

## Research report

# Organization of projections from the juxtacapsular nucleus of the BST: a PHAL study in the rat

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**Abstract**

The axonal projections of the juxtacapsular nucleus of the anterior division of the bed nuclei of the stria terminalis (BSTju) were examined with the *Phaseolus vulgaris*-leucoagglutinin (PHAL) method in the adult male rat. Our results indicate that the BSTju displays a relatively simple projection pattern. First, it densely innervates the medial central amygdalar nucleus and the subcommissural zone and caudal anterolateral area of the BST — cell groups involved in visceromotor responses. Second, it provides inputs to the ventromedial caudoputamen (CP) and anterior basolateral amygdalar nucleus — areas presumably modulating somatomotor outflow. Third, the BSTju sends dense projections to the caudal substantia innominata, a distinct caudal dorsolateral region of the compact part of the substantia nigra, and the adjacent mesencephalic reticular nucleus and retrorubral area. And fourth, the BSTju provides light inputs to the prelimbic, infralimbic, and ventral CA1 cortical areas; to the posterior basolateral, posterior basomedial, and lateral amygdalar nuclei; to the paraventricular and medial mediodorsal thalamic nuclei; to the subthalamic and parasubthalamic nuclei of the hypothalamus; and to the ventrolateral periaqueductal gray. These projections, in part, suggest a role for the BSTju in circuitry integrating autonomic responses with somatomotor activity in adaptive behaviors. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Autonomic; Bed nuclei of the stria terminalis; Central nucleus of the amygdala; Somatomotor; Substantia innominata

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**1. Introduction**

The gray matter in the cerebral hemispheres that surround the stria terminalis, and extend from the temporal pole caudally to the base of the olfactory peduncle rostrally, was defined as the bed of the stria terminalis by Johnston [31]. The temporal end of Johnston's bed of the stria terminalis is now regarded as part of the amygdala, and only a few neurons can be traced along the body of the stria terminalis in the rat [38]. In contrast, the rostral end of Johnston's bed of the stria terminalis, an area situated just ventral to the lateral septal nucleus near the crossing of the anterior commissure, is now commonly designated the bed nuclei (or nucleus) of the stria terminalis (BST) in mammals.

Most amygdalar nuclei send a dense projection to the BST [13,26,36,76], and collectively, they probably constitute a large majority of neural inputs to the BST [48,72]. In

1972, de Olmos, in his account of amygdalar inputs, retained the parcellation of the BST into medial and lateral divisions by Bleier [7]: the medial division was characterized by inputs from the medial nucleus, whereas the lateral division was characterized by inputs from the central (CEA) and basolateral nuclei. Variations on this basic medial/lateral division remain in common usage [2,8,14,29,36,51,55,58,66,72]. In contrast, developmental evidence suggests a fundamental anterior/posterior (rostral/caudal) division [3], and Ju and Swanson [32] and Ju et al. [33] arrived at the same conclusion in the adult rat based on cyto- and chemoarchitectonic observations. The adult anterior division was further parcellated into dorsal, lateral, and ventral areas, and within them 10 distinct cell groups (nuclei) were identified.

The "lateral part of the BST" recently has attracted considerable attention because of its bidirectional connections with the CEA, parabrachial nucleus, and nucleus of the solitary tract [2,29,36,41,42,51,55,58,66], all three of which form part of the central system modulating autonomic responses (for reviews, see Refs. [39,69]). Not

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surprisingly, the “lateral BST” itself has been implicated in modulating autonomic responses [11,15,27]. In the nomenclature of Ju and Swanson [32] and Ju et al. [33], the “lateral part of the BST” corresponds approximately to the anterolateral area of the anterior BST, which itself consists of a large undifferentiated region with three relatively distinct nuclei embedded within it — juxtacapsular, rhomboid (BSTrh), and oval (BSTov).

The BSTju appears to have features that distinguish it from the rest of the anterolateral area of the BST. McDonald [40] first recognized the nucleus, with its distinctive medium-sized, spiny neurons in far lateral regions of the BST, immediately adjacent to the internal capsule. The connection pattern of the BSTju also appears to differ from the rest of the anterolateral BST. Unlike the rest of the latter, it does not receive inputs from the CEA [40,49], and it does not share dense connections with the parabrachial nucleus [2,41,42].

Almost nothing is known about the output of the BSTju, mainly because its tiny volume has discouraged anterograde tracer experiments. Nevertheless, we decided to examine the organization of its axonal projections with the anterograde tracer *Phaseolus vulgaris*-leucoagglutinin (PHAL) because it produces small injection sites and is very sensitive. This information can be used as a starting point for subsequent retrograde tracer and histochemical — as well as functional — analysis of BSTju projections.

## 2. Materials and methods

Eighteen adult male Harlan Sprague–Dawley rats (300–350 g) received a single, stereotactically placed iontophoretic injection of a 2.5% solution of PHAL (Vector Laboratories, Burlingame, CA), prepared in 0.01 M sodium phosphate-buffered saline (NaPBS), into the region of the BSTju through a glass micropipette (15  $\mu$ m tip diameter) by applying a positive current (5  $\mu$ A, 7 s off/on intervals) for 7–10 min. Animals were anesthetized for stereotaxic surgery (50 mg ketamine, 10 mg xylazine/ml; 1 ml/kg body weight).

After a survival time of 14–16 days, the rats were deeply anesthetized with pentobarbital and perfused transcardially with 150 ml of 0.9% NaCl followed by 300 ml of ice-cold 4% paraformaldehyde in 0.1 M borate buffer (pH 9.5). The brains were removed, post-fixed overnight at 4°C in the same fixative containing 10% sucrose, and frozen, and then serial 30  $\mu$ m-thick sections (one-in-four) were cut in the transverse plane on a sliding microtome. One complete series of sections was processed to detect PHAL using the immunohistochemical procedure described elsewhere [20,49]. PHAL-containing cells (in the injection sites) and fibers were plotted with the aid of a camera lucida onto cytoarchitectonic drawings of adjacent thionin-stained sections, and then transferred onto a series of standard drawings of the rat brain [60] with the aid of a

computer (Apple, Power Macintosh 7600/132; Adobe Illustrator 7). Parcellation of the rat brain, and the terminology for describing morphological features of PHAL-labeled axons, follows Swanson [60].

## 3. Results

### 3.1. Parcellation

Before describing the projections of the BSTju, it is important to consider the boundaries adopted here for the nucleus because different nomenclatures have been used in the past and no real consensus has emerged.

