Neuroscience 135 (2005) 155–179

THE BED NUCLEUS OF THE STRIA TERMINALIS IN THE SYRIAN HAMSTER: SUBNUCLEI AND CONNECTIONS OF THE POSTERIOR DIVISION

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Abstract—The bed nucleus of the stria terminalis is a key part of a ring of cells extending between the centromedial amygdala and bed nucleus of the stria terminalis referred to as the extended amygdala. The present study describes the architecture of the bed nucleus of the stria terminalis and the connections of subnuclei in posterior bed nucleus of the stria terminalis. The hamster bed nucleus of the stria terminalis is readily allotted to anterior and posterior divisions separated by the fibers of the body of the anterior commissure. The anterior division has four subnuclei: anteromedial, anterointermediate, anterolateral, and anteroventral. Within the posterior division, there are three distinct regions: posteromedial, posterointermediate, and posterolateral. In hamsters, the posterior bed nucleus of the stria terminalis contributes to male sexual behavior, particularly chemoinvestigation. Moreover, the posterior bed nucleus of the stria terminalis is part of a neural circuit essential for mating, including the medial amygdaloid nucleus and medial preoptic area. The connections of bed nucleus of the stria terminalis, posteromedial part, bed nucleus of the stria terminalis, posterointermediate part and bed nucleus of the stria terminalis, posterolateral part were visualized by co-injection of anterograde (*Phaseolus vulgaris* leucoagglutinin) and retrograde (cholera toxin B) tract tracers. The bed nucleus of the stria terminalis, posterointermediate part and bed nucleus of the stria terminalis, posteromedial part have dense bidirectional connections with medial amygdaloid nucleus and cortical amygdala via the stria terminalis and ventral amygdalofugal pathway. These subnuclei also maintain bidirectional connections with steroid-concentrating areas including lateral septum, medial preoptic area, hypothalamus, and periaqueductal gray. The bed nucleus of the stria terminalis, posterointermediate part and bed nucleus of the stria terminalis, posteromedial part receive projections from the subiculum and send projections to deep mesencephalic nuclei. By contrast, the bed nucleus of the stria terminalis, posterolateral part is connected with the central amygdala, lateral hypothalamus, subthalamic nucleus, nucleus accumbens, substantia innominata, substantia nigra and thalamus. Thus, the bed nucleus of the stria terminalis, posterointermediate part and bed nucleus of the stria terminalis, posteromedial part have similar connections with areas involved in social behaviors. The bed nucleus of the stria terminalis, posterolateral part maintains connections with areas involved in motivational circuits. This supports the concept of distinct circuits within the extended amygdala which differentially link the centromedial amygdala and bed nucleus of the stria terminalis.

Key words: amygdala, cytoarchitecture, chemoarchitecture, cholera toxin, BDA.

