

WHOLE-BRAIN MAPPING OF AFFERENT PROJECTIONS TO THE BED NUCLEUS OF THE STRIA TERMINALIS IN TREE SHREWS

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Abstract—The bed nucleus of the stria terminalis (BST) plays an important role in integrating and relaying input information to other brain regions in response to stress. The cytoarchitecture of the BST in tree shrews (*Tupaia belangeri chinensis*) has been comprehensively described in our previous publications. However, the inputs to the BST have not been described in previous reports. The aim of the present study was to investigate the sources of afferent projections to the BST throughout the brain of tree shrews using the retrograde tracer Fluoro-Gold (FG). The present results provide the first detailed whole-brain mapping of BST-projecting neurons in the tree shrew brain. The BST was densely innervated by the prefrontal cortex, entorhinal cortex, ventral subiculum, amygdala, ventral tegmental area, and parabrachial nucleus. Moreover, moderate projections to the BST originated from the medial preoptic area, supramammillary nucleus, paraventricular thalamic nucleus, pedunculopontine tegmental nucleus, dorsal raphe

nucleus, locus coeruleus, and nucleus of the solitary tract. Afferent projections to the BST are identified in the ventral pallidum, nucleus of the diagonal band, ventral posteromedial thalamic nucleus, posterior complex of the thalamus, interfascicular nucleus, retrorubral field, rhabdoid nucleus, intermediate reticular nucleus, and parvocellular reticular nucleus. In addition, the different densities of BST-projecting neurons in various regions were analyzed in the tree shrew brains. In summary, whole-brain mapping of direct inputs to the BST is delineated in tree shrews. These brain circuits are implicated in the regulation of numerous physiological and behavioral processes including stress, reward, food intake, and arousal. © 2016 Published by Elsevier Ltd on behalf of IBRO.

Key words: prefrontal cortex, amygdala, hypothalamus, hippocampus, ventral tegmental area, parabrachial nucleus.

INTRODUCTION

The bed nucleus of the stria terminalis (BST), surrounding the anterior commissure and anterior to the hypothalamus, is sometimes referred to as a key part of the extended amygdala (de Olmos and Heimer, 1999;

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Abbreviations: 2, layer 2 of cortex; 3, layer 3 of cortex; 10N, dorsal motor nucleus of vagus; 12n, root of hypoglossal nerve; 12N, hypoglossal nucleus; 3N, oculomotor nucleus; 3PC, oculomotor nucleus, parvocellular part; 3V, 3rd ventricle; 4n, trochlear nerve; 4N, trochlear nucleus; 4V, 4th ventricle; 6n, root of abducens nerve; 6N, abducens nucleus; 7N, facial nucleus; 7n, facial nerve; 8cn, cochlear root of the vestibulocochlear nerve; 8vn, vestibular root of the vestibulocochlear nerve; AA, anterior amygdaloid area; Ab, auditory belt area; AB, accessory basal nucleus; Ac, auditory core area; ac, anterior commissure; Acb, accumbens nucleus; AcbC, accumbens nucleus, core; AcbSh, accumbens nucleus, shell; aci, anterior commissure, intrabulbar part; ACo, anterior cortical amygdaloid nucleus; acp, anterior commissure, posterior part; AD, anterodorsal thalamic nucleus; AHi, amygdalohippocampal area; AHy, anterior hypothalamic area; alv, alveus of the hippocampus; AM, anteromedial thalamic nucleus; Amb, ambiguous nucleus; AmbC, ambiguous nucleus, compact part; AOD, anterior olfactory nucleus, dorsal part; AOE, anterior olfactory nucleus, external part; AOL, anterior olfactory nucleus, lateral part; AOM, anterior olfactory nucleus, medial part; AOV, anterior olfactory nucleus, ventral part; AP, area postrema; APT, anterior pretectal nucleus; APTD, anterior pretectal nucleus, dorsal part; APTV, anterior pretectal nucleus, ventral part; Aq, aqueduct; Arc, arcuate hypothalamic nucleus; ArcP, arcuate hypothalamic nucleus, posterior part; ASt, amygdalostriatal transition area; AV, anteroventral thalamic nucleus; B, brachium of the superior colliculus; BLA, basolateral amygdaloid nucleus; BMA, basomedial amygdaloid nucleus; BST, bed nucleus of the stria terminalis; CA1, field CA1 of the hippocampus; CA2, field CA2 of the hippocampus; CA3, field CA3 of the hippocampus; cc, corpus callosum; CC, central canal; Cd, caudate nucleus; CeA, central amygdaloid nucleus; Cg, cingulate cortex; CG, central gray; Cl, claustrum; CLi, caudal linear nucleus of the raphe; CM, central medial thalamic nucleus; CnF, cuneiform nucleus; cp, cerebral peduncle; csc, commissure of the superior colliculus; Cu, cuneate nucleus; cu, cuneate fasciculus; D3V, dorsal 3rd ventricle; das, dorsal acoustic stria; DCN, dorsal cochlear nucleus; DFC, dorsal frontal cortex; DG, dentate gyrus of the hippocampus; DLG, dorsal lateral geniculate nucleus; DMH, dorsomedial hypothalamic nucleus; DpG, deep gray layer of the superior colliculus; DpWh, deep white layer of the superior colliculus; DR, dorsal raphe nucleus; DS, dorsal subiculum; dsc, dorsal spinocerebellar tract; DTg, dorsal tegmental nucleus; dtgx, dorsal tegmental decussation; E, ependyma and subependymal layer; EA, sublentiform extended amygdala; EAC, sublentiform extended amygdala, central part; Ect, entorhinal cortex; ECu, external cuneate nucleus; EGP, external globus pallidus; Ent, entorhinal cortex; EPI, external plexiform layer of the olfactory bulb; EPIA, external plexiform layer of the accessory olfactory bulb; EW, Edinger-Westphal nucleus; f, fornix; FG, Fluoro-Gold; fi, fimbria of the hippocampus; fmi, forceps minor of the corpus callosum; fr, fasciculus retroflexus; g7, genu of the facial nerve; GCL, granule cell layer of the olfactory bulb; Gem, gemini hypothalamic nucleus; Gi, gigantocellular reticular nucleus; GL, glomerular layer of the olfactory bulb; GlA, glomerular layer of the accessory olfactory bulb; Gr, gracile nucleus; GrA, granule cell layer of the accessory olfactory bulb; GrDG, granular layer of the dentate gyrus; Hip, hippocampus; IAM, interanteromedial thalamic nucleus; ic, internal capsule; IC, inferior