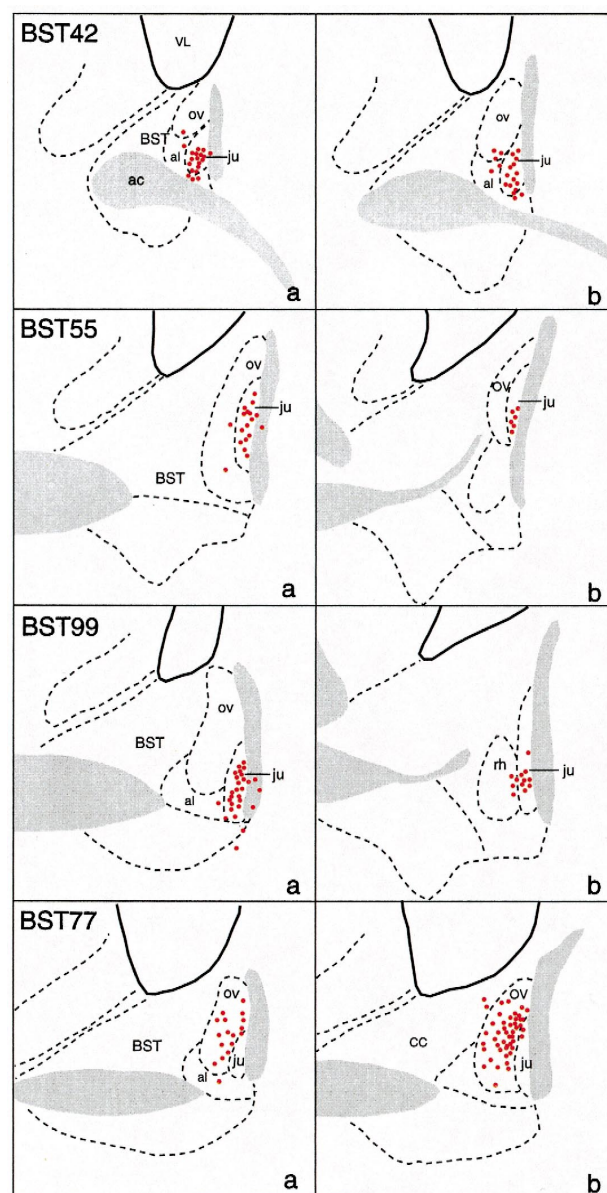


Fig. 1. Camera lucida plots of transverse histological sections with labeled neurons following PHAL injections into the BSTju (experiments BST42, BST55, and BST99) and BSTov (experiment BST77). In each case, (a) is rostral to (b).

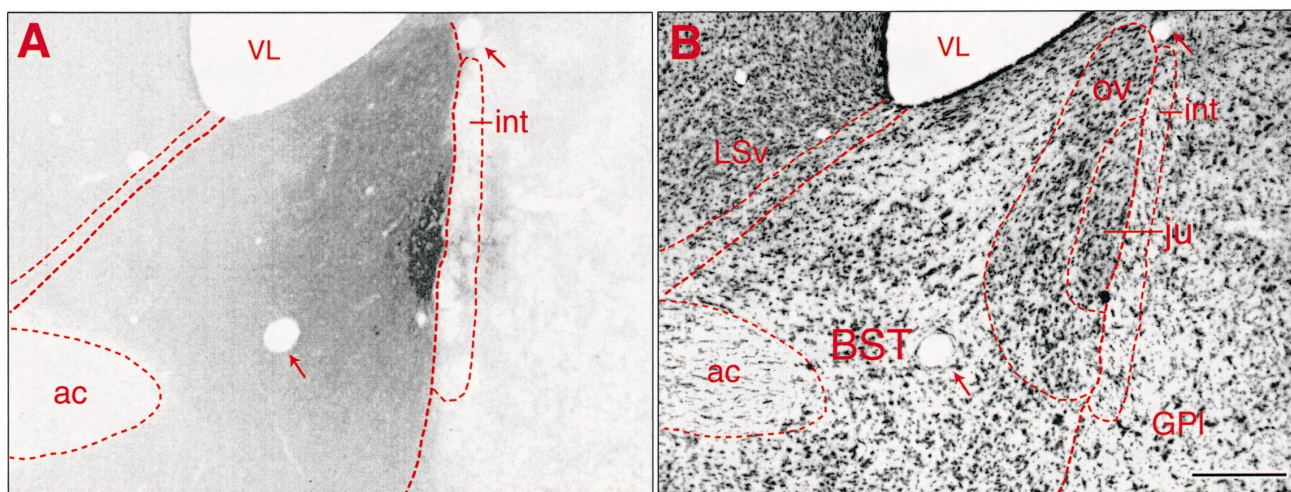


Fig. 2. Brightfield photomicrographs illustrating the appearance of the PHAL injection site in experiment BST55 (A), and the caudally adjacent thionin-stained transverse section (B). The injection in this experiment was centered in mid-rostrocaudal levels of the BSTju (see Fig. 1, BST55a). Arrows point to the same two blood vessels in the photomicrographs. Scale bar indicates 250  $\mu$ m.

The parcellation of the BST adopted here follows that of Ju and Swanson [32] and Ju et al. [33]. The BSTju is a narrow vertical strip of cells adjacent to the internal capsule, just ventral and lateral to mid-rostrocaudal levels of the BSTov (Fig. 1). In fact, dorsal regions of the BSTju are wedged between the internal capsule and the BSTov. In Nissl preparations, the BSTju contains medium-sized, round to oval neurons that are much like those in the BSTov, except that they tend to be somewhat smaller. A preliminary estimate based on counts of neuronal nuclei in

one-in-four series of 30- $\mu$ m thick Nissl-stained frozen sections ( $N = 5$  animals) suggests that the BSTju contains  $1353 \pm 102$  neurons (after applying a simple Abercrombie [1] correction for double counting errors).

The BSTju was first named the “juxtacapsular subdivision of the BST” by McDonald [40], who observed in Golgi preparations that its neurons appear different from those in the rest of the “lateral BST”. The nucleus was also called the “lateral subdivision of the BST, juxtacapsular” (JXC) by Moga et al. [42] and the “lateral division of

