detailed description of this region in an avian species. J. Comp. Neurol. 396:141–157, 1998.

The bed nucleus of the stria terminalis (BST) has been studied intensively in mammals, whereas its location and characteristics are still a matter of discussion in other classes of vertebrates. Traditionally, this nucleus has been divided into a medial and a lateral subdivision (Krettek and Price, 1978; De Olmos et al., 1985) that consist of several subnuclei (Del Abril et al., 1987; Moga et al., 1989; Hines et al., 1992). The medial subdivision (BSTm) is part of the circuitry that controls mating behavior. It receives inputs from the accessory olfactory bulb and the medial amygdala, and it sends projections to the medial preoptic area and the ventromedial hypothalamus (De Olmos and Ingram, 1972; De Olmos et al., 1978; Krettek and Price, 1978; Weller and Smith, 1982; Simerly and Swanson, 1986, 1988; Akesson et al., 1988; Simerly et al., 1989; Canteras et al., 1995). These regions are involved in the control of sexual motivation and/or performance (for recent reviews, see Segovia and Guillamon, 1993; Van Furth et al., 1995). In contrast, the lateral subdivision (BSTl) is characterized by reciprocal connections with nuclei that are involved in central autonomic regulation (for a review of the literature, see Moga et al., 1989).

Several anatomical (Del Abril et al., 1987; Allen and Gorski, 1990; Hines et al., 1992; Segovia and Guillamon, 1993) have studied the BST in avian species. Although the BST has been demonstrated to be present in various avian species (Simerly and Swanson, 1991; Van Furth et al., 1995), its location and characteristics are still a matter of discussion. This is due to the fact that the BST is a complex region that shows a high degree of variability in its anatomical and neurochemical organization. In the present study, we have provided anatomical, immunohistochemical, and hodological data on a prosencephalic region in Japanese quail (Coturnix japonica) in which the nomenclature is still a matter of discussion. This region is located just dorsal to the anterior commissure and extends from the level of the medial part of the preoptic area at its most rostral end to the caudal aspects of the nucleus preopticus medialis. At this caudal level, it reaches its maximal elongation and extends from the ventral tip of the lateral ventricles to the dorsolateral aspects of the paraventricular nucleus. This area contains aromatase-immunoreactive cells and a sexually dimorphic population of small, vasotocinergic neurons. The Nissl staining of adjacent sections revealed the presence of a cluster of intensely stained cells outlining the same region delineated by the vasotocin-immunoreactive structures. Cytoarchitectonic, immunohistochemical, and in situ hybridization data support the notion that this area is similar and is probably homologous to the medial part of the nucleus of the stria terminalis of the mammalian brain. The present data provide a clear definition of this nucleus in quail: They show for the first time the presence of sexually dimorphic vasotocinergic neurons in this region of the quail brain and provide the first detailed description of this region in an avian species.
1993) and neurochemical (Woodhams et al., 1983; Walter et al., 1991) characteristics of the BSTm or of its subdivisions are sexually dimorphic and are organized in early life by steroid hormones (for review, see Guillamon and Segovia, 1997). In particular, sex differences that favor males compared with females affect the number of vasopressin-immunoreactive (VP-ir) neurons and the VP content of BSTm in the rat brain (De Vries et al., 1994a; Wang et al., 1994). Moreover, the rodent BSTm is an important site of testosterone aromatization (transformation of testosterone into 17β-estradiol), as shown by measures of the enzymatic activity and immunocytochemical detection of the protein (Roselli, 1991; Roselli and Resko, 1993; Jakab et al., 1993; Shinoda et al., 1994; Tsuuo et al., 1994; Foidart et al., 1995a). Recently, the presence of nitric oxide synthase has been demonstrated in many of the nuclei that control the rodent mating behavior, including the BST (Hadeishi and Wood, 1996).

In the rat, the BSTm is one element of the pathway that connects the vomeronasal organ to the preoptic region-hypothalamus; therefore, it is implicated in the control of various aspects of reproductive behavior that are governed by chemosensory stimuli (Segovia and Guillamon, 1993; Guillamon and Segovia, 1997). Several studies indicate that lesions aimed at the rat BST disrupt consummatory and/or motivational aspects of male and female sexual behavior (Emery and Sachs, 1976; Valcourt and Sachs, 1979; Lopez and Carrer, 1982; Claro et al., 1995; Takeo et al., 1995) and impair maternal behavior (Numan and Numan, 1996). Moreover, a recent study suggests that the volume of the central subdivision of the BST, as identified by vasoactive intestinal polypeptide immunoreactivity, is related to gender identity in humans (Zhou et al., 1995). However, despite numerous studies investigating morphological and functional characteristics of the BST in mammals, the definition of the homologous nuclei in other classes of vertebrates is still a matter of controversy.

The Japanese quail is an experimental model that has been employed widely in the study of the neural and endocrine bases of male sexual behavior (for recent reviews, see Balthazart and Foidart, 1993; Panzica et al., 1996b). The action of steroids in the quail preoptic-hypothalamic region is necessary and sufficient to activate male copulatory behavior (Balthazart and Surlemont, 1990a,b); accordingly, this area contains large numbers of cells that express steroid receptors (Watson and Adkins Regan, 1988; Balthazart et al., 1989, 1992b). Aromatization of testosterone into estrogens is a limiting step in the activation of male quail copulatory behavior; consequently, the distribution and regulation of preoptic aromatase (ARO) activity and ARO-containing neurons have been intensively studied (for recent reviews, see Balthazart et al., 1996b; Balthazart, 1997). ARO-ir neurons are present in the nucleus preopticus medialis (POM), the tuberal region, an area dorsal to the anterior commissure (CA), and a V-shaped structure extending from a region ventral to the lateral septal area to the caudal aspects of the POM (Balthazart et al., 1990a,b, 1997; Foidart et al., 1995b). With the exception of the POM, which is outlined clearly by ARO-ir cells and can be observed also in Nissl-stained material, the regions containing ARO-ir cells in the quail brain do not match exactly the structures that have been defined previously based on Nissl-stained sections. Their identification and nomenclature is therefore somewhat unclear.

Numerous peptidergic elements have also been identified within the quail septopreoptic-hypothalamic region (Panzica et al., 1992a; Aste et al., 1997). In particular, several studies have been devoted to the vasotocin (VT)-ir fibers of the POM and of the lateral septum, because these peptidergic structures are sexually dimorphic and steroid-sensitive (Viglietti-Panzica et al., 1992, 1994; Panzica et al., 1996a; Aste et al., 1997; for review see Panzica et al., 1997). However, these studies have paid little attention to the distribution of this neuropeptide in the aforementioned region of the quail brain, which is located between the septum and the caudal aspects of the POM.