Oler et al., 2016). It is organized into several subdivisions (Franklin and Paxinos, 2007; Paxinos and Watson, 2007; Lebow and Chen, 2016). Different BST subdivisions are connected with different parts of the brain in rodents by anterograde and retrograde tracing methods (Dong et al., 2001; Dong and Swanson, 2003, 2004a,b, 2006a, b; Wood and Swann, 2005). The afferent and efferent projections of the BST have been examined in non-human primates (deCampo and Fudge, 2013; Oler et al., 2016), rodents (Dong and Swanson, 2006b; Kudo et al., 2012), cat (Holstege et al., 1985), and pigeon (Berk, 1987; Atoji et al., 2006). These neural circuits indicate the possible role of the BST in addiction-related behaviors (Stamatakis et al., 2014), ingestive behaviors (Dong and Swanson, 2003; Naka et al., 2013), and stress response (Davis et al., 2010; Radley and Sawchenko, 2011).

Tree shrews are day-active animals that live in arboreal habitats in South and Southeast Asia (Peng et al., 1991). According to recent studies, tree shrews are the closest living relatives of primates (Janecka et al., 2007; Kriegs et al., 2007; Fan et al., 2013; McCollum and Roberts, 2014). Many researchers focus on stress-related brain structures of tree shrews using chronic psychosocial stress model, such as the BST, amygdala, hippocampus, and prefrontal cortex (Flugge, 1996; Fuchs and Flugge, 2003; Kozicz et al., 2008; Zambello et al., 2010). However, no information is available regarding the connections between the BST and the latter regions in the tree shrew brain.

Many publications have reported on the brain neuroanatomy of tree shrews (*Tupaia belangeri*) (Airaksinen et al., 1989; Kozicz et al., 2008; Rice et al.,