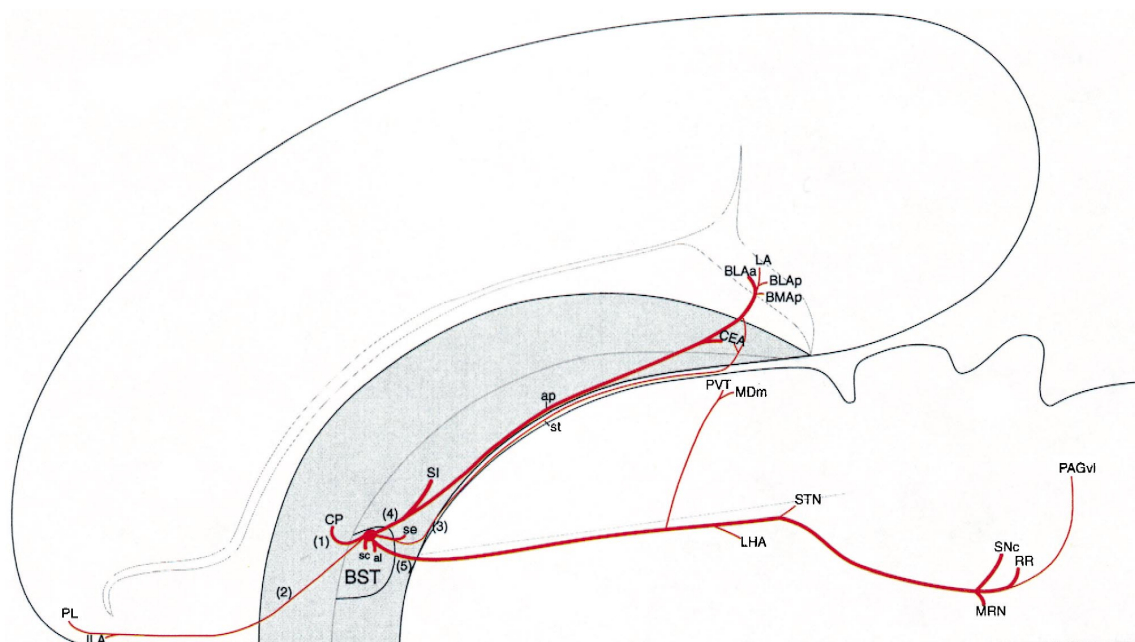
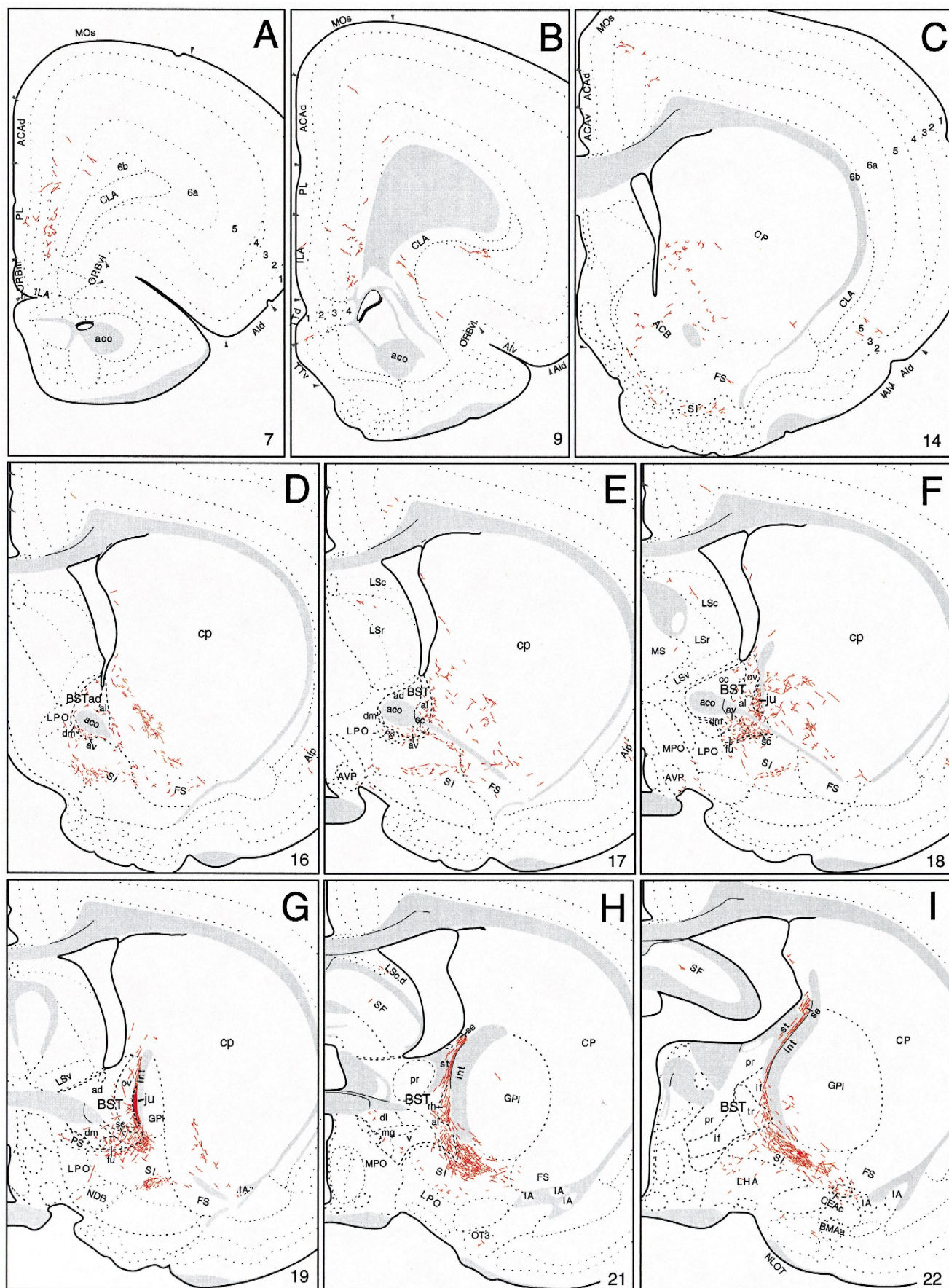
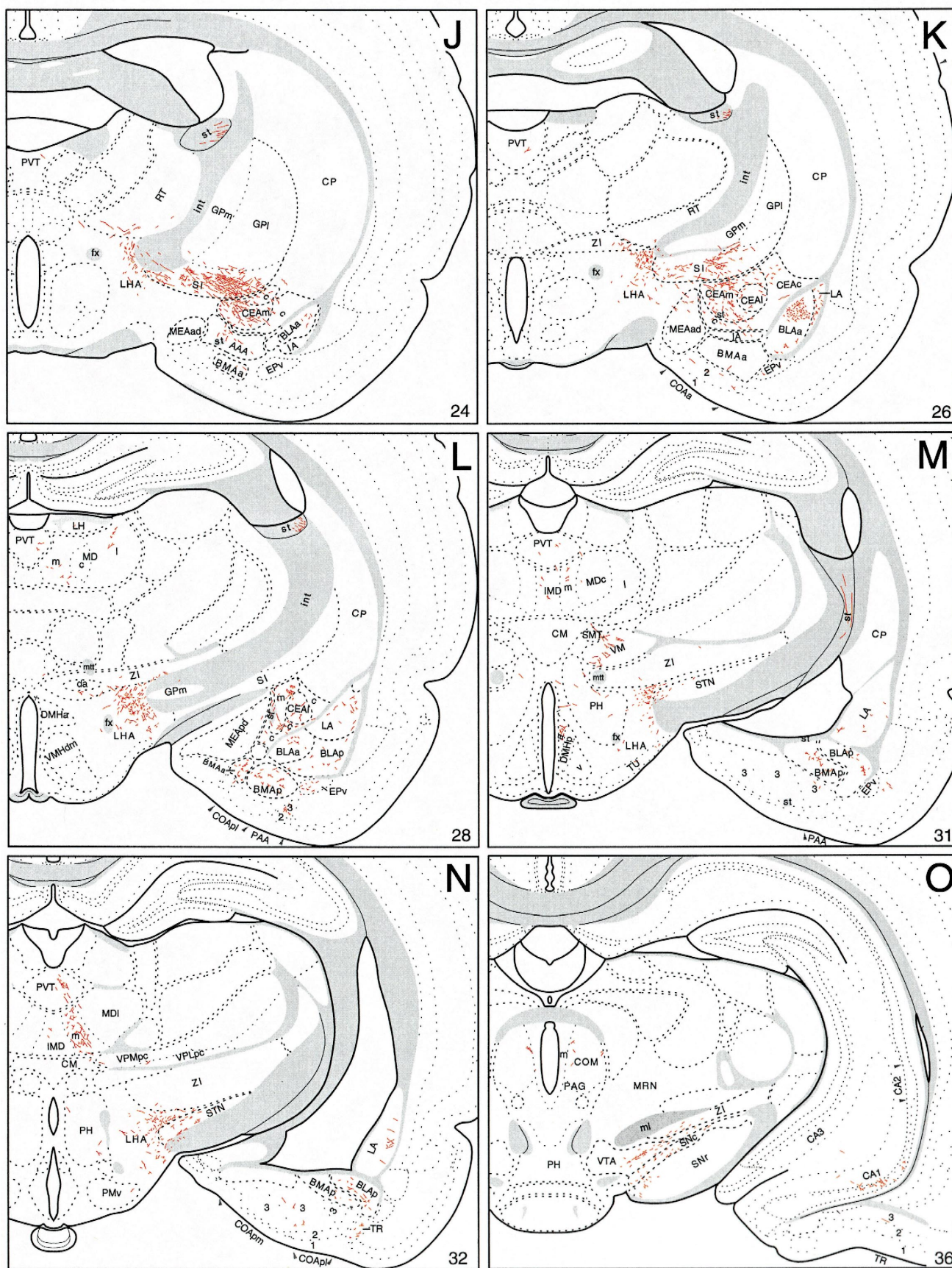


