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# Structural Organization, Neurochemical Characteristics, and Connections of the Reticular Nucleus of the Thalamus

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This review analyzes current concepts of the structural organization and ultrastructure of the reticular nucleus of the thalamus (RNT) and the neurochemical characteristics of its neurons. The topography, cytoarchitectonics, and neuronal organization of this nucleus are considered in detail, as are questions of its neurogenesis. Neurochemical data clarifying the representation of neurotransmitter systems in the RNT and data on neuropeptides synthesized in its neurons are systematized. The complex ultrastructural organization of the RNT is characterized in terms of recent data from state-of-the-art immunocytochemical methods allowing localization of glutamatergic and GABAergic receptors on synaptic elements. Data on the afferent and efferent connections of the RNT demonstrate its influences on various parts of the brain and the specific features of its interactions with cortical formations.

**KEY WORDS:** reticular nucleus of the thalamus, neuronal organization, neurochemistry, ultrastructure and connections.

Fifty years ago, the reticular nucleus of the thalamus (RNT) was regarded as a diffusely organized cell group tightly appressed to the brainstem reticular formation; it is now regarded as a complex with a clear internal organization and a modulatory role in controlling corticothalamic interactions [45]. Studies in recent years have demonstrated that it is involved in the pathogenetic mechanisms of absence epilepsy [6], investigations of which have also thrown light on fundamental questions of the interaction of the neocortex and the non-specific systems of the brain [3].

The aim of the present review was to analyze current concepts of the structural organization and ultrastructure of the RNT, as well as the neurochemical characteristics of its neurons.

**General Features.** All authors studying RNT structure describe it as a grouping of neurons forming a narrow band located lateral to the other thalamic nuclei. The RNT is located between the internal capsule (capsula interna), which forms its outer margin, and the external medullary plate (lamina medullaris externa) located internally to the cell groups of the nucleus. The nucleus is penetrated by corticothalamic and thalamocortical fibers [4, 31, 82].

This nucleus was first described in 1889 by Nissl , who termed it the *Gitterschicht*, characterized as a "grid layer" [80]. The term "reticular nucleus" was introduced by Munzer and Wiener in 1902 and became widely accepted by all subsequent authors [79].

Some authors regard the RNT as part of the dorsal thalamus [4, 28, 50, 53], while others include it among the structures of the ventral thalamus, in view of its neurogenesis [5, 11, 12, 85, 89]. Topographically, the RNT, having a significant dorsoventral extent, is among the structures of the dorsal (located laterally) and the ventral thalamus, tightly contacting the indeterminate zone (zone incerta).

Experiments based on lesioning of different areas of the cortex, along with results obtained from tracer studies, have demonstrated that the efferent fibers of the RNT do not reach the neocortex but are directed into the cerebral cortex via a variety of thalamic nuclei [39, 52, 53, 73, 90, 91, 95, 100].

**Cytoarchitectonics of the RNT.** Nissl [80] identified three areas in the rabbit RNT: a dorsal area, a ventral area, and a lateral area. Studies of the RNT in carnivores (cats) and rodents (weasels) showed it to contain three subnuclei. These were termed the main body of the reticular nucleus,

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the perireticular nucleus, and the parvocellular nucleus [31]. Studies of the topography of the afferent connections of the rostral area of the RNT revealed three parts, identified as the medial, intermediate, and lateral parts [19, 32]. The medial part, as shown by illustrations presented by these authors, includes a ventral portion of the reticular nucleus which, in accord with the arcuate configuration of the nucleus, is located closer to the midline of the brain on frontal sections, and a lateral portion, which is its dorsal portion.

The appropriateness of identifying dorsal and ventral parts in the main body of the RNT is supported by a number of studies [14, 33, 38]. The authors of these studies demonstrated that the ventral part of the RNT is approached by larger brainstem pathways, by which catecholamines can be delivered to neurons in the nucleus.

