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Abstract

Thalamic neurons projecting to both the head of the caudate nucleus and the premotor cortex in the cat were studied by the retrograde fluorescent double labeling technique. After injections of Evans blue into the caudate nucleus, and diamidino-phenylindol into the premotor cortex, a small number of double labeled neurons appeared in the ventral anterior, ventral lateral, anteromedial, rhomboid, central dorsal, central lateral, central medial, paracentral and parafascicular nuclei, in addition to numerous single-labeled neurons. This indicates that some neurons in the thalamic nuclei send bifurcating axons to both the head of the caudate nucleus and the premotor cortex. The caudatal projections of these thalamic neurons are organized in a topical manner.

KEYWORDS: thalamus, axon collateral, fluorescent tracer, caudate nucleus, premotor cortex

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**THE ORGANIZATION OF THALAMIC NEURONS PROJECTING
TO THE PREMOTOR CORTEX AND THE CAUDATE
NUCLEUS IN THE CAT STUDIED BY A
FLUORESCENT RETROGRADE DOUBLE
LABELING TECHNIQUE**

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Abstract. Thalamic neurons projecting to both the head of the caudate nucleus and the premotor cortex in the cat were studied by the retrograde fluorescent double labeling technique. After injections of Evans blue into the caudate nucleus, and diaminodiphenylindol into the premotor cortex, a small number of double labeled neurons appeared in the ventral anterior, ventral lateral, anteromedial, rhomboid, central dorsal, central lateral, central medial, paracentral and parafascicular nuclei, in addition to numerous single-labeled neurons. This indicates that some neurons in the thalamic nuclei send bifurcating axons to both the head of the caudate nucleus and the premotor cortex. The caudatal projections of these thalamic neurons are organized in a topical manner.

Key words : thalamus, axon collateral, fluorescent tracer, caudate nucleus, premotor cortex.

It is well-known that thalamic neurons projecting to the premotor cortex (area 6) are present in the ventral anterior and ventral lateral nuclear complex (VA-VL) (1-4) and the intralaminar nuclei (3-8). It has been confirmed that the caudate nucleus (NC) receives fibers from the intralaminar nuclei (8-17), and from the ventral anterior nucleus (15, 17). Earlier retrograde cell degeneration studies using the monkey has suggested that the projections of the intralaminar neurons to the striatum may be by way of the collaterals of the thalamo-cortical fibers (10). Recent anatomical studies using iron dextran and horseradish peroxidase in the rat has demonstrated the presence of neurons in the central lateral nucleus (CL) which send bifurcating axons to both the anterior striatum and the motor cortex (18). Electrophysiological data also has indicated that the neurons sending collateral axons to both the striatum and the pericruciate cortex in the cat are present in the ventral nuclei and the intralaminar nuclei (19-21). Some authors, however, has denied the existence of such neurons in the intralaminar nuclei (22).

The present study, using the retrograde fluorescent double labeling technique, was undertaken to demonstrate the presence of thalamic neurons projecting to both the NC and the premotor cortex (area 6) by divergent axons in the cat,

and to clarify the precise distribution of these neurons in the thalamus. A preliminary report of the present findings was given earlier (23).

MATERIALS AND METHODS

Twenty-six normal adult cats (32 hemispheres) were used in the present investigation. Prior to surgery, each cat was anesthetized with ketamin hydrochloride (Ketalar) by intramuscular injection (40 mg/kg). Evans blue (EB) and 4'-6-diamidino-2-phenylindol 2HCl (DAPI) were chosen as the fluorescent retrograde tracers (24). A total of 0.2-0.5 μ l of 10 % EB (w/v) solution containing 1 % poly-L-ornithine was injected stereotactically, according to the atlas of Reinoso-Suárez (25), into the head of the NC, and a total of 0.1-0.2 μ l of 2.5 % DAPI (w/v) aqueous suspension was injected ipsilaterally into the premotor cortex using a Hamilton syringe. The NC was entered by a conventional stereotaxic approach, in which the injection needle passed vertically through the overlying cortex and subcortical white matter. To prevent the uptake of dye along the vertical needle track, an oblique approach was also tried (C117R, C131R). After a survival period of 60-72 h, the animals were deeply anesthetized with sodium pentobarbital (Nembutal) and perfused transcardially with 200 ml of 0.9 % saline (w/v) followed by 3000 ml of 10 % formalin in saline. After 4-5 h, the brain was removed and soaked in 30 % cacodylated-buffered sucrose (pH 7.2) for 12 h. Frozen sections were cut transversely at 50 μ m, mounted from cacodylate buffer solution (pH 7.2) onto gelatine coated slides, air dried, and coverslipped with glycerol.