In a number of immunocytochemical studies analyzing the distribution of ARO-ir or VT-ir structures in quail and other avian species (fowl, canary, zebra finch), this region was named the nucleus of the stria terminalis (Kiss et al., 1987; Balthazart et al., 1990b; Viglietti-Panzica et al., 1992; Voorhuis and De Kloet, 1992; Foidart et al., 1995b; Shen et al., 1995; Jurkevich et al., 1997). However, the

---

**Abbreviations**

<table>
<thead>
<tr>
<th>Ac</th>
<th>nucleus accumbens</th>
</tr>
</thead>
<tbody>
<tr>
<td>AM</td>
<td>nucleus anterior medialis hypothalami</td>
</tr>
<tr>
<td>ARO</td>
<td>aromatase</td>
</tr>
<tr>
<td>BSTm</td>
<td>bed nucleus striae terminalis, pars medialis</td>
</tr>
<tr>
<td>CA</td>
<td>commissura anterior</td>
</tr>
<tr>
<td>CPA</td>
<td>commissura pallii</td>
</tr>
<tr>
<td>DLA</td>
<td>nucleus dorsolateralis anterior thalami</td>
</tr>
<tr>
<td>FPL</td>
<td>fasciculus prosencephali lateralis (lateral forebrain bundle)</td>
</tr>
<tr>
<td>GLv</td>
<td>nucleus geniculatus lateralis, pars ventralis</td>
</tr>
<tr>
<td>HA</td>
<td>hyperstriatum accessorium</td>
</tr>
<tr>
<td>HP</td>
<td>hippocampus</td>
</tr>
<tr>
<td>HV</td>
<td>hyperstriatum ventrale</td>
</tr>
<tr>
<td>ir</td>
<td>immunoreactive</td>
</tr>
<tr>
<td>LA</td>
<td>nucleus lateralis anterior thalami</td>
</tr>
<tr>
<td>LHV</td>
<td>nucleus lateralis hypothalami</td>
</tr>
<tr>
<td>LPO</td>
<td>lobus parolfactorius (medial part of the dorsal striatum)</td>
</tr>
<tr>
<td>LV</td>
<td>lateral ventricle</td>
</tr>
<tr>
<td>N</td>
<td>neostriatum</td>
</tr>
<tr>
<td>nCPa</td>
<td>nucleus commissurae pallii</td>
</tr>
<tr>
<td>NI</td>
<td>neostriatum intermedium</td>
</tr>
<tr>
<td>OM</td>
<td>occipitomesencephalic tract</td>
</tr>
<tr>
<td>PA</td>
<td>paleostriatum augmentatum (lateral part of the dorsal striatum)</td>
</tr>
<tr>
<td>POA</td>
<td>nucleus preopticus anterior</td>
</tr>
<tr>
<td>POM</td>
<td>nucleus preopticus dorsalis</td>
</tr>
<tr>
<td>PP</td>
<td>paleostriatum primitivum (dorsal pallidum)</td>
</tr>
<tr>
<td>PVN</td>
<td>nucleus paraventricularis</td>
</tr>
<tr>
<td>OF</td>
<td>tractus quintofrontalis</td>
</tr>
<tr>
<td>ROT</td>
<td>nucleus rotundus</td>
</tr>
<tr>
<td>SCNI</td>
<td>nucleus suprachiasmaticus, pars lateralis</td>
</tr>
<tr>
<td>SCNm</td>
<td>nucleus suprachiasmaticus, pars medialis</td>
</tr>
<tr>
<td>SL</td>
<td>nucleus septal lateralis</td>
</tr>
<tr>
<td>SM</td>
<td>nucleus septal medialis</td>
</tr>
<tr>
<td>Tn</td>
<td>nucleus taeniae</td>
</tr>
<tr>
<td>TPO</td>
<td>area temporoparietooccipitalis</td>
</tr>
<tr>
<td>TSM</td>
<td>tractus septomesencephalicus</td>
</tr>
<tr>
<td>VML</td>
<td>nucleus ventromedialis hypothalami</td>
</tr>
<tr>
<td>VP</td>
<td>ventral paleostriatum (ventral pallidum)</td>
</tr>
<tr>
<td>VT</td>
<td>vasotocin</td>
</tr>
</tbody>
</table>
One series was stained with toluidine blue for Nissl that sections placed in the same well were 90 µm apart. Sections were collected in three separate series, so were collected in multiwell plates filled with PBS. Addition with a solution containing 20% sucrose in PBS, brains were dissected brains were postfixed in the same fixative for 12 hours at 4°C and washed with 0.01 M phosphate buffer.

Brains were cut in 30-µm-thick coronal sections that were placed in 4% paraformaldehyde in 0.1 M phosphate buffer, pH 7.2. The boundaries and exact localization of the BST and its position relative to the nucleus accumbens, therefore, have not been defined consistently in different studies (compare Brauth et al., 1978; Reiner et al., 1983; Kitt and Brauth, 1986a,b; Berk, 1987; Anderson and Reiner, 1991; Veenman et al., 1995). There has been also a lack of detailed anatomical investigations describing the full extent of this nucleus, which probably explains the discrepancies in the nomenclature of this region across and within the avian species.

Neurochemical markers provide a useful method to analyze homology between brain structures (Gahr, 1997). Therefore, the present study was designed to provide a detailed description of this region in quail and attempts to establish its homology with the mammalian BSTm based on topographical and neurochemical criteria. Special attention was paid here to the VT-ir and ARO-ir structures that are clear anatomical markers of the BSTm in mammals.

MATERIALS AND METHODS

Subjects

The experiments described in this paper were carried out on adult male and female Japanese quail (Coturnix japonica) that were obtained from local breeders in Belgium (Dujardin Farms, Lierneu) or Italy (Morni, Modena). Throughout their life, they received water and food ad libitum and were submitted to a photoperiod of 16 hours of light and 8 hours of darkness. All experimental procedures have been reviewed by the appropriate authorities and are in compliance with the relevant laws and regulations of Italy, Germany, and Belgium that govern the treatment of experimental animals.