Fig. 3. Summary diagram to indicate the general organization of projections from the BSTju. The relative size of each pathway is roughly proportional to the thickness of the line representing it. Numbers in parentheses correspond to the five pathways discussed in the text (Section 3.3). Flatmap is based on Ref. [60].









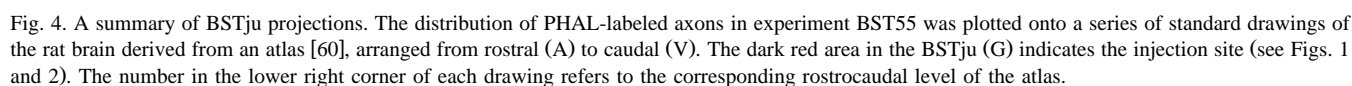


to the BSTju. In experiment BST55, the only spread of the effective injection site was to several labeled neurons in the BSTov. Therefore, the results of four PHAL experiments with an injection confined to the BSTov were examined as controls (e.g., experiment BST77, Fig. 1).

### 3.3. Projections from the BSTju

Our analysis suggests that axons from BSTju neurons use five distinct pathways (summarized in Fig. 3, below) to reach their terminal fields.

From the injection site, a group of PHAL-labeled axons extends into the rostral end of the BSTju, where individual axons display many branches with very dense terminal boutons (Fig. 4F and G). Farther rostrally, in the anterolat-





eral area of the BST and immediately adjacent to the caudoputamen (CP), the number of fibers and boutons is much less. Interestingly, the BSTov and anterodorsal area of the BST — areas immediately adjacent to the BSTju — receive only very sparse inputs from the BSTju. Instead, a moderate number of axons turn laterally to enter the CP where they branch extensively and display many terminal boutons in ventromedial regions (Fig. 4C–G, Fig. 5A). A few axons also extend into the fundus of the striatum (Fig. 4C–F).

### 3.3.2. The ventral pathway (2)

Another bundle of labeled axons from the BSTju courses rostroventrally to innervate densely the subcommissural zone of the BST (Fig. 4E–G), and a few axons with terminal boutons also extend into the fusiform nucleus of the BST (Fig. 4F and G). Most of these axons continue through the anteroventral area of the BST into the nucleus accumbens, whereas only a few scattered fibers leave the caudal BST to enter the ventral substantia innominata (Fig. 4D–F). Axons within the anteroventral BST and nucleus accumbens may be primarily fibers of passage because

they generate few boutons. After traveling through ventromedial regions of the nucleus accumbens, they enter the rostromedial substantia innominata (Fig. 4C) where they generate moderate numbers of boutons. A few of these axons extend caudally to merge with axons arriving via the ansa peduncularis pathway (see Section 3.3.4) in the caudodorsal substantia innominata (Fig. 4C–H). Finally, a small number of axons continue rostrally to provide light inputs to the deep layers of the prelimbic and infralimbic cortical areas (Fig. 4A and B), and a few axons were also observed in the agranular insular and secondary motor cortical areas (Fig. 4A–F).

### 3.3.3. The stria terminalis pathway (3)

From the injection site, a small group of PHAL-labeled fibers travels dorsally and caudally to enter the stria terminalis. Curiously, most of them end in the strial extension of the BST (Fig. 4H and I), and only a few continue caudally in the stria terminalis to reach the amygdala (Fig. 4L) where they cannot be distinguished from labeled axons arriving via the ansa peduncularis pathway (see Section 3.3.4).