The material was examined with a Leitz Ploemopak fluorescence microscope equipped with filter system A and N2 providing excitation light of 360 nm and 550 nm wavelength, respectively. A photographic record of the labeled neurons was kept in order to determine their exact location in the thalamus. Finally, the sections were counterstained with 0.1 % cresyl violet. The thalamic nuclei were classified and named following Niimi and Kuwahara (26).

RESULTS

In most of our experiments, EB was injected into the head of the NC, and DAPI into the premotor cortex on the same side of each cat. EB was injected into the central portion of the head of the caudate nucleus (C79R, C82L, R, C86L, C90R, C91L, C92L, R, C93R, C100R, C104L, C108R, C109R, C110L, C117R, C131R) or into the lateral portion (C79L, C81R, C86R, C90L, C91R, C97R, C98R). DAPI was injected into the premotor cortex (6a β of Hassler and Muhs-Clement (27)) at about coordinates between 24 and 27 in the frontal plane. DAPI injection sites were in the rostromedial sector of the ventral lip of the cruciate sulcus (C82L, R, C86L, C90L, R, C91L, R, C98R, C106R, C109R, C110L, C117R), in the rostromedial half of the ventral wall of the cruciate sulcus (C75L, C79L, R, C81R, C92L, R, C93R, C97R, C100R, C104L, C108R, C131R) and in the rostromedial surface of the hemisphere belonging to area 6 (C86R). In addition, the following control experiments were made: DAPI was injected into the head of the NC, and EB into the premotor cortex (C85L and C85R).

At an excitation wave length of 550 nm, EB-labeled neurons showed red fluorescent cytoplasm (Fig. 1A). In 18 cases, retrograde EB-labeled neurons were ob-