Immunocytochemistry

Seven male and seven female quail were used for immunocytochemical investigations. They were injected with 0.1 ml of heparin solution (30 mg/ml; Sigma, St. Louis, MO) into the wing vein and deeply anaesthetized with an overdose of Hypnodil (50 mg/kg; Janssen Pharmaceutica, Beerse, Belgium). The animals were then perfused intracardially with a saline solution followed by 4% paraformaldehyde in 0.1 M phosphate buffer, pH 7.2. The dissected brains were postfixed in the same fixative for 12 hours at 4°C and washed with 0.01 M phosphate buffer containing 0.125 M NaCl, pH 7.2 (PBS). After cryoprotection with a solution containing 20% sucrose in PBS, brains were rapidly frozen on dry ice and stored at −80°C.

Brains were cut in 30-µm-thick coronal sections that were collected in multiwell plates filled with PBS. Adjacent sections were collected in three separate series, so that sections placed in the same well were 90 µm apart. One series was stained with toluidine blue for Nissl material, and two series were submitted to immunocytochemical procedures.

Sections were stained by immunocytochemistry for VT and ARO by using procedures that have been described in previous studies (Aste et al., 1995; Foidart et al., 1995b). Briefly, after a 30-minute wash in PBS containing 0.2% Triton X-100 (PBST) and inhibition of endogenous peroxidase activity by an incubation in hydrogen peroxide, sections were incubated with normal serum (Vectastain Elite Labtek; Vector Laboratories, Burlingame, CA) for 20 minutes at room temperature. Adjacent sections were then incubated overnight at room temperature in a primary antibody diluted in PBST (anti-VT, 1:8,000; anti-ARO, 1:1,000).

The polyclonal anti-VT serum was developed originally by Dr. D. Gray at the Max Plank Institute of Clinical and Physiological Research of Bad Nauheim, Germany (Gray and Simon, 1983). The characteristics and specificity of this antibody for the detection of quail VT were reported in a previous study (Viglietti-Panzica et al., 1994). The polyclonal anti-ARO serum (kindly provided by Dr. N. Harada, Fujita Health University, Toyoake, Japan) was raised in rabbit against quail recombinant ARO, as described by Foidart et al. (1995b).

On the next day, sections were incubated for 45 minutes in a secondary biotinylated antibody and for 30 minutes in an avidin-biotin-peroxidase complex (Vectastain Elite Labtek; Vector Laboratories). The peroxidase activity was revealed with a solution containing 0.187 mg/ml 3,3'-diaminobenzidine and 0.003% hydrogen peroxide in 0.05 M Tris-HCl, pH 7.6. Several rinses in PBS were made after each step. The sections were mounted on slides, dehydrated, and coverslipped with Entellan (Merck, Milano, Italy). The sections were photographed with a Zeiss Axiosplan microscope (Thornwood, NY) with a Kodak Wratten 44 or 75 gelatine filter (Eastman Kodak, Rochester, NY) to increase the contrast.

In situ hybridization

Five adult male and five adult female quail were killed by decapitation. The brains were quickly dissected and frozen on dry ice. Coronal sections were cut on a cryostat at 20 µm thickness, serially collected on 3-aminopropylsilane-coated slides, and fixed by immersion for 5 minutes in 4% paraformaldehyde in 0.1 M phosphate buffer, pH 7.2.

After dehydration, the slides were incubated for 2 hours at 52°C in prehybridization buffer (50% formamide, 5/ Denhardt’s solution, 0.75 M NaCl, 25 mM PIPES, 25 mM EDTA, 0.2% sodium dodecylsulfate [SDS], 10 mM DTT, and 250 µg/ml herring sperm DNA). The hybridization proceeded overnight at 52°C in prehybridization buffer plus 10% sodium dextran sulfate. The AVT-specific probe (a 260-bp cDNA directed toward the 3’ distal part of the chicken AVT gene; Hamann et al., 1992) was labeled with [35S]dCTP by using the random priming method (Megaprime DNA labeling system; Amersham, Buckingham, Germany). Approximately 4,000 cpm/µl of [35S]dCTP-labeled probe were used for each section. The specificity of this probe for quail AVT mRNA was described in a previous study (Aste et al., 1996).

Sections were then washed three times in 5× standard saline citrate (SSC; 3 M NaCl, 0.3 M Na-citrate, pH 7.0), washed three more times in 2× SSC at room temperature for 5 minutes, and dried under a vacuum. Slides were
coated with autoradiography emulsion (LM-1; Amersham, Little Chalfont, UK) and exposed for 4 days at 6°C. The sections were finally counterstained with Toluidine blue to help in the identification of brain nuclei. They were photographed on a Leitz Diaplan microscope (Wetzlar, Germany) by using darkfield illumination.

The nomenclature used in this study is based largely on the chicken atlas of Kuenzel and Masson (1988) with some modifications, according to our previous studies on the quail preoptic region (Panzica et al., 1991, 1996b), and on some recent studies on the pigeon prosencephalon (Veenman et al., 1995; Medina and Reiner, 1997). The drawings in Figure 1 summarize the distribution of nuclei in the quail prosencephalon as they are used in this paper. Discussion of some of the choices made for nomenclature can be found below (see Results and Discussion).

RESULTS

VT Immunoreactivity in males

The septopreoptic-hypothalamic area of male quail contains several discrete clusters of VT-ir structures (cells and fibers). In agreement with previous observations on quail (Viglletti-Panzica, 1986; Panzica et al., 1992a, 1996a; Viglletti-Panzica et al., 1992, 1994; Aste et al., 1997), VT-ir fibers are observed in the lateral septum, the periventricular hypothalamus, and the tuberal region. In particular, at the level of the preoptic area, a dense cluster of VT-ir fibers outlines the whole POM throughout its entire rostral-to-caudal extent (Viglletti-Panzica et al., 1994). VT-ir neurons are found in a periventricular position, lining the ependymal wall of the third ventricle, close to the pial surface of the preoptic area and in the nucleus paraventricularis. They are also seen more laterally in the lateral and dorsal thalamic areas (see Fig. 2E–H).

In addition, VT-ir cells and fibers are observed in a discrete area located above and caudal to the anterior commissure, where they have never been described in detail previously in the quail brain. This region, as discussed below, corresponds to an identifiable cell cluster in Nissl-stained sections (Fig. 2A–D). This cluster has been named nucleus of the stria terminalis in a number of previous publications, but this identification was never evaluated critically. It is the purpose of the present paper to provide neurochemical criteria confirming and specifying this nomenclature. In this section, we describe the data and use the term BSTm without making any additional comments on the name. In the Discussion, a critical evaluation of this decision is presented.