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Abbreviations: AAA, anterior amygdaloid area; aca, anterior limb of the anterior commissure; Acb, accumbens nucleus; ACo, anterior cortical amygdaloid nucleus; AH, anterior hypothalamic area; AHA, amygdalohippocampal area; AI, agranular insular cortex; ARC, arcuate hypothalamic nucleus; AVPe, anteroventral periventricular nucleus; BL, basolateral amygdaloid nucleus; BM, basomedial amygdaloid nucleus; BST, bed nucleus of the stria terminalis; BSTAI, bed nucleus of the stria terminalis, anterointermediate part; BSTAL, bed nucleus of the stria terminalis, anterolateral part; BSTAM, bed nucleus of the stria terminalis, anteromedial part; BSTAV, bed nucleus of the stria terminalis, anteroventral part; BSTPI, bed nucleus of the stria terminalis, posterointermediate part; BSTPL, bed nucleus of the stria terminalis, posterolateral part; BSTPM, bed nucleus of the stria terminalis, posteromedial part; Ce, central amygdaloid nucleus; Cg2, cingulate cortex, area 2; Cl, claustrum; CLi, caudal linear nucleus of the raphe; CPu, caudate putamen (striatum); CTB, cholera toxin beta; DAB, diaminobenzidine; DpMe, deep mesencephalic nucleus; ER, estrogen receptor; f, fornix; fmi, forceps minor of the corpus callosum; GP, globus pallidus; HRP, horseradish peroxidase; IL, infralimbic cortex; La, lateral amygdaloid nucleus; LH, lateral hypothalamic area; LOT, nucleus of the lateral olfactory tract; LPAG, lateral periaqueductal gray; LPO, lateral preoptic area; LS, lateral septal nucleus; LSV, lateral septal nucleus, ventral part; LV, lateral ventricle; Me, medial amygdaloid nucleus; MeA, medial amygdaloid nucleus, anterior part; MeP, medial amygdaloid nucleus, posterior part; MOB, main olfactory bulb; MPN, medial preoptic nucleus; MPNmag, medial preoptic nucleus, magnocellular part; MPO, medial preoptic area; NDB, nucleus of the diagonal band of Broca; NPY, neuropeptide Y; Pa, paraventricular hypothalamic nucleus; PAG, periaqueductal gray; PB, phosphate buffer; PBS, phosphate-buffered saline; Pha-l, *Phaseolus vulgaris* leucoagglutinin; PIR, piriform cortex; PLCo, posterolateral cortical amygdaloid nucleus; PMCo, posteromedial cortical amygdaloid nucleus; PMnR, paramedian raphe nucleus; PMV, premammillary nucleus, ventral part; PPTg, pedunculopontine tegmental nucleus; PrL, prelimbic cortex; PSTh, parasubthalamic nucleus; S, subiculum; SCN, suprachiasmatic nucleus; SI, substantia innominata; sm, stria medullaris; SNC, substantia nigra, compact part; SPFp, subparafascicular thalamic nucleus; st, stria terminalis; vaf, ventral amygdalofugal pathway; VMH, ventromedial hypothalamic nucleus; VP, ventral pallidum; VTA, ventral tegmental area.

The bed nucleus of the stria terminalis (BST) first described by Johnston in the 1920s (Johnston, 1923) is a key part of the "extended amygdala" (reviewed by deOlmos and Heimer, 1999). More recent analysis has described the BST as a ring of cells extending between the centromedial amygdala and preoptic area. Focus on the extended amygdala has increased interest in the role of the BST in a number of physiological and behavioral functions including fluid regulation (Zardetto-Smith et al., 1994), stress mediation (Koolhaas et al., 1998; Marshall and Garakani, 2002), motivation (Schulz and Canbeyli, 2000),