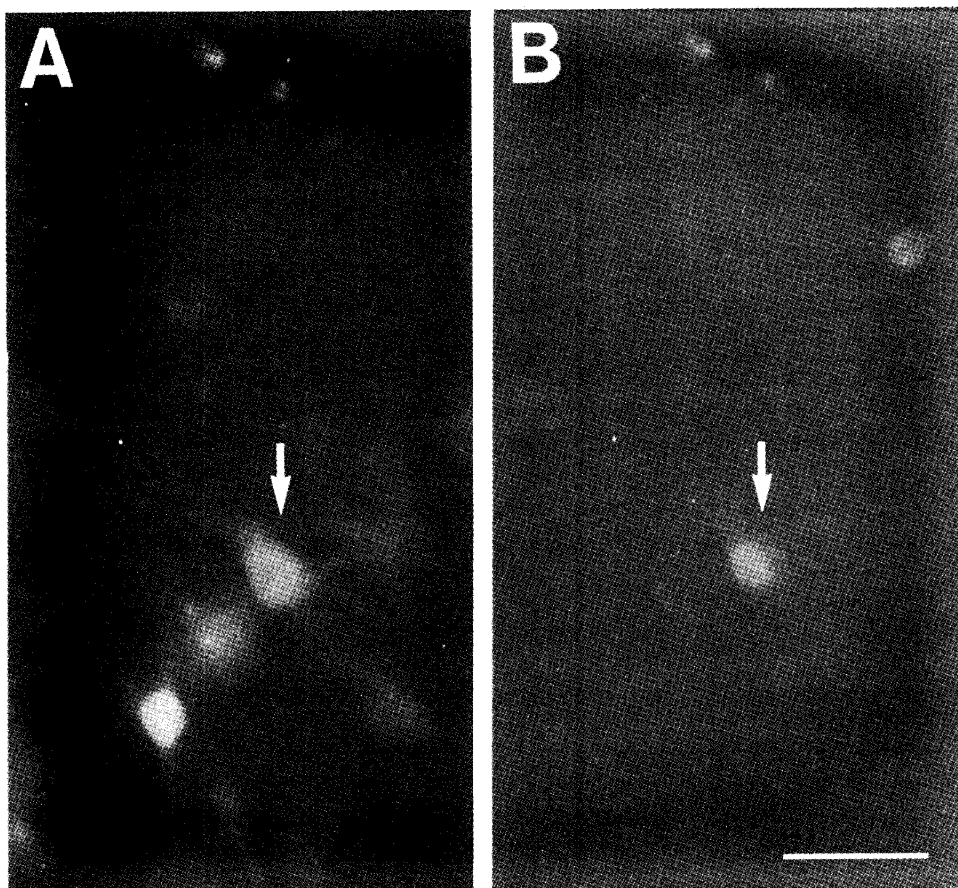


Fig. 1. Photomicrographs of fluorescent retrogradely-labeled neurons in the central lateral nucleus of the thalamus after injections of EB into the head of the caudate nucleus, and DAPI into the premotor cortex. A: EB-labeled neurons with red fluorescence in the cytoplasm (550 nm excitation wavelength). B: DAPI-labeled neurons with blue nuclear fluorescence (360 nm excitation wavelength). A and B show the same fields. The arrows indicate a neuron double-labeled with EB and DAPI. The white bar at the lower right = 50 μ m.

served in the thalamus. Numerous EB-labeled neurons were seen in the central lateral nucleus at its middle levels, and in the central dorsal (CD), centre médian (CeM) and parafascicular (Pf) nuclei at posterior thalamic levels. Occasional labeled cells were detected in the anteromedial (AM), paracentral (Pc), central medial (CM), rhomboid (Rh) and central anterior nuclei. Some labeled cells were found in the ventral anterior (VA) and ventral lateral (VL) nuclei. Cells labeled with EB were seen in the medial and central parts of the VA-VL. At middle thalamic levels, EB labeled cells were seen in the dorsal part of the Pf (PfD), CD,

CL, Pc, CM and Rh, surrounding the mediodorsal nucleus (MD). The distribution of labeled cells in the CL shifted from the dorsal part to the medial part toward caudal levels. Within the Pc, the labeling was found almost exclusively in its medial part. At caudal levels numerous labeled cells were detected in the CeM, spreading medially to the Pf. The fluorescence in the VA and VL was somewhat duller than that in the intralaminar nuclei.

At an excitation wave length of 360 nm, DAPI-labeled neurons displayed a blue fluorescence in the cell nucleus (Fig. 1B). In 19 cases, DAPI was transported in a retrograde direction to the thalamocortical neurons. The DAPI-labeled cells were found most abundantly in the VA and VL. Many labeled cells were also present in the ventral medial (VM), MD, Pf, CL and CD nuclei. Some cells in the CM, CeM, Pc, PfD and medial pulvinar (PM) nuclei were labeled with DAPI. Only a few labeled cells were found in the AM, Sm and Rh. Within the VA-VL, labeled cells were seen in the central part of the VA at middle levels, and in the medial half of the VL. In the VM, labeling was seen in its lateral part at anterior levels, spreading caudally to its posteriormost part. The labeling in the medial part of the CL spread into the lateral part of the MD, and caudally to the Pf. Some labeled cells were also detected in the PfD and CD, and a few in the adjoining portion of the PM.

Comparing the distribution of EB-labeled cells with that of DAPI-labeled cells, there was striking overlapping and interdigitation in the VA, VL, Pf, PfD, CD, CL, Pc, CM, CeM, AM and Rh. In 11 of 17 cases, in which EB or DAPI single-labeled cells were observed, a number of cells double-labeled with both EB and DAPI were found in the VA, VL, AM, Rh, CD, CL, CM, Pc and Pf (Fig. 1). The distribution patterns of these single- or double-labeled cells were classified into three groups. In the first group, double-labeled cells were detected in the VA-VL, but not in the intralaminar nuclei, where cells single-labeled with EB and those single-labeled with DAPI were intermingled (C79L, R, C81R, C86R, C117R). The second group is represented by double-labeled cells present in both the VA-VL and the intralaminar nuclei (C86L, C93R, C110L, C131R). In the third group, double-labeled cells were seen in the intralaminar nuclei or the midline nuclei, but not in the VA or VL (C108R, C109R). In 3 of the 5 cases in the first group, injections of EB were fairly well localized in the lateral part of the head of the NC at middle levels. In all of the cases in the second group, injected EB dye was located mainly in the central part of the head of the NC at middle levels spreading somewhat laterally. The third group consisted of two cases where the injection sites of EB were restricted to the central part of the head of the NC at middle levels, not including its lateral part. In the first and second groups, the distribution patterns of double-labeled cells in the VA and VL were almost the same. The cells double-labeled with EB and DAPI were distributed mainly in the central part of the VL, and appeared medially toward caudal levels, and some double-labeled cells were also detected in the central part of the VA at anterior levels. (Fig. 2). Such double-labeled cells in-