VT-ir structures are present in the entire area connecting the lateral septum with the medial preoptic region. However, they are distributed heterogeneously, and higher densities of immunoreactive structures are observed in the BSTm. These structures are located ventral to the septal area and extend in the rostrocaudal direction from about 100 μm rostral to the CA to sections located 200–300 μm caudal to the commissure and above the level of the peroxidase reaction.

In slightly more caudal sections, where the first signs of the CA become visible, this cluster expands to form a larger structure that also contains a few scattered, immunopositive cell bodies (Figs. 2E, 3C,E). When the CA reaches its full extension, VT-ir cells are seen in larger numbers above the commissure, and the cluster of VT-ir fibers extends above and below the commissure (Figs. 2F, 3G). More caudally, in sections where the CA is reduced or is no longer visible, numerous vasotocinergic cells and fibers cover an ovoid area that is positioned in oblique manner (dorsolateral-to-ventromedial direction) and border the dorsal edge of the occiptomesencephalic tract (OM) and of the lateral forebrain bundle (FPL; Figs. 2G,H, 4B,F, 5B,D). The most rostral aspect of this ovoid structure merges at its ventral edge with the most dorsal and caudal aspects of the VT-ir structures, identifying the POM (Figs. 2G, 3G). This cluster of VT-ir cells and fibers suddenly disappears in more caudal sections. The VT-ir fibers defining the BSTm (Figs. 3E, 4D) are associated only with a few punctate structures. These VT-ir fibers are often organized in basket-like ring structures around immunonegative cells (Fig. 4D).

Scattered VT-ir cells are also present in the most caudal aspects of the POM at the level of the CA (Figs. 2E–G, 3G, 4B,C). These cells are similar morphologically to those observed in the BSTm (Figs. 3E, 4D, 5D). Although the VT-ir cells are not distributed homogeneously in the BSTm, and although they increase in number as one progresses in rostrocaudal direction (compare Fig. 3E with Fig. 5D), their morphological characteristics are similar in the entire region. These cell bodies are round or slightly elongated, mainly bipolar, and their diameter ranges between 5 μm and 12 μm. The density of the immunoreactive material in these cells is variable (Figs. 4C, 5D), but, in general, it is lower than in the magnocellular elements observed in the lateral, periventricular, and subpial groups (Fig. 3G; see also Viglletti-Panzica, 1986; Viglletti-Panzica et al., 1994).

Distribution of VT mRNA in males

Detection of mRNA for VT by using in situ hybridization revealed a distribution of large and small elements that is in agreement with a previous study (Aste et al., 1996). Magnocellular elements were observed bordering the third ventricle wall and were also found in a more lateral position (Fig. 6B,D). In addition, smaller and weakly labeled cells were revealed by using in situ hybridization in the septopreoptic region and had a general distribution that was similar to that of the VT-ir cells described above in the BSTm and the POM. In particular, a group of VT gene-expressing cells could be observed easily that corresponded topographically to the group of VT-ir cells located just above the CA from the rostral edge of this structure to a level slightly caudal to the end of the POM (Fig. 6B,D).

The small variation in the number of VT-ir cells that has been described in the rostrocaudal extent of the BSTm based on the immunocytochemistry could also be observed at the level of the mRNA. More VT gene-expressing cells were observed in the caudal portion (Fig. 6D) than in the rostral portion of the BSTm (Fig. 6B). In situ hybridization also confirmed the presence of VT gene-expressing cells in the caudal part of the POM (Fig. 6B,D).

Sexual dimorphism of vasotocinergic structures

A qualitative sexual dimorphism in the number of VT-ir cells could be observed in the entire BSTm. VT-ir cells were detectable only in males (compare Figs. 3G, 4F, 5B,D, and 7A–D), and no VT-ir cell body could be observed in this area of the female brain, even after prolonged development of the peroxidase reaction.
Fig. 1. A–H: Schematic drawings throughout the rostral to caudal (A through H) prosencephalon of the Japanese quail illustrating the organization of the preoptic and telencephalic nuclei in this species. Hatched areas represent the major fiber tracts of the region. The nomenclature used in these drawings is based largely on the chicken atlas of Kuenzel and Masson (1988), with some more recent modifications for the preoptic region (Panzica et al., 1991, 1996b) and the limbic system (Veenman et al., 1995; Medina and Reiner, 1997). For abbreviations, see list.
Fig. 2. A–D: Schematic drawings of Nissl-stained sections throughout the male quail septopreoptic-hypothalamic area, including the medial part of the bed nucleus of the stria terminalis (BSTm) throughout its rostrocaudal extent. Shaded areas indicate the presence of Nissl-stained cell clusters. E,F: Schematic distribution of the vasotocin-immunoreactive (VT-ir) cells in the quail septopreoptic region. Small and large dots indicate the parvocellular and magnocellular perikarya, respectively. I–L: Distribution of aromatase (ARO)-ir cells (triangles) in the quail septopreoptic region. LV, lateral ventricle; BSTi, lateral part of the bed nucleus of the stria terminalis; nCPa, nucleus of the pallial commissure; POM, medial preoptic nucleus; CA, anterior commissure; FPL, lateral forebrain bundle. For other abbreviations, see list.
Fig. 3. A: Low-power enlargement of a Nissl-stained section of the male quail septopreoptic area. Arrow indicates the rostral pole of the bed nucleus of the stria terminalis (BSTm). The relationship of this region (arrow) with the lateral septum, the lateral ventricle, and the anterior commissure can be appreciated. B,C: Consecutive sections illustrating the clustered, Nissl-stained cells (B) and vasotocin (VT)-ir structures (C) in the rostral part of the BSTm. The two arrows indicate two blood vessels for reference. The VT-ir elements in C (identified by the dashed line) cover the denser Nissl-stained region that is observed in B (dashed line). D: High magnification of aromatase (ARO)-ir elements in the BSTm that are visible in F. E: High magnification of the VT-ir cells and fibers shown in C. Small bipolar elements are visible (arrows) among the network of positive fibers. F,G: Topographical correspondence between the ARO-ir neurons (F) and VT-ir structures (G) in the medial preoptic nucleus (POM) and in the BSTm in adjacent sections. Asterisks indicate the lateral ventricle and the third ventricle. CA, anterior commissure; FPL, lateral forebrain bundle. For abbreviations, see list. Scale bars = 200 µm in A,B,C, 100 µm in D–G.
Fig. 4.  
A: Nissl-stained section at the level of the pallial commissure (CPa). The medial preoptic nucleus (POM) and the bed nucleus of the stria terminalis (BSTm) are at caudal levels, where they merge. 
B: Adjacent section showing the distribution of vasotocin (VT)-ir structures. 
C,D: High magnification of VT-ir cells and fibers in the POM (C) and the BSTm (D). Cell bodies are round and weakly stained. A broad network of ir fibers is also present. 
E,F: Consecutive sections representing the caudal BSTm and its merging with the POM. Note the correspondence of the blood vessels (arrows) and their identical relationship between the Nissl-stained cluster of cells (E) and the VT-ir structures (F). Asterisk indicates the third ventricle. Scale bars = 200 µm in A,B,E,F, 100 µm in C,D.
Fig. 5. A–D: Caudal portion of the male quail bed nucleus of the stria terminalis (BSTm). A,C: Distribution of aromatase (ARO)-ir elements. B,D: Distribution of vasotocin (VT)-ir elements. Cells and fibers positive for these two markers are distributed in the same region. ARO-ir cell bodies are more numerous than VT-ir perikarya, whereas the number of VT-ir fibers is higher than the number of ARO-ir fibers. Asterisks in B indicate the large VT-ir elements of the magnocellular system. Scale bars = 200 µm in A,C (also apply to B,D, respectively).
VT-ir fibers also formed a less compact network in females than in males (compare Figs. 3E and 4D with Fig. 7B,D), and VT-ir fibers were often seen surrounding negative cell bodies (compare Fig. 3G,D with Fig. 7B,D) in both sexes.