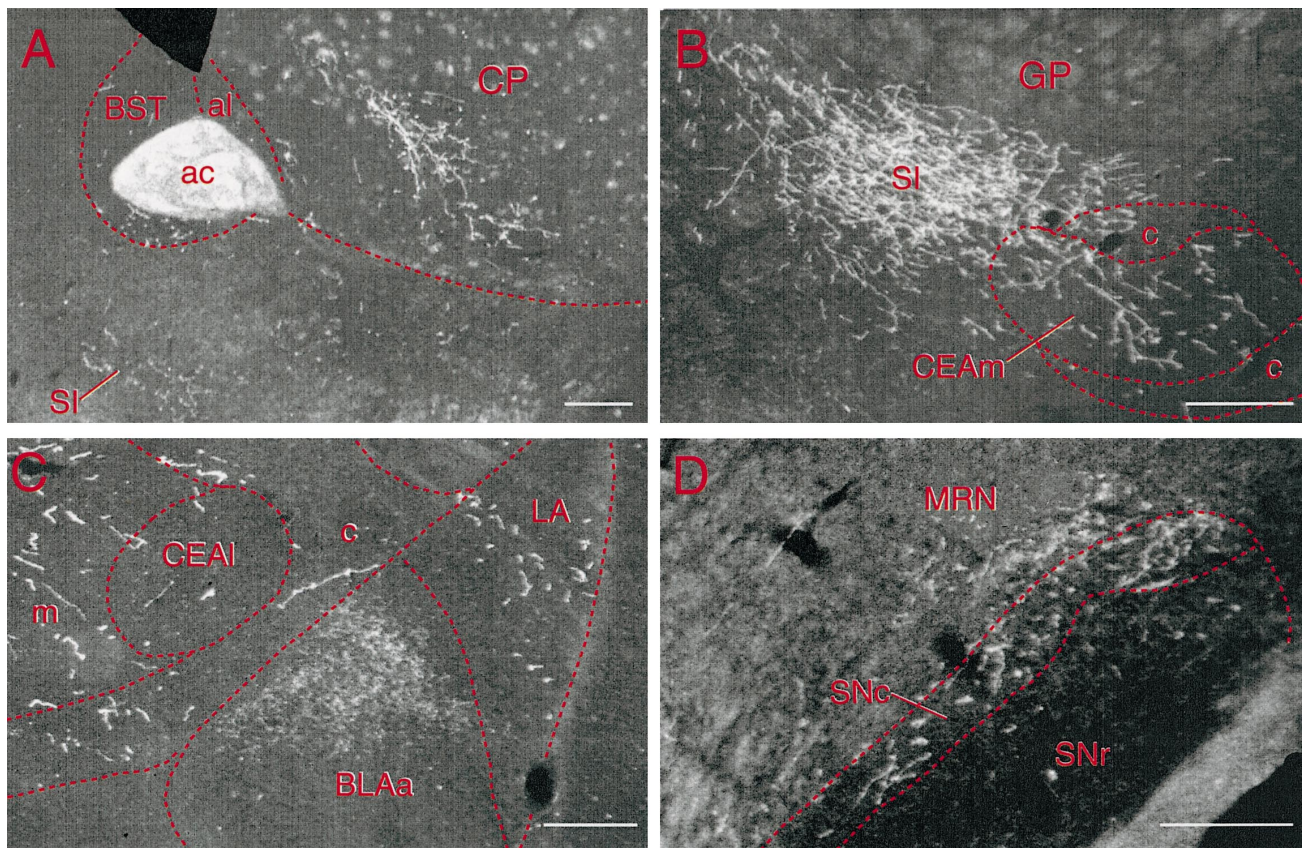


Fig. 5. Darkfield photomicrographs showing the appearance of PHAL-labeled axons in transverse histological sections. (A) This ventromedial region of the CP receives a moderate number of fibers (see Fig. 4D). (B) A very dense plexus of PHAL-labeled fibers in the substantia innominata (SI). A substantial number of fibers were also observed in the CEAm (see Fig. 4J). (C) A plexus of very thin PHAL-labeled fibers in dorsal regions of the anterior basolateral amygdalar nucleus (BLAa). PHAL-labeled fibers are also seen in the lateral amygdalar nucleus (LA) and in the CEA (see Fig. 4K). (D) The caudal dorsolateral compact substantia nigra (SNc) and adjacent mesencephalic reticular nucleus (MRN) are innervated by PHAL-labeled fibers from the BSTju (see Fig. 4P). All scale bars indicate 250  $\mu$ m.

### 3.3.4. The ansa peduncularis pathway (4)

The vast majority of PHAL-labeled axons from the BSTju stream ventrocaudally through the BSTrh and caudal anterolateral area of the BST to enter caudal dorsolateral regions of the substantia innominata (Fig. 4G and H). Within the BSTrh, labeled fibers are poorly branched with only occasional boutons. In contrast, fibers in the caudal anterolateral area of the BST display many boutons of passage as well as terminal boutons (Fig. 4H). Caudally, some fibers also course through the interfascicular and transverse nuclei of the posterior division of the BST to enter the substantia innominata (Fig. 4I).

This massive group of highly branched fibers with very rich terminal boutons and varicosities provides a very dense input to the caudal substantia innominata, from the level of the crossing of the anterior commissure to its caudal tip (Fig. 4G–K, Fig. 5B). Overall, this is the densest output from the BSTju observed in the present study. Many fibers extend caudally through the substantia innominata, displaying numerous boutons of passage along their way toward the amygdala (Fig. 4G–K).

A moderate number of fibers in the substantia innominata reach the amygdala, where abundant branches with terminal boutons provide a dense input to the medial part of the central nucleus (CEAm) (Fig. 4I–L, Fig. 5B and C). The capsular part of the CEA contains only a small number of labeled fibers caudally (Fig. 4L), while the lateral part was almost free of PHAL labeling except for an occasional axon. We also observed a dense terminal field of PHAL labeling in the anterior basolateral amygdalar nucleus. This distinctive terminal field appears to consist of very thin fibers with a very rich plexus of terminal bouton-laden branches (Fig. 4K and L, Fig. 5C). The lateral, posterior basolateral, and basomedial amygdalar nuclei, and the anterior amygdalar areas contain a small number of PHAL-labeled fibers with terminal boutons (Fig. 4J–N, Fig. 5C). Finally, a few labeled axons continue farther ventrocaudally to innervate the ventral part of the endopiriform nucleus, postpiriform transition area, and ventral region of hippocampal field CA1 (Fig. 4O).

### 3.3.5. The descending (medial forebrain bundle) pathway (5)

This is a major route for axons from the BSTju to reach the caudal interbrain and midbrain. A moderate number of PHAL-labeled axons from the BSTju course medial to the substantia innominata to enter the lateral hypothalamic area, and some may enter the lateral hypothalamic area from the substantia innominata itself (Fig. 4I). These fibers travel caudally through the most lateral part of the lateral hypothalamic area, and display a small number of branches and boutons, especially in tuberal levels and in a caudolateral part of the lateral hypothalamic area that may correspond to the parasubthalamic nucleus illustrated by Wang and Zhang [71] (Fig. 4L–N). The subthalamic nucleus,

located just ventrolateral to the lateral hypothalamic area, also contains a few bouton-laden fibers (Fig. 4N). At this level, a few axons course medially through the posterior hypothalamic nucleus to reach the midline nuclei of the thalamus, where fibers with terminal boutons were observed in caudal regions of the medial part of the mediodorsal nucleus and in the paraventricular nucleus (Fig. 4N). Most fibers descending from the lateral hypothalamic area course through the ventral tegmental area, zona incerta, and rostral compact part of the substantia nigra to innervate densely a caudal dorsolateral region of the latter (Fig. 4P, Fig. 5D). A dense terminal plexus was also observed in the adjacent mesencephalic reticular nucleus and retrorubral area, where the A8 dopamine cell group is located [12] (Fig. 4P and Q, Fig. 5D). This terminal field extends into the adjacent most caudal region of the reticular part of the substantia nigra (Fig. 4Q). Only a few axons descend past the retrorubral area and mesencephalic reticular nucleus to end in the ventrolateral division of the periaqueductal gray (Fig. 4R–T), and a very few scattered fibers were identified in the pedunculopontine nucleus, medial parabrachial nucleus, and rostral locus coeruleus (Fig. 4U and V).

### 3.4. Contralateral projections

The BSTju does not provide significant contralateral projections except for a very few labeled axons in the paraventricular thalamic nucleus (Fig. 4M), retrorubral area (Fig. 4Q), and ventrolateral division of the periaqueductal gray. The location of these axons is typically a mirror image of the ipsilateral labeling.