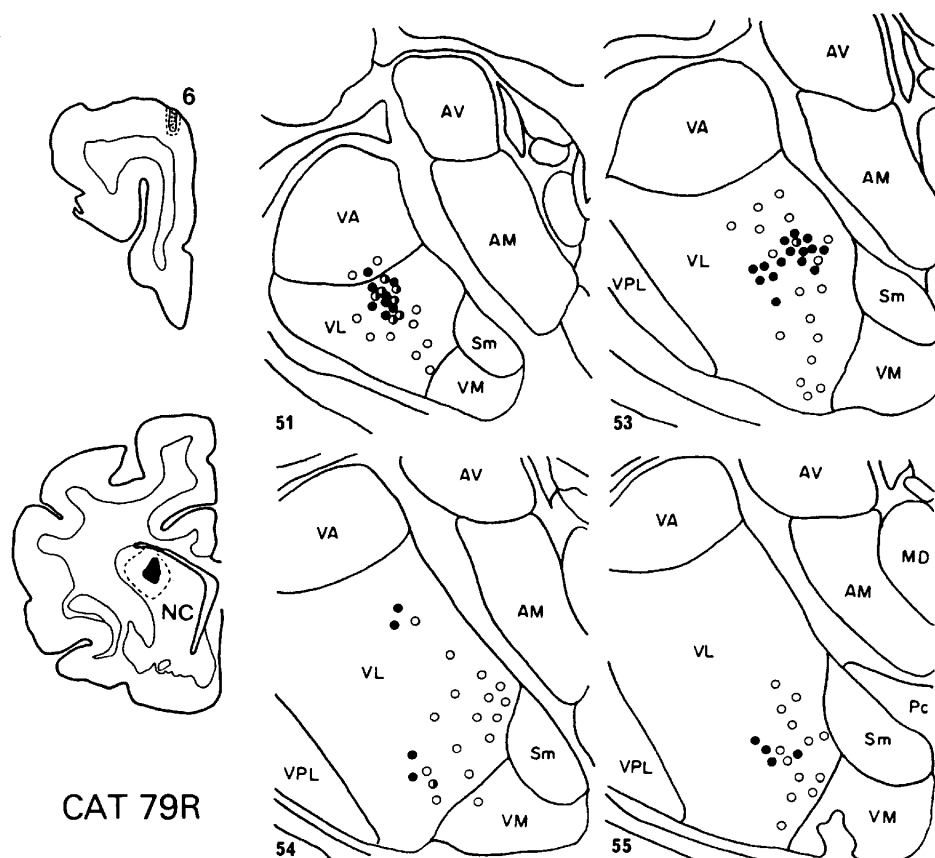


Fig. 2. The distribution of single- and double-labeled cells in the ventral lateral nucleus of the dorsal thalamus (51-55) following injections of DAPI (dotted area) into the premotor area (6), and EB (black area) into the head of the caudate nucleus (NC) in cat 79R. Dotted lines indicate the limitation of diffused dye. Each open circle and solid dot represents three cells single-labeled with DAPI and EB, respectively, and each half-solid circle represents one double-labeled cell. AM, anteromedial nucleus; AV, anteroventral nucleus; CD, central dorsal nucleus; CeM, centre médian nucleus; CL, central lateral nucleus; CM, central medial nucleus; LP, lateral posterior nucleus; MD, dorsomedial nucleus; Pc, paracentral nucleus; Pf, parafascicular nucleus; PiD, dorsal part of parafascicular nucleus; PMD, dorsolateral part of medial pulvinar nucleus; PMM, medial part of medial pulvinar nucleus; PMV, ventrolateral part of medial pulvinar nucleus; Sg, supragenicular nucleus; Sm, submedial nucleus; VA, ventral anterior nucleus; VL, ventral lateral nucleus; VM, ventral medial nucleus; VPL, ventral posterolateral nucleus; VPM, ventral posteromedial nucleus; VPML, lateral part of VPM; VPMM, medial part of VPM.

creased in number when injections were made in the lateral portion of the central part of the head of the NC. In the VA-VL, EB single-labeled cells were fewer than DAPI single-labeled cells, and only 10 % or less of these EB labeled cells were also labeled with DAPI.