0306-4522/05$30.00+0.00
doi:10.1016/j.neuroscience.2005.05.029

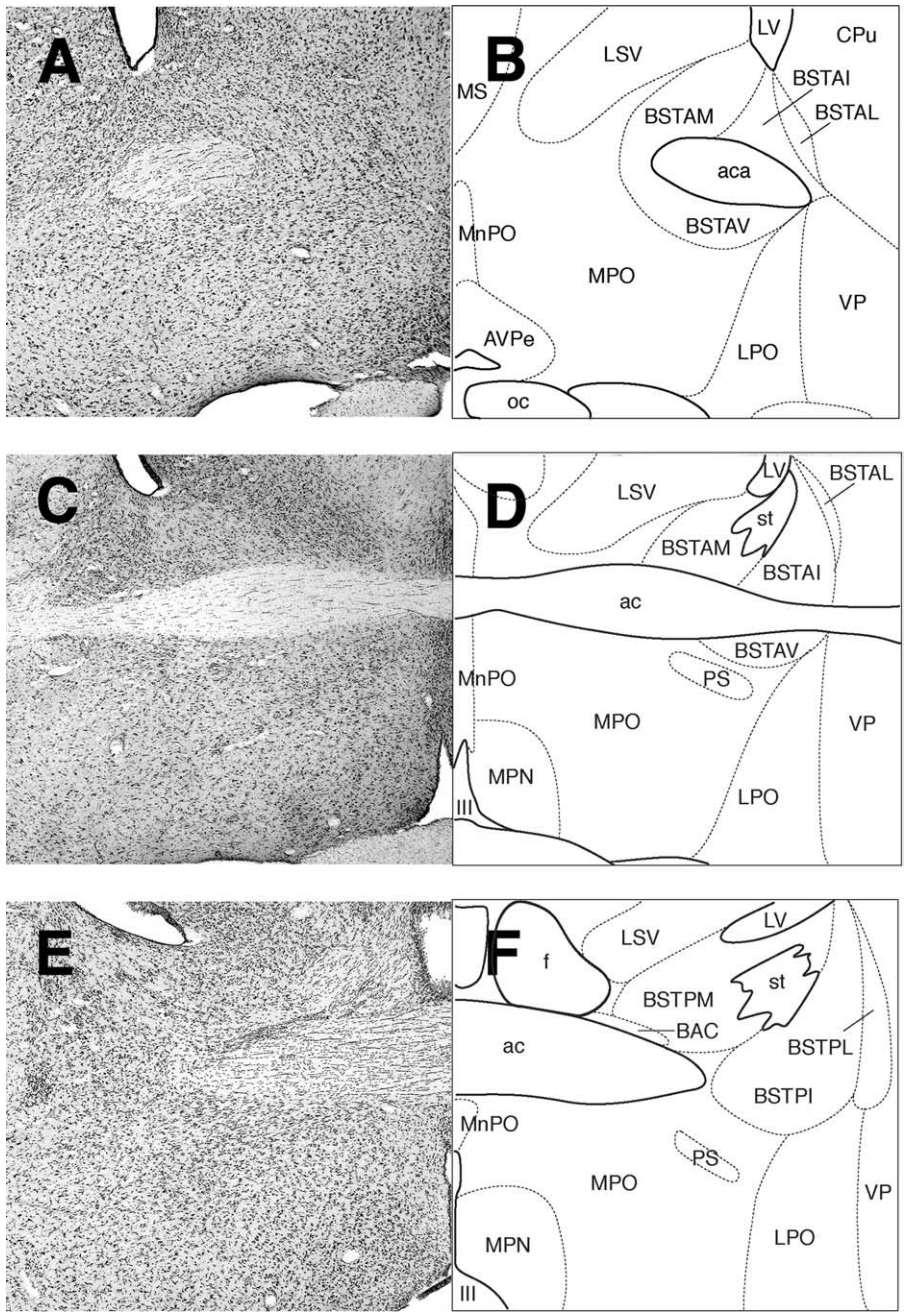

Fig. 1. Photomicrographs of Nissl-stained coronal brain sections in a representative male hamster throughout the rostral-caudal extent of BST illustrating the subnuclei of the anterior (A–D) and posterior (E–L) BST. Sections are spaced about 0.24 mm apart.

copulation (Kollack-Walker and Newman, 1997), parenting (Numan and Sheehan, 1997), and learning and memory (Gewirtz et al., 1998). Lesion studies suggest that these functions can be relegated to different aspects of the BST (Van de Kar, 1996; Powers et al., 1987; Gewirtz et al., 1998). The role of these areas may be tempered by differential connections to the centromedial amygdala. For example the anterior lateral bed nucleus of the stria terminalis (BSTAL) maintains connections with the central nucleus of the amygdala, Ce (Zahm et al., 1999). Both Ce and BSTAL play similar roles in fluid regulation (Johnson et al., 1999), stress (Gray et al., 1993) and fear (Davis, 1998). The medial nucleus of the amygdala maintains bidirectional connections with the posterior BST (Coolen and Wood, 1998). Both Me and posterior BST have been implicated in the regulation of social behaviors, (Joppa et al., 1995; Lehman et al., 1980; Stack et al., 2002; Yahr et al., 1994).

In contrast to the wealth of detailed tract tracing studies of the central (Cassell et al., 1986) and medial amygdaloid nuclei (Gomez and Newman, 1992; Canteras et al., 1995; Coolen and Wood, 1998), only a few