colliculus; ICj, islands of Calleja; icp, inferior cerebellar peduncle; IF, interfascicular nucleus; IG, indusium griseum; IGL, intergeniculate leaf; IGP, internal globus pallidus; IL, infralimbic cortex; IM, intercalated amygdaloid nucleus, main part; IMD, intermediodorsal thalamic nucleus; InC, interstitial nucleus of Cajal; InG, intermediate gray layer of the superior colliculus; Ins, insular cortex; Int, interposed cerebellar nucleus; InWh, intermediate white layer of the superior colliculus; IO, inferior olive; IPA, interpeduncular nucleus, apical subnucleus; IPAC, interstitial nucleus of the posterior limb of the anterior commissure; IPC, interpeduncular nucleus, caudal subnucleus; IPI, internal plexiform layer of the olfactory bulb; IPL, interpeduncular nucleus, lateral subnucleus; IPR, interpeduncular nucleus, rostral subnucleus; IRd, infraradiata dorsalis; IRt, intermediate reticular nucleus; IRv, infraradiata ventral area; IT, inferior temporal cortex; Lat, lateral cerebellar nucleus; LC, locus coeruleus; LD, laterodorsal thalamic nucleus; LDTg, laterodorsal tegmental nucleus; lfp, longitudinal fasciculus of the pons; LHA, lateral hypothalamic area; LHb, lateral habenular nucleus; LHbL, lateral habenular nucleus, lateral part; LHbM, lateral habenular nucleus, medial part; LL, nucleus of the lateral lemniscus; ll, lateral lemniscus; LM, lateral mammillary nucleus; LMoL, lacunosum moleculare layer of the hippocampus; lo, lateral olfactory tract; LOT, nucleus of the lateral olfactory tract; LPB, lateral parabrachial nucleus; LPO, lateral preoptic area; LRT, lateral reticular nucleus; LSd, lateral septal nucleus, dorsal part; LSi, lateral septal nucleus, intermediate part; LSS, lateral stripe of the striatum; LSv, lateral septal nucleus, ventral part; LV, lateral ventricle; M1, primary motor cortex; M2, secondary motor cortex; MCL, mitral cell layer of the olfactory bulb; mcp, middle cerebellar peduncle; MD, mediodorsal thalamic nucleus; MdD, medullary reticular nucleus, dorsal part; MdV, medullary reticular nucleus, ventral part; ME, median eminence; me5, mesencephalic trigeminal tract; Me5, mesencephalic trigeminal nucleus; MeA, medial amygdaloid nucleus; Med, medial cerebellar nucleus; MFC, medial frontal cortex; MG, medial geniculate nucleus; MGD, medial geniculate nucleus, dorsal part; MGV, medial geniculate nucleus, ventral part; MHb, medial habenular nucleus; MiA, mitral cell layer of the accessory olfactory bulb; MiTg, microcellular tegmental nucleus; ml, medial lemniscus; ML, medial mammillary nucleus, lateral part; mlf, medial longitudinal fasciculus; mlx, medial lemniscus decussation; MM, medial mammillary nucleus, medial part; MnR, median raphe nucleus; MoDG, molecular layer of the dentate gyrus; MPA, medial preoptic area; MPB, medial parabrachial nucleus; MPO, medial preoptic nucleus; MPT, medial pretectal nucleus; MRe, mammillary recess of the 3rd ventricle; mRt, mesencephalic reticular formation; MS, medial septal nucleus; mt, mammillothalamic tract; MT, medial terminal nucleus of the accessory optic tract; Mx, matrix region of the medulla; NDB, nucleus of the diagonal band; oc, olivocerebellar tract; oc/dsc, olivocerebellar tract and dorsal spinocerebellar tract; och, optic chiasm; OFC, orbital frontal cortex; ONL, olfactory nerve layer; Op, optic nerve layer of the superior colliculus; opt, optic tract; OPT, olivary pretectal nucleus; Or, oriens layer of the hippocampus; OV, olfactory ventricle (olfactory part of lateral ventricle); P5, peritrigeminal zone; PaA, paraventricular hypothalamic nucleus, anterior part; PAG, periaqueductal gray; PBG, parabigeminal nucleus; PBP, parabrachial pigmented nucleus of the VTA; PBS, phosphate-buffered saline; PC, paracentral thalamic nucleus; Pc, central nucleus of the pulvinar; pc, posterior commissure; PCRt, parvicellular reticular nucleus; Pd, dorsal nucleus of the pulvinar; Pe, paraventricular hypothalamic nucleus; PeF, perifornical nucleus; PF, parafascicular thalamic nucleus; PG, pineal gland; PH, posterior hypothalamic nucleus; PHA, posterior hypothalamic area; Pir1, piriform cortex, layer 1; PLH, peduncular part of lateral hypothalamus; Pn, pontine nuclei; PN, paranigral nucleus of the VTA; PnC, pontine