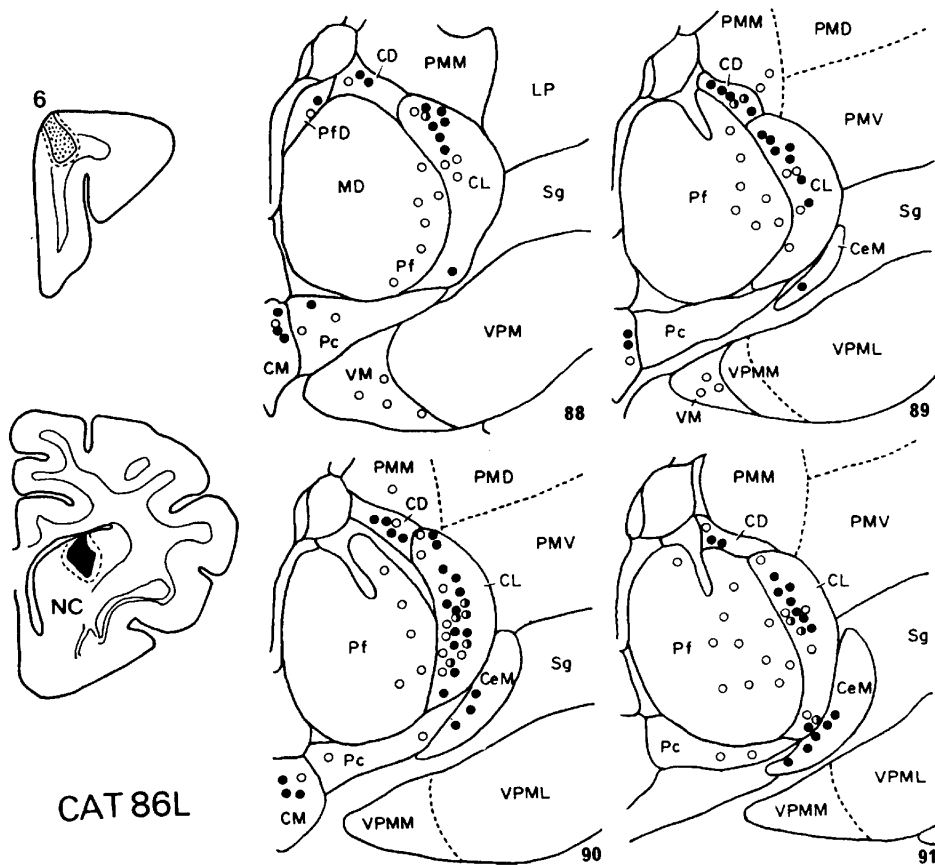


Fig. 3. The distribution of single- and double-labeled cells in the dorsal thalamus at middle levels (88-91) in cat 86L. Symbols and abbreviations as in Fig. 2.

In six cases of the second and third groups (C86L, C93R, C108R, C109R, C110L, C131R), some double labeled cells were also detected in the intralaminar nuclei, and a few in the midline nuclei (Fig. 3). In these cases most double labeled cells were seen in the CL and CD. At levels just rostral to the lateral geniculate body (LGB), many double labeled cells were found in the dorsal portion of the CL and the CD, which spread caudally to the medial portion of the CL nucleus. Some double labeled cells were detected in the CM and Pc at levels just rostral to the LGB. In C108R, a few double-labeled cells were also encountered in the AM and Rh at anterior thalamic levels, while in C93R many were observed in the dorsolateral portion of the Pf at the anterior level of the LGB. No double labeling was encountered in the CeM, in which cells single-labeled with EB were concentrated.

Control experiments with injections into the NC through an oblique approach

(C117R, C131R) revealed some double-labeled cells in the thalamus, in addition to numerous single-labeled cells.