A sexual dimorphism affecting the vasotocinergic perikarya was also observed at the level of gene expression. The sex difference observed at this level, however, was not as dramatic as the difference observed by using immunocytochemistry. VT gene-expressing neurons were present in the BSTm of both sexes (Fig. 6), but, in males, the density of grains on the autoradiography was obviously higher over each cell than in females, suggesting a sex difference in the amount of expressed mRNA per cell (compare Fig. 6A,C with Fig. 6B,D, respectively). This sex difference did not appear to affect the magnocellular cell bodies.

**Distribution of ARO-ir elements**

In agreement with previously published studies (Balthazart et al., 1990b; Foidart et al., 1994, 1995b), a dense cluster of ARO-ir cells was observed in the septopreoptic region in the exact same location as the dense cluster of VT-ir fibers (Fig. 2I–L). When moving in a rostral-to-caudal direction, this cell group was first observed in sections just rostral to the CA. It then increased progressively in size at the level of the CA (Fig. 2I,J), and, in sections caudal to this commissure, the group of ARO-ir cells appeared as an oblique structure that extended from the ventral tips of the lateral ventricles to the dorsocaudal aspects of the POM, which is also identified by a dense cluster of ARO-ir neurons (Fig. 2K). These two clusters of cells eventually merged to form an extended group of immunoreactive cells and then disappeared abruptly (Fig. 2L).

The analysis of consecutive sections that were immunostained for VT or ARO indicated a clear topographical overlapping between the area covered by the VT-ir structures and the area that contained ARO-ir neurons (compare Figs. 3F and 5A, respectively, with Figs. 3G and 5B). ARO-ir cells were distributed uniformly and showed the same morphological characteristics in the whole area (Fig. 3D, anterior BSTm; Fig. 5C, posterior BSTm). The ARO-ir cells located in this region and those located in the POM were observed to merge at the same rostrocaudal level where the fusion of the VT-ir structures occurred (Fig. 5A,B). It must be stressed that ARO-ir cells were more numerous by far than VT-ir cells in the BSTm.
Analysis of Nissl-stained sections

A comparison of the sections stained by immunocytochemistry with the alternate Nissl-stained sections revealed the presence of a cluster of Nissl-stained cells that had never been identified precisely before the topographical data derived from the immunocytochemical studies were available. This cell group is characterized by a higher cell density than the surrounding area and allows one to define the extension of the BSTm. The cells in this cluster are also stained in a slightly denser manner than in the surrounding area.

Throughout most of the rostrocaudal extent of the BSTm (Fig. 2A–D), a perfect match was observed between the boundaries of this cell cluster: They could be drawn at low magnification based on the distribution of either the VT-ir fibers and cells, the ARO-ir cells, or the densely packed, Nissl-stained cells (compare Figs. 3B and 4A,E, respectively, with Figs. 3C and 4B,F). However, in the rostral part of the region, scattered ARO-containing cells were also present outside the boundaries of the BSTm, and the cluster of Nissl-stained cells was very small and was not easily recognizable. At the very rostral tip of the BSTm (rostral to the beginning of the CA), sometimes, no match could be made between the distribution of the densely packed, Nissl-stained neurons and the distribution of VT-ir fibers.

When it was observed in Nissl-stained sections, the BSTm first appeared at its most rostral level as a dense cell group located above and, to a lesser extent, below the CA (Fig. 2A,B). At this level, the dense cluster of Nissl-stained cells matched perfectly the group of ARO-ir cells, but there was only a partial overlap with VT-ir structures: The correspondence was good in the area dorsal to the CA, but the Nissl-stained cell group located below the CA did not correspond to matching VT-ir material (Fig. 2A,B, E,F,I,J).

Caudal to the CA, the overlap between Nissl staining, ARO-ir cells, and VT-ir cells and fibers was very reliable. The staining of the BSTm increased gradually in a rostrocaudal gradient, reaching a maximum where the BSTm merges with the POM (Fig. 4E). Visual inspection of the sections did not reveal significant cytoarchitectural differences between the Nissl-stained cells of the POM and those of the BSTm (Fig. 4A). When, at their most caudal level, these two nuclei merge, they constitute a single, oblique structure in which no subdivision can be made based on cell characteristics (Fig. 4E).
**DISCUSSION**

The present study describes the location and some neurochemical characteristics of a region of the quail forebrain that has been identified previously by different names. Its rostral portion has been named the dorsal diencephalon, the caudal paleostriatum pars ventralis, or the septal area (Kiss et al., 1987; Voorhuis et al., 1988; Balthazart et al., 1992a; Voorhuis and De Kloet, 1992; Foidart et al., 1995b). This study also provides the first evidence for the presence of a sexually dimorphic population of vasotocinergic neurons within this region of the quail brain. The ARO-ir cells and the VT-ir cells and fibers in this region can be considered as neurochemical markers of a clearly recognizable cluster of Nissl-stained cells that bear the anatomical characteristics of a nucleus. These data further confirm the existence of a dose association between ARO-ir cells and VT-ir fibers that was observed previously in the quail brain (Balthazart et al., 1997).