### 3.5. Control experiments

Because the BSTju is so tiny, each of our experiments with a PHAL injection centered within it also labeled a few neurons in adjacent cell groups, and in the experiment just described, this included a few neurons in the BSTov. Therefore, it is possible that some of the smaller pathways illustrated in Fig. 4 may be due to a few PHAL-labeled neurons in the BSTov. The results of our four experiments with a PHAL injection centered in the BSTov will be described in detail elsewhere. Here we will simply examine whether the BSTov projects moderately or heavily to areas lightly labeled by PHAL injections centered in the BSTju. In short, these lightly labeled areas include (1) the striatal fundus; (2) the fusiform nucleus of the BST, and the infralimbic, prelimbic, agranular insular, and secondary motor cortical areas; (3) the stria terminalis; (4) the capsular and lateral parts of the central, and the lateral, posterior basolateral, and basomedial amygdalar nuclei; the anterior amygdalar area; the endopiriform nucleus; and ventral hippocampal field CA1; and (5) the lateral and parasubthalamic parts of the lateral hypothalamic area, subthalamic nucleus, mediodorsal and paraventricular thalamic nuclei,



ventrolateral periaqueductal gray, pedunculopontine nucleus, medial parabrachial nucleus, and locus coeruleus. The BSTov sends a very dense input to the fusiform nucleus of the BST, and moderate inputs to the capsular and lateral parts of the central amygdalar nucleus, parabrachial nucleus of the lateral hypothalamic area, and ventrolateral division of the periaqueductal gray. Therefore, the light projections from our BSTju injections to these areas may arise only in the BSTov, or in the BSTov and BSTju. Retrograde tracer experiments are needed to clarify this ambiguity. The BSTov does not send significant projections to the rest of the areas listed, suggesting that light projections to them probably arise in the BSTju.

#### 4. Discussion

Our results suggest that the BSTju displays a relatively simple pattern of projections, and densely innervates only a few targets. Within the BST, it provides a dense input to the subcommissural zone, and moderate inputs to the caudal anterolateral area and strial extension. Outside the BST, its most dense projection is to a restricted caudal region of the substantia innominata, and it also projects densely to the ventromedial CP, CEAm, and anterior basolateral amygdalar nucleus, and to a continuous midbrain terminal field that includes the caudal dorsolateral compact part of the substantia nigra and adjacent regions of the mesencephalic reticular nucleus and retrorubral area.

##### 4.1. Projections from the BSTju

The lack of projections to the parabrachial nucleus observed in the present study is the most striking distinction between the BSTju and the rest of the anterolateral BST. This result confirms the work of Moga et al. [41,42] who found no retrogradely labeled neurons in the BSTju after fast blue or WGA–HRP injections into the parabrachial nucleus. In contrast, all other parts of the anterolateral BST send topographically organized projections to the parabrachial nucleus [41,42]. Furthermore, we did not observe projections from the BSTju to the nucleus of the solitary tract, which is innervated by the rest of anterolateral BST (our unpublished observations with PHAL). This lack of a projection to the nucleus of the solitary tract cannot be confirmed by previous retrograde tracer studies because the BST parcellation in them was not sufficiently detailed [55,58,66]. The BSTju appears to provide very light inputs to the lateral hypothalamic area and the ventrolateral periaqueductal gray, whereas these two areas receive moderate to dense inputs from the rest of the anterolateral BST [23,62]. Gray and Magnuson [23] observed scattered retrograde labeling in the BSTju after large fluorescent tracer injections into the periaqueductal gray.

On the other hand, the BSTju does share certain terminal fields with the rest of the anterolateral BST. The BSTju projects very densely to the caudal substantia innominata and CEAm, which is common for all cell groups of the anterolateral BST (our unpublished results with PHAL). Following WGA–HRP injections into dorsal regions of the substantia innominata, Grove [24] found dense retrograde labeling of cell bodies in the “lateral part” of the BST. Ottersen [45] did not report retrograde labeling in the BST after HRP injections in the CEA, probably due to the insensitivity of the HRP method used at the time.

We observed here a dense input to a caudal dorsolateral region of the compact substantia nigra and to adjacent regions of the mesencephalic reticular nucleus and retrorubral area after PHAL injections in the BSTju. With [<sup>3</sup>H]leucine injected into the “lateral part” of the BST, Holstege et al. [29] observed dense projections to the compact substantia nigra of the cat. However, their injection sites involved the entire lateral BST. After rhodamine and WGA–HRP injections into the lateral compact substantia nigra, including what they called the “lateral part of the substantia nigra”, Vankova et al. [67] also found many retrogradely labeled neurons in the “lateral part of the BST”. The other nuclei in the anterolateral area of the BST project very lightly to the compact substantia nigra, except for the BSTrh, which provides a moderate input to the caudolateral compact substantia nigra (our unpublished results with PHAL). Thus, it appears likely that BST inputs to the caudolateral compact substantia nigra mainly arise in the BSTju itself. In contrast, the entire anterolateral area of the BST projects very densely to the areas adjacent to the caudolateral substantia nigra — the mesencephalic reticular nucleus and retrorubral area (our unpublished results).

Finally, after PHAL injections into the BSTju, we observed dense projections to the ventromedial CP and to the anterior basolateral amygdalar nucleus — areas that do not receive significant inputs from the rest of the anterolateral BST (our unpublished results with PHAL).

Little is known about neurotransmitters synthesized by neurons in the BSTju. However, most neurons in the anterolateral area of the BST, including the BSTju, appear to be GABAergic [59]. Furthermore, the BSTju and lateral part of the BSTov express very high levels of enkephalin and dynorphin [16,17]. Dense enkephalin- and dynorphin-immunoreactive fibers have been reported in the CEAm, caudal substantia innominata, ventromedial CP, compact substantia nigra, and retrorubral area [16] — all of which are projection fields of the BSTju, as shown here.

##### 4.2. Inputs to the BSTju

Very little is known about direct neural inputs to the BSTju. Curiously, axons from the CEA, which innervate quite heavily all other parts of the anterolateral BST, avoid entering the BSTju [40,49]. Because the dendrites of BSTju

neurons are more or less restricted to the confines of the nucleus [40], it seems likely that the CEA does not provide a direct input to neurons of the BSTju. Instead, direct amygdalar inputs to the BSTju arise in the posterior basolateral nucleus and the postpiriform transition area (Fig. 6) (Ref. [36], our unpublished results with PHAL). These two areas are highly interconnected and appear to belong to the main olfactory system [64]. The postpiriform transition area (TR) appears to be a “main olfactory association cortical area” because of its major inputs from the main olfactory bulb (for review, see Ref. [64]). The posterior basolateral nucleus appears to be the “claustrum” for the postpiriform transition area, and is also a major target of projections from the anterior basolateral and lateral amygdalar nuclei [48,50,54], via which it presumably also receives visual, auditory, visceral, and gustatory sensory information [50,54,64]. In addition, the posterior basolateral nucleus receives direct inputs from the medial prefrontal cortex [46], the ventral two-thirds of hippocampal field CA1 and the adjacent ventral subiculum, the thalamic paraventricular nucleus, and the parabrachial nucleus [5,10,43,46]. Thus, the posterior basolateral amygdalar nucleus presumably relays converged unimodal and polymodal sensory information (including trisynaptic circuit information from the hippocampal formation) to the BSTju (see Fig. 6).