reticular nucleus, caudal part; PnO, pontine reticular nucleus, oral part; Po, posterior complex of the thalamus; PoDG, polymorph layer of the dentate gyrus; PoMn, posteromedian thalamic nucleus; Post, postsubiculum; pPAG, p1 periaqueductal gray; Ppc, posterior parietal caudal area; Ppd, posterior parietal dorsal area; PPr, posterior parietal rostral area; Pr, prepositus nucleus; Pr5, principal sensory trigeminal nucleus; PrC, precommissural nucleus; PrEW, pre-Edinger-Westphal nucleus; PRh, perirhinal cortex; PrL, prelimbic cortex; PrS, presubiculum; pRt, p1 reticular formation; PT, paratenial thalamic nucleus; PTg, pedunculopontine tegmental nucleus; Pu, putamen; Pv, ventral nucleus of the pulvinar; PVA, parietal ventral area; PVA, paraventricular thalamic nucleus, anterior part; PVN, paraventricular hypothalamic nucleus; PVP, paraventricular thalamic nucleus, posterior part; py, pyramidal tract; Py, pyramidal cell layer of the hippocampus; pyx, pyramidal decussation; Rad, radiatum layer of the hippocampus; Rbd, rhabdoid nucleus; Re, reuniens thalamic nucleus; Rh, rhomboid thalamic nucleus; RLI, rostral linear nucleus of the raphe; RMC, red nucleus, magnocellular part; Ro, nucleus of Roller; RPa, raphe pallidus nucleus; RPC, red nucleus, parvicellular part; RRF, retrorubral field; rs, rubrospinal tract; RSg, retrosplenial granular cortex; Rt, reticular thalamic nucleus; RtTg, reticulotegmental nucleus of the pons; S1, primary somatosensory cortex; S2, secondary somatosensory cortex; s5, sensory root of the trigeminal nerve; SCC, somatosensory caudal cortex; SCN, suprachiasmatic nucleus; scp, superior cerebellar peduncle; scpd, superior cerebellar peduncle, descending limb; SFi, septofimbrial nucleus; SFO, subfornical organ; SGe, supragenual nucleus; SHi, septohippocampal nucleus; SHy, septohypothalamic nucleus; sm, stria medullaris of the thalamus; SNC, substantia nigra, compact part; SNL, substantia nigra, lateral part; SNR, substantia nigra, reticular part; SO, superior olive; Sol, solitary nucleus; SON, supraoptic nucleus; Sp5, spinal trigeminal nucleus; sp5, spinal trigeminal tract; SPTg, subpeduncular tegmental nucleus; SpVe, spinal vestibular nucleus; st, stria terminalis; STh, subthalamic nucleus; SThy, striohypothalamic nucleus; STA, bed nucleus of the stria terminalis, anterior part; STAL, bed nucleus of the stria terminalis, anterolateral part; STAM, bed nucleus of the stria terminalis, anteromedial part; STP, bed nucleus of the stria terminalis, posterior part; STPL, bed nucleus of the stria terminalis, posterolateral part; STPM, bed nucleus of the stria terminalis, posteromedial part; STV, bed nucleus of the stria terminalis, ventral part; str, superior thalamic radiation; Su5, supratrigeminal nucleus; Sub, submedial thalamic nucleus; SubC, subcoeruleus nucleus; SuG, superficial gray layer of the superior colliculus; SuM, supramammillary nucleus; SuML, supramammillary nucleus, lateral part; SuMM, supramammillary nucleus, medial part; sumx, supramammillary decussation; TC, temporal cortex; tpf, transverse fibers of the pons; Tl, temporal inferior area; TS, triangular septal nucleus; th, trigeminothalamic tract; Tu, olfactory tubercle; Tu1, layer 1 of olfactory tubercle; tz, trapezoid body; Tz, nucleus of the trapezoid body; V1, primary visual cortex; V2, secondary visual cortex; VCA, ventral cochlear nucleus, anterior part; VCN, ventral cochlear nucleus; Ves, vestibular nucleus; VL, ventrolateral thalamic nucleus; VLG, ventral lateral geniculate nucleus; VLN, ventrolateral reticular nucleus; VM, ventromedial thalamic nucleus; VMH, ventromedial hypothalamic nucleus; VP, ventral pallidum; VPM, ventral posteromedial thalamic nucleus; VPO, ventral periolivary nucleus; VPPC, ventral posterior nucleus of the thalamus, parvicellular part; VPT, ventral posterior thalamic nucleus; VS, ventral subiculum; vsc, ventral spinocerebellar tract; VTAR, ventral tegmental area, rostral part; VTg, ventral tegmental nucleus; vtgx, ventral tegmental decussation; VTM, ventral tuberomammillary nucleus; xscp, decussation of the superior cerebellar peduncle; ZI, zona incerta; Zo, zonal layer of the superior colliculus.

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