VP (the mammalian homologue of VT in birds) and ARO are two neurochemical markers of the rat BSTm. This nucleus is also defined as a part of the accessory olfactory pathway due to its afferents, which originate from the medial amygdala. The rat BSTm also shows special topographical relationships with the lateral portion of the CA that are similar to those of the region investigated here. Therefore, the data presented in this paper strongly suggest that the cluster of Nissl-stained neurons that is located dorsal to the CA and that matches the ARO-ir and VT-ir structures fulfills the requirements to be identified as the avian homologue of the BSTm.

**Similarity of connections and of topographical organization**

A detailed description of the olfactory inputs to the septopreoptic region of the avian brain was proposed originally for the pigeon by Zeier and Karten (1971). In that study, the authors defined the stria terminalis as a portion of the dorsal occipitomesencephalic tract (OM) that showed degenerating fibers ending in a region ventral to the lateral septum and the lateral ventricle after lesions of the postero medial archistriatum, including the nucleus taeniae. In more recent studies, which were performed mainly in pigeons, the BST has been described as a distinct, small, round region that bulges into the lateral base of the lateral ventricles throughout nearly the entire rostrocaudal extent of the paraolfactory lobe. At its most caudal level, the BST extends laterally and ventrally toward the archistriatal complex (see drawings and discussion in Veenman et al., 1995; Medina and Reiner, 1997). However, this region was previously named the nucleus accumbens (Karten and Hodos, 1967; Reiner et al., 1983), whereas the name BST was employed to indicate different parts of the septohypothalamic area or was not used at all in some brain atlases (see above). A recent study (Veenman et al., 1995; see Fig. 1) presented a graphical description of the relative positions of the BST, paraolfactory lobe, and nucleus accumbens in the pigeon basal telencephalon. The same authors also emphasized that some neurochemical characteristics are comparable between the pigeon BST and the mammalian BST (Moga et al., 1989). In particular, both are relatively poor in dopaminergic innervation (Reiner et al., 1994) and in substance P-containing fibers and cells (Reiner et al., 1983), whereas neurotensin fibers and neurons are relatively abundant (Reiner and Carr-away, 1987). In our previous studies in quail, we also demonstrated a paucity of substance P-ir elements as well as a prominent population of corticotropin releasing factor (CRF)-like-positive neurons in the same region (Panzica et al., 1986; Aste et al., 1995). Tract-tracing studies have also demonstrated a peculiar reciprocal connection of pigeon BST with the parabrachial region and with the nucleus of the solitary tract (Arends et al., 1988; Wild et al., 1990). Comparing these data in birds with the wide literature in mammals (for a list of references, see Moga et al., 1989), it appears that many of these characteristics are not typical to the entire BST but chiefly to its lateral portion (BSTl). In particular, the BSTl is distinguished by its reciprocal connections with nuclei involved in central autonomic regulation, including the parabrachial nucleus. Moreover, it is characterized by a large population of CRF- and neurotensin-positive neurons (Moga et al., 1989). Therefore, here, we propose to name this region in the pigeon (and the quail homologue) the BSTl, whereas the area that we have described in the present study would be named the BSTm.

The name BST had been used previously to describe the caudal portion of this region in quail (Balthazart et al., 1990b, 1992a; Panzica et al., 1991, 1994; Foidart et al., 1995b) as well as in other avian species (Kiss et al., 1987; Balthazart et al., 1990b, 1996a; Voorhuis and De Kloet, 1992; Shen et al., 1995; Deviche et al., 1996; Jurkevich et al., 1996, 1997). Topographically, the anterior portions of the quail and the rat BSTm show similar relationships with the lateral ventricle, the septal area, and the caudal portion of this region in quail (Balthazart et al., 1997; Panzica et al., 1991, 1994; Foidart et al., 1995b) as well as in other avian species (Kiss et al., 1987; Balthazart et al., 1990b, 1996a; Voorhuis and De Kloet, 1992; Shen et al., 1995; Deviche et al., 1996; Jurkevich et al., 1996, 1997). Topographically, the anterior portions of the quail and the rat BSTm show similar relationships with the lateral ventricle, the septal area, and the CA. In particular, the BSTm is partitioned at this level by the lateral edge of the CA, which creates a very characteristic anatomical relationship. Similarly, the caudal portion of this nucleus in quail and in mammals forms a structure running from the ventral edge of the lateral ventricle to the dorsolateral aspects of the periventricular region (De Olmos et al., 1985; present study). Thus, overall, the appearance and connectivity of the BSTm in mammals and quail are very similar.

**Neurochemical criteria**

VP has been considered classically to be a useful marker of the medial portion of the BST (De Vries and Buijs, 1983; Millier et al., 1989). However, whether the population of VP-ir cells and fibers is restricted to the BSTm or is only most intense in this region is unclear. In the present study, fibers immunoreactive for VP, the avian homologue of VP, were shown to identify the full extent of the structure that we suggest to be homologous to the mammalian BSTm. We demonstrated also the presence of VT-ir cells in this brain area, which provides an additional similarity with the mammalian BSTm. The distribution of VT- or VP-ir cells follows a similar rostrocaudal gradient in these two nuclei, which are more abundant in their caudal aspects than in their rostral aspects (Van Leeuwen and Caffeé, 1983; Van Leeuwen et al., 1985; present study). This differential distribution allows a distinction between a rostral portion of the nucleus (which shows a relatively low content in VP- or VT-ir cells) and a caudal portion (where these neurons are more abundant).

In the present study, a cluster of intensely Nissl-stained cells was also observed just ventral to the lateral aspects of the CA in a location that is reminiscent of the ventral subdivision of the rat BSTm (Del Abril et al., 1987). This portion of the BSTm contains VP-ir cells in rat (De Vries et
DEFINITION OF THE NUCLEUS OF THE STRIA TERMINALIS IN BIRDS

by A. Steiger, 1994; Wagner and Morrell, 1996). Thus, the presence of a sexual dimorphism in the number of VT-ir fibers in quail depends in this species on an organizational effect of gonadal hormones (Panzica et al., 1997).