The BSTju does not receive direct inputs from the parabrachial nucleus, which sends topographically organized projections to the rest of the anterolateral BST [2]. However, the medial division of the parabrachial nucleus, which presumably relays gustatory and viscerosensory information, may indirectly influence the BSTju via its

projections to the posterior basolateral amygdalar nucleus, subcommissural zone of the BST, and caudal substantia innominata [2,5], all of which in turn project to the BSTju (Ref. [25], our unpublished results with PHAL, and personal communication with B. Spann and L.W. Swanson). The subcommissural zone of the BST and the caudal substantia innominata also receive dense projections from the CEAm [36,48], which receives sensory information from the parabrachial nucleus and nucleus of the solitary tract [5,51].

The BSTju also receives a dense input from the ventrolateral periaqueductal gray, based on PHAL injections into this region [9]. This division of the periaqueductal gray receives a dense projection from the superficial region of the spinal dorsal horn [6], and thus may relay nociceptive and/or thermal information to the BSTju. In the present study, we observed a light projection from the BSTju back to the ventrolateral periaqueductal gray.

In addition, a dense terminal field in the BSTju is labeled with antisera to tyrosine hydroxylase (presumably dopaminergic fibers) and cholecystokinin, and this terminal field(s) may arise in or near the ventral tegmental area [19,28]. It is not yet known whether dopamine and cholecystokinin are coexpressed in the same fibers, but it is very interesting that the same overlapping pattern of immunostaining was observed in two targets of BSTju projections — the ventromedial CP and CEA [28].

Finally, the BSTju contains a dense vasoactive intestinal polypeptide (VIP)-immunoreactive terminal field that appears to arise in the posterior basolateral nucleus [73].

#### 4.3. Relationship to motor systems

The results presented here suggest that the BSTju is in a position to modulate both autonomic and somatic motor circuits (Fig. 6). On one hand, it sends direct projections to the CEAm, and to the subcommissural zone and caudal anterolateral area of the BST, all of which project to brainstem autonomic areas [41,55,58,69]. The BSTju may also influence the CEAm indirectly via its projections to the lateral and posterior basolateral amygdalar nuclei, as well as to the subcommissural zone and caudal anterolateral area of the BST, because all of these cell groups in turn send dense projections to the CEAm (Refs. [48,50,54], our unpublished results with PHAL).

On the other hand, the BSTju may influence somatomotor responses in a number of ways, including via its projections to the anterior basolateral amygdalar nucleus and ventromedial CP. First, the anterior basolateral amygdalar nucleus provides an extraordinarily dense input to premotor and motor cortical areas and to the entire CP — except for a small ventromedial region [35,48,57]. Interestingly, the BSTju sends direct projections to just this ventromedial region of the CP. This area, which is avoided by

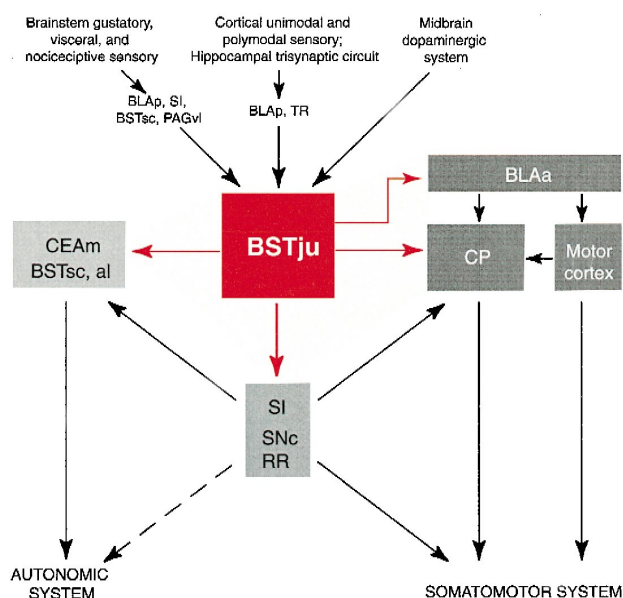


Fig. 6. A diagrammatic summary of major known connections of the BSTju. See text for details.



inputs from the anterior basolateral amygdalar nucleus, also receives inputs from medial prefrontal (prelimbic and infralimbic) and agranular insular cortical areas, and from the basolateral amygdala (lateral, posterior basolateral, and basomedial nuclei) [30,48,52,53,56,65,74], and projects to far medial regions of the substantia nigra [61]. Thus, the BSTju influences complementary regions of the dorsal striatum (CP), directly via its projections to the ventromedial CP, and indirectly via the anterior basolateral amygdalar nucleus, which projects to the rest of the CP. In addition, the BSTju may influence the caudolateral CP via its direct projections to the caudolateral compact substantia nigra and retrorubral area (see below).

The second way the BSTju may influence the somatomotor system is via its most dense projection — to a caudolateral region of the substantia innominata that corresponds in part to what has been referred to as “the sublenticular substantia innominata” [14]. The latter has been suggested to modulate somatomotor responses through direct projections to the subthalamic and mesencephalic locomotor regions [44,63]. However, the projections of strictly that region of the substantia innominata that receives BSTju inputs remain to be determined.

And third, the BSTju sends a dense projection to a region in the ventral midbrain that includes the caudal dorsolateral compact substantia nigra, and adjacent mesencephalic reticular nucleus and retrorubral area. The latter two regions contain the A9 and A8 dopaminergic cell groups, respectively [12]. The caudolateral region of the compact substantia nigra projects to the dorsolateral CP [4,68], which in rats has been shown to receive inputs from premotor and motor cortical areas [34], whereas the retrorubral area projects to a wider region of the CP [68].

Of equal interest, the caudal dorsolateral region of the compact substantia nigra and the retrorubral area also have bidirectional connections with the CEA. Using PHAL, Gonzales and Chesselet [21] found dense projections from the CEAm to lateral regions of the compact part of the substantia nigra, as well as to the retrorubral area. These areas in turn provide dopaminergic and cholecystokinergic inputs to the CEAm [18]. In addition, the “caudal dorsolateral substantia nigra” and adjacent retrorubral area reportedly project to motor pattern generators in the hind-brain reticular formation that mediate complex orofacial reflexes [70]. Finally, the caudal dorsolateral substantia nigra also sends non-dopaminergic projections to the “shell” of the inferior colliculus, which has been suggested to modulate orienting movements of the head and eyes via its projections to the superior colliculus [37,75]. Thus, the evidence suggests that the BSTju influences somatic motor pattern generators that influence orofacial movements and orienting movements of the eyes and head.