DISCUSSION

Our data on the distribution of thalamic neurons projecting to the premotor area and to the caudate nucleus agree with the results of previous reports using horseradish peroxidase (3, 4, 6, 15-17). Our study provides direct evidence that some cells in the thalamic nuclei (VA, VL, AM, CD, CL, Pc, CM, Rh, Pf) give rise to diverging axons to both the premotor cortex and the head of the NC. These results have been published in the form of an abstract (23). Recently, Royce (28) and Macchi *et al.* (29), using the double labeling method, arrived at similar conclusions. In addition, our data demonstrate the differences in the distribution pattern of double labeled neurons caused by shifting the injection site in the head of the NC.

Concerning the VA and VL neurons, it appears that there are some differences between the neurons to the premotor cortex and those to the caudate nucleus. In the intralaminar nuclei, both cells labeled with EB and DAPI were quite brilliant. In the VA and VL, however, the labeling with EB was less intense than the DAPI labeling, although the distance from the VA and VL to the NC is shorter than that from the VA and VL to cortical area 6. This result may be due to the small transport capacity for dye of these VA and VL neurons projecting to the NC. Electrophysiological data indicates that the latencies of the antidromic responses of the VA neurons to the NC stimulation are longer than those to the medial portion of the anterior sigmoidal gyrus (area 6) (21). These electrophysiological data together with ours suggests that the fibers projecting to the NC have small diameters. Therefore, the VA and VL bifurcating neurons seem to send the stem axon to the cortex and the collateral branch to the NC. Electrophysiological data also indicates that low frequency repetitive stimulation of the entopeduncular nucleus (ENT) and/or globus pallidus (GP) fired the VA neurons projecting to both the NC and the medial portion of the anterior sigmoid gyrus synchronously with the cortical recruiting responses (21). These VA, and probably VL, branching neurons may receive input from the ENT and the GP and take part in the generation of the recruiting response in the cortex.

Our results indicate that the CD and CL neurons sending bifurcating axons to both the premotor cortex and the NC terminate in a certain part of the head of the NC. In most cases, many cells single-labeled with EB and DAPI were intermingled in the CD and CL nuclei. In a few cases, however, some cells double-labeled with EB and DAPI were also found in these nuclei (C86L, C93R, C108R, C109R, C110L, C131R). This may be due to the difference in the EB injection sites in the NC. Only in cases with EB injections into the head of the caudate nucleus, including the lateral portion of the central part, these double-labeled cells

can be seen in the CD and CL. It is probable that the double-labeled neurons in the CD and CL terminate predominantly in the lateral portion of the central part in the NC. It has been reported that projections of thalamic neurons to the NC are arranged topographically (16, 17). Especially, the parvocellular part of the CL (CLp) projects topically to the dorsolateral portion of the NC in the rostro-caudal direction (17). The present study reveals that the collateral fibers of the CLp neurons projecting to the ventromedial part of the pericruciate gyrus (area 6) terminate mainly in the lateral portion of the central part of the head of the NC.

The intralaminar nuclei receive ascending input from the brainstem reticular formation (30-32). It appears that this ascending input influences the discharge of the CL and Pc neurons and gives a general activating effect on the cerebral cortex (22). In the cat, the lateral part of the CL is considered to be the termination site of the spinothalamic fibers (33, 34), and seems to have some cells which emit axon collaterals to both the pericruciate cortex and the anterior suprasylvian gyrus (35). By contrast, the medial parvocellular part of the CL receives fibers from the intermediate and deep layers of the superior colliculus (15, 36, 37), the cerebellar nuclei (38, 39), the pretectal nuclei (37, 40), the perihypoglossal nuclei (41) and the ventral lateral geniculate nucleus (42, 43), and plays a significant role in the visuo-oculomotor mechanism (44, 45). However, there is no information on the participation of the NC in this mechanism. Moreover, the substantia nigra sends fibers to the intralaminar nuclei (38). It should be assumed that this motor-related information is integrated in the intralaminar nuclei, a part of which sends outputs simultaneously to the premotor cortex and the NC by axonal collateralization.

In conclusion, the present findings demonstrate ascending thalamic pathways to both the premotor cortex and the NC by means of divergent axons. The site of termination of these neurons in the head of the NC is mainly in the lateral portion of its central part.

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