The presence of a sexual dimorphism in the number of VT-ir neurons and in the density of the in situ hybridization signal in the quail BSTm provides an additional criterion that supports the homology of this region with the mammalian BSTm. The number of the vasopressinergic neurons in the rat BST, defined by using in situ hybridization or immunocytochemistry for the peptide, is higher in males than in females (Voorhuis et al., 1988). On the other hand, an analogous hormonal treatment performed in gonadectomized female quail fails completely to increase the vasotocinergic immunoreactivity of this region (Viglietti-Panzica et al., 1992). These data suggest that the sexual dimorphism in VT-ir fibers in quail is typical of the mammalian BST (mostly in the BSTm): galanin (Planas et al., 1994) and nitric oxide synthase (Hadeishi and Wood, 1996). A subpopulation of galanin-expressing neurons is associated specifically with VP neurons in the rat BSTm (Planas et al., 1995). In quail, the distribution of galanin and its binding sites have been studied recently (Azumaya and Tsutsui, 1996), but no details have been provided concerning the presence of this peptide in the region of the BST. In contrast, our study of the distribution of nicotinamide adenine dinucleotide phosphate (NADPH)-diaphorase (the enzymatic activity associated with nitric oxide synthase) in the quail brain (Panzica et al., 1994) described a population of positive neurons in a region corresponding to the posterior part of the BSTm (see Fig. 68 in Panzica et al., 1994). In the hamster, NADPH-diaphorase activity is also highly concentrated in the posterior BSTm (Hadeishi and Wood, 1996).

Sex differences

A comparison between the present data and previous studies on other avian species indicates that the presence of a sexual dimorphism in vasotocinergic elements is a common feature of the BST, although interspecific differences do occur (for reviews, see Jurkevich et al., 1996; Panzica et al., 1997). VT-ir cells or VT gene-expressing cells are present in canary, zebra finch, and fowl in a region corresponding to the quail BSTm (Kiss et al., 1987; Voorhuis and De Kloet, 1992; Aste et al., 1996; Deviche et al., 1996; Jurkevich et al., 1997).

Incidentally, it must also be observed that the present study, by using optimized immunocytochemical procedures for VT immunocytochemistry, has identified for the first time the presence of a small number of VT-ir perikarya within the boundaries of the POM. The presence of these cells was confirmed independently by using in situ hybridization. Whether these VT-ir cells located in the POM and BSTm are the origin of the immunoreactive fibers that outline these two nuclei remains to be analyzed experimentally with tract-tracing studies combined with immunocytochemistry.

A high level of ARO activity has been reported to be present in the BST of rats (Roselli et al., 1985; for recent review, see Roselli et al., 1997). Surprisingly, however, immunocytochemical studies have largely failed to identify high numbers of ARO-ir cells in this structure (Sanghera et al., 1991; Shinoda et al., 1994), with the exception of one study by Jakab et al. (1993). This failure must be due to technical problems associated with the relative lack of specificity of antibodies, because more recent work using in situ hybridization has confirmed that the rat BSTm can be identified both during ontogeny and in adulthood by a high density of ARO-expressing cells (Lauber and Lichtensteiger, 1994; Wagner and Morrell, 1996). Thus, the presence of a dense cluster of ARO-ir cells in the quail BSTm, as defined here, provides additional evidence for the homology of this nucleus with the mammalian BSTm.

The presence of ARO-ir cells or VT-ir fibers within the boundaries of a nucleus (as defined by the observation of Nissl-stained sections) had been reported previously only for the POM (Balthazart et al., 1990a; Viglietti-Panzica et al., 1994). Therefore, this nucleus shows considerable similarities with the region investigated in this study. The definition of the boundaries between the POM and the BSTm has always represented a difficult question. In our previous work, we decided to proceed operationally on the premise that the POM ends caudally, where it fuses with the dorsal cell group that we define here as the caudal portion of the BSTm (Panzica et al., 1991). By using neurochemical markers (ARO and VT), it is impossible to distinguish two separate subpopulations at this level. It is possible that the dorsocaudal POM and the ventral portion of the BSTm fuse caudally in a single morphological structure that is still composed of two functionally distinct units. Alternatively the elongated structure might be considered to be entirely part of the BSTm. The cytoarchitectonic and neurochemical criteria used in the present study do not permit differentiation between these two interpretations.

Two other neurochemical markers have been considered to be typical of the mammalian BST (mostly in the BSTm): galanin (Planas et al., 1994) and nitric oxide synthase (Hadeishi and Wood, 1996). A subpopulation of galanin-expressing neurons is associated specifically with VP neurons in the rat BSTm (Planas et al., 1995). In quail, the distribution of galanin and its binding sites have been studied recently (Azumaya and Tsutsui, 1996), but no details have been provided concerning the presence of this peptide in the region of the BST. In contrast, our study of the distribution of nicotinamide adenine dinucleotide phosphate (NADPH)-diaphorase (the enzymatic activity associated with nitric oxide synthase) in the quail brain (Panzica et al., 1994) described a population of positive neurons in a region corresponding to the posterior part of the BSTm (see Fig. 68 in Panzica et al., 1994). In the hamster, NADPH-diaphorase activity is also highly concentrated in the posterior BSTm (Hadeishi and Wood, 1996).
enable us to see these cells in female quail, as suggested by the fact that cells containing a low level of mRNA were detected in the female BSTm. To our knowledge, no study is available so far on the rate of VT gene transcription vs. translation or on the stability of the mRNA for VT in the two sexes of quail. The specific absence of VT mRNA translation in female quail, therefore, cannot be ruled out completely.

**Functional significance of the quail BSTm**

The vasotocinergic system of the quail BSTm that is described in detail in the present study is known to be exquisitely steroid-sensitive (Viglietti-Panzica et al., 1992). A similar sensitivity to steroids has also been demonstrated for the VT-ir fibers in the lateral septum and in the POM (Viglietti-Panzica et al., 1992, 1994; Panzica et al., 1996a). All of these studies demonstrated a prominent effect of testosterone, but it is not known at present whether this steroid needs to be aromatized into an estrogen in order to exert its effects, as shown previously in mammals (De Vries and Duetz, 1984; De Vries et al., 1986, 1994b; Brot et al., 1993). This may be the case, because numerous estrogen receptors containing cells are present in the area (Watson and Adkins Regan, 1988; Balthazart et al., 1989). However, we do not know at this point whether these estrogen receptors are colocalized specifically with VT. The VT-ir innervation of these regions decreases whenever a drop in circulating testosterone occurs, either after surgical castration (Viglietti-Panzica et al., 1992, 1994), after exposure to a short-day photoperiod, or during aging (Viglietti-Panzica et al., 1992; Panzica et al., 1996a). This effect can be reversed completely by testosterone replacement therapy or by exposure to a long-day photoperiod (Viglietti-Panzica et al., 1992, 1994; Panzica et al., 1996a).