In summary (see diagram in Fig. 6), the evidence reviewed here suggests that there are three major classes of neural inputs to the BSTju, and that the outputs of the latter may serve to coordinate autonomic and somatomotor

responses. Virtually every major class of sensory information potentially can reach the BSTju, either from the brainstem or from the cerebral cortex; and there also appears to be a dopamine and cholecystokinin-containing input(s) to the BSTju from the ventral midbrain. After processing this varied information, the BSTju transmits it to both the autonomic and somatomotor systems. First, the BSTju sends axons to the CEAm (recently suggested to be the “visceromotor striatum” [64]), and to two terminal fields of the CEAm, the subcommissural zone and caudal anterolateral area of the BST. Second, the BSTju projects directly to the ventromedial CP, and projects indirectly to the rest of the CP via a direct projection to the anterior basolateral amygdalar nucleus (which also projects directly to the primary and secondary cortical motor areas). It is firmly established that the CP (dorsal striatum) influences somatomotor outflow. And third, the BSTju sends its densest output to the substantia innominata (ventral pallidum of [60]) and brainstem motor regions (substantia nigra, mesencephalic reticular nucleus, and retrorubral area) that also project to parts of the autonomic and somatomotor control systems that receive direct and indirect inputs from the BSTju. Thus, the neuroanatomical evidence suggests that the BSTju is in a position to coordinate autonomic and somatomotor responses during adaptive behaviors associated with affective components. Physiological work is needed to test this hypothesis.

## 5. Abbreviations

AAA	anterior amygdalar area
ACAd	anterior cingulate area, dorsal part
ACAv	anterior cingulate area, ventral part
ACB	nucleus accumbens
ac	anterior commissure
aco	anterior commissure, olfactory limb
AId	agranular insular area, dorsal part
AIv	agranular insular area, ventral part
AQ	cerebral aqueduct
AVP	anteroventral preoptic nucleus
BLAa	basolateral amygdalar nucleus, anterior part
BLAp	basolateral amygdalar nucleus, posterior part
BMAa	basomedial amygdalar nucleus, anterior part
BMAp	basomedial amygdalar nucleus, posterior part
BST	bed nuclei of the stria terminalis
BSTad	bed nuclei of the stria terminalis, anterodorsal area
BSTal	bed nuclei of the stria terminalis, anterolateral area
BSTav	bed nuclei of the stria terminalis, anteroventral area
BSTdl	bed nuclei of the stria terminalis, dorsolateral nucleus
BSTdm	bed nuclei of the stria terminalis, dorsomedial nucleus

BSTfu	bed nuclei of the stria terminalis, fusiform nucleus	LS	lateral septal nucleus
BSTif	bed nuclei of the stria terminalis, interfascicular nucleus	LSc	lateral septal nucleus, caudal part
BSTmg	bed nuclei of the stria terminalis, magnocellular nucleus	LSr	lateral septal nucleus, rostral part
BSTov	bed nuclei of the stria terminalis, oval nucleus	LSv	lateral septal nucleus, ventral part
BSTpr	bed nuclei of the stria terminalis, principal nucleus	MD	mediodorsal nucleus thalamus
BSTrh	bed nuclei of the stria terminalis, rhomboid nucleus	MDc	mediodorsal nucleus thalamus, central part
BSTsc	bed nuclei of the stria terminalis, subcommissural zone	MDl	mediodorsal nucleus thalamus, lateral part
BSTtr	bed nuclei of the stria terminalis, transverse nucleus	MDm	mediodorsal nucleus thalamus, medial part
BSTv	bed nuclei of the stria terminalis, ventral nucleus	MEAad	medial nucleus amygdalar, anterodorsal part
CA1	field CA1, ammon's horn	MEApd	medial nucleus amygdalar, posterior part
CA2	field CA2, ammon's horn	MEV	mesencephalic nucleus of the trigeminal
CA3	field CA3, ammon's horn	ml	medial lemniscus
CEA	central nucleus amygdala	MOs	secondary motor area
CEAc	central nucleus amygdala, capsular part	MPO	medial preoptic area
CEAl	central nucleus amygdala, lateral part	MRN	mesencephalic reticular nucleus
CEAm	central nucleus amygdala, medial part	MS	medial septal nucleus
CLA	claustrum	mtt	mammillothalamic tract
CLI	central linear nucleus raphé	NDB	nucleus of the diagonal band
CM	central medial nucleus thalamus	NLOT	nucleus of the lateral olfactory tract
COAa	cortical nucleus amygdala, anterior part	NTS	nucleus of solitary tract
COApI	cortical nucleus amygdala, posterior part, lateral zone	PAA	piriform-amygdalar area
COApm	cortical nucleus amygdala, posterior part, medial zone	PAG	periaqueductal gray
COM	commissural nucleus, periaqueductal gray	PAGd	periaqueductal gray, dorsal division
CP	caudoputamen	PAGdl	periaqueductal gray, dorsolateral division
DMH	dorsomedial nucleus hypothalamus	PAGm	periaqueductal gray, medial division
DMHa	dorsomedial nucleus hypothalamus, anterior part	PAGvl	periaqueductal gray, ventrolateral division
DMHp	dorsomedial nucleus hypothalamus, posterior part	PB	parabrachial nucleus
DMHv	dorsomedial nucleus hypothalamus, ventral part	PBlc	parabrachial nucleus, central lateral part
EPV	endopiriform nucleus, ventral part	PBld	parabrachial nucleus, dorsal lateral part
FS	fundus of the striatum	PBLE	parabrachial nucleus, external lateral part
fx	columns of the fornix	PBlv	parabrachial nucleus, ventral lateral part
IA	intercalated nuclei amygdala	PBmm	parabrachial nucleus, medial medial part
ICe	inferior colliculus, external nucleus	PCG	pontine central gray
ILA	infralimbic cortical area	PH	posterior hypothalamic nucleus
int	internal capsule	PL	prelimbic cortical area
IMD	intermediodorsal nucleus thalamus	PMv	ventral premammillary nucleus
LA	lateral amygdalar nucleus	PP	peripeduncular nucleus
LC	locus coeruleus	PPN	pedunclopontine nucleus
LDT	laterodorsal tegmental nucleus	PS	parastrial nucleus
LH	lateral habenula	PVT	paraventricular nucleus thalamus
LHA	lateral hypothalamic area	RL	rostral linear nucleus raphé
LPO	lateral preoptic area	RR	mesencephalic reticular nucleus, retrorubral area
		SCdg	superior colliculus, deep gray layer
		SCP	superior cerebellar peduncle
		SF	septohippocampal nucleus
		SI	substantia innominata
		SN	substantia nigra
		SNe	substantia nigra, compact part
		SNr	substantia nigra, reticular part
		st	stria terminalis
		SUT	supratrigeminal nucleus
		TTd	taenia tecta, dorsal part
		TTv	taenia tecta, ventral part
		TR	postpiriform transition area
		TU	tuberal nucleus



VTA	ventral tegmental area
ZI	zona incerta
ZIda	zona incerta, dopaminergic group

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