The location of VT-ir cells that give rise to the steroid-sensitive fibers innervating the lateral septum, the BSTm, and the POM is unknown. In rat, the vasopressinergic innervation of the lateral septal area is also sexually dimorphic, testosterone-sensitive, and affected by aging (for reviews, see De Vries et al., 1994a; De Vries, 1995). These aspects of the septal vasopressinergic innervation correlate qualitatively with those of VP-ir or VP gene-expressing cells in the BST and in the medial amygdala, so that these two nuclei are supposed to be the major source of the septal vasopressinergic innervation (De Vries et al., 1984, 1994a). Based on the available data in quail, it is impossible to identify the cell bodies that are responsible for the VT-ir innervation of the POM, lateral septum, and BSTm. VT-ir cells are present in large numbers in the caudal part of the BSTm and, to a lesser extent, in the rostral part of this nucleus and in the POM. Tract-tracing studies have demonstrated a reciprocal connection between the POM and the lateral septum (Panza et al., 1992b; Balthazart et al., 1994; Balthazart and Ablsi, 1997), but no evidence is available so far for the existence of projections from the BSTm to the POM and septum. Additional work should be performed to answer this question.

The sex differences and steroid-induced changes in VT immunoreactivity closely parallel changes of male sexual behavior that are observed in the same situations. These correlations suggest that VT is actually implicated in the control of copulatory behavior, as also indicated by hodological and recent pharmacological evidence (Panza et al., 1992b; Balthazart et al., 1994; Balthazart and Ablsi, 1997; Castagna et al., 1998). The specific part of the quail vasotocinergic system that is implicated in behavior control, however, has not been identified so far. Electrolytical lesions or testosterone implantation in the POM exert potent effects on male copulatory behavior in quail, but the same manipulations aimed at the anterior part of the BSTm do not appear to have major behavioral effects (Balthazart and Ball, 1997). In mammals, the BSTm is implicated in the regulation of several behavioral systems, including male copulatory behavior and maternal behavior. This nucleus receives sensory inputs mainly from the olfactory centers and projects to the medial preoptic area. This projection is supposed to modulate the motivational aspects of reproductive activities (Emery and Sachs, 1976; Valcourt and Sachs, 1979; Claro et al., 1995). However, the specific role of the VP circuitry originating in the BST in the control of these behaviors still remains to be demonstrated.

In quail, the presence of afferent connections from the archistriatum to the BSTm (Balthazart and Ablsi, 1997), together with the functional and morphological data collected in mammals, suggests a possible participation of the BST in the elaboration of limbic information. The archistriatum, specifically, the nucleus taeniae (the avian homologue of the medial amygdala of mammals), is known to receive olfactory inputs, at least in pigeon (Reiner and Karten, 1985). The significance of putative olfactory and/or pheromonal inputs to the quail BST, however, remains to be assessed. Although the importance of the olfactory perception in birds is still a matter of discussion, some studies support the hypothesis that olfaction may play a modulatory role in the control of avian reproductive activities or other behaviors (Balthazart and Schoffeniels, 1979; Papi, 1989; Papi, 1990; Burne and Rogers, 1996; Jones and Roper, 1997).

In conclusion, this paper provides a clear anatomical definition and neurochemical characterization of the medial portion of the BST in the quail brain and supports the notion that this nucleus is homologous to the mammalian BSTm. In view of the involvement of the mammalian BSTm in the control of different aspects of reproductive activities, it will be important now to determine whether this structure plays a similar role in the control of quail reproduction.

**ACKNOWLEDGMENTS**

N.A. was a 3-month fellow of ESF in Celle.

**LITERATURE CITED**


Shinoda, K., M. Nagano, and Y. Osawa (1994) Neuronal aromatase expression in preoptic, striatal, and amygdaloid regions during late prenatal
nucleus: A Phascolus vulgaris leucoagglutinin anterograde tract-
Simerly, R.B., B.J. Young, M.A. Capozza, and L.W. Swanson (1989) Estro-
gen differently regulates neuropeptide gene expression in a sexually
diencephalon, and mesencephalon of the canary, Serinus canaria, in
Takeo, T., M. Kudo, and Y. Sakuma (1995) Stria terminalis conveys a
Tsuruo, Y., K. Ishimura, H. Fujita, and Y. Osawa (1994) Immunohistochemi-
cal localization of aromatase-containing neurons in the rat brain during
Valcourt, R.J. and B.D. Sachs (1979) Penile reflexes and copulatory
behavior in male rats following lesions in the bed nucleus of the stria
masculine sexual behaviour: Involvement of brain opioids and dopa-
Van Leeuwen, F.W. and A.R. Caffé (1983) Vasopressin-immunoreactive cell
bodies in the bed nucleus of the stria terminalis of the rat. Cell Tissue Res. 228:525–534.
Van Leeuwen, F.W., A.R. Caffé, and G.J. De Vries (1985) Vasopressin cells in
the bed nucleus of the stria terminalis of the rat: Sex differences and the
corticostriatal projection system: A retrograde and anterograde path-
of vasotocin reading neurons in avian diencephalon. J. Hirnforsch 27:559–566.
Viglietti-Panzica, C., G.C. Anselmetti, J. Balthazart, N. Aste, and G.C.
Panzica (1992) Vasotocinergic innervation of the septal region in the
Japanese quail: Sexual differences and the influence of testosterone.
Vasotocinergic innervation of sexually dimorphic medial preoptic
Voorhuis, T.A.M. and E.R. De Kloet (1992) Immunoreactive vasotocin in the
Testosterone-sensitive vasotocin-immunoreactive cells and fibers in the
regulation of aromatase mRNA expression in the forebrain of adult
male and female rats: A cellular level analysis using in situ hybridiza-
of immunohistochemical markers in the bed nucleus of the stria
differences in the effects of cohabitation on vasopressin messenger RNA
expression in the bed nucleus of the stria terminalis in prairie voles
(Microtus ochrogaster) and meadow voles (Microtus pennsylvanicus).
Brain Res. 650:212–218.
sex steroid-concentrating cells in the Japanese quail (Coturnix ja-
ponica): Autoradiography with (3H)-testosterone, (3H)-estradiol, and
Weller, K.L. and D.A. Smith (1982) Afferent connections to the bed nucleus
branchial nucleus in the pigeon (Columbia livia), J. Comp. Neurol. 293:499–523.
tion of neuropeptides in the limbic system of the rat: The bed nucleus of the stria
terminalis, septum and preoptic area. Neuroscience 8:677–703.
Zeier, H. and H.J. Karten (1971) The archistriatum of the pigeon: Organiza-
tion of afferent and efferent connections. Brain Res. 31:313–326.
difference in the human brain and its relation to transsexuality. Nature
378:68–70.