Some authors believe that the rat RNT contains a single neuron type, with ellipsoid bodies with a cross-sectional area usually of 10–20 μm. The longer diameters on frontal sections are aligned parallel to the long, dorsoventral axis of the nucleus [82]. This characteristic of the nucleus corresponds to earlier data showing that only fusiform neurons were found in the RNT [86, 95].

Detailed studies of the cytoarchitectonics of the RNT performed in the 1990s were initiated because of electrophysiological and tract course studies [43, 54]. These suggested that the rostral part is related to supporting motor and limbic functions, the intermediate part to somatosensory functions, and that the posterior part has connections with the visual centers and the statokinetic and auditory analyzers.

Further studies of the connections between the three areas of the RNT found successively in the rostrocaudal direction and cortical areas and other thalamic nuclei have now demonstrated that there is essentially no correspondence between defined functions and parts of the reticular nucleus. Each sector of the RNT is connected with more than one thalamic nucleus and neocortical area [44]. The authors of this study recognized that each sector has its own connections, though they noted that the RNT operates as a network in which functionally different cortical areas and thalamic nuclei can interact, modifying thalamocortical transmission via inhibitory connections running from the RNT to relay nuclei in the thalamus.

Studies of the cytoarchitectonic and cytological characteristics of RNT neurons in WAG/Rij rats (providing a model of absence epilepsy) showed that most RNT neurons are of intermediate and large size and are dark or light depending on their functional state. The authors also identified small neurons, accounting for 5–8% of all the neurons in this nucleus [7–10].

**Neuronal Organization of the RNT.** Data on the neuronal organization of the RNT are found in many reports from many authors [5, 72, 83, 96]. The most complete descriptions are from studies of the brains of carnivores [5]. All cells in the RNT were shown to be quite large, to have long axons, and to be reticular neurons, which have small numbers of long, straight and sparsely branched radial dendrites. Apart from typical reticular neurons, the RNT also contains transitional forms between reticular and densely branched neurons. These are characterized by short and more extensively branched dendrites, though in terms of a number of characteristics they resemble the brush neurons of other nuclei of the dorsal thalamus [5].

The reticular neurons of the RNT, unlike those of other thalamic nuclei, are characterized by having 2–3 terminal branches, which run parallel and form a dendritic bundle. It has been suggested that dendrodendritic contacts and interneuronal electrotonic interactions may exist in these bundles [5]. The dendrites also have numerous long, rod-like spines, which appear to be piliform spines [5]. Similar descriptions of the characteristics of dendrites in the intermediate areas of the RNT have also been provided by other authors [95]. The existence of fine outgrowths from dendrites gives RNT neurons a characteristic "shaggy" appearance.

The RNT has a very complex axon system [5]. Although the author of this study was unable to find typical short-axon neurons in the RNT, attention was drawn to the fact that the nucleus contained reticular neurons with axons distributed within their own dendritic territories, which is typical of short-axon cells. Various autapses were also detected, these being contacts between the processes of reticular nucleus neurons with other parts of the same cells, including contacts between axons and dendrites, which under the electron microscope should be seen as synapses along the axon (en passant). One of the characteristic features of the axons of RNT neurons is their division into thick, bifurcating branches which, leaving the nucleus, are directed to variety nuclei in the dorsal thalamus [5].

Studies of the cellular composition of the RNT have shown it to contain three types of neuron [96]. Large neurons with round bodies, which the authors designated R cells, were found predominantly in the rostral part of the nucleus, in its dorsal area. They have four primary dendrites running from the neuron body in different directions. The dendritic territory of these neurons is spherical in shape. The second population consists of large neurons with fusiform cell bodies (F cells), located in different areas of the nucleus. F cells have primary dendrites running from the different poles of the cells. A characteristic feature of these neurons is that they have a dendritic field such that dendrite branching is located in the horizontal plane (flattened horizontal dendritic fields). Small fusiform neurons (f cells) are located in the marginal zones of the nucleus, mainly in the middle third of its dorsoventral axis. The architectonic features of the dendrites of these cells are clearly demonstrated on horizontal sections. Secondary and distal dendritic branches are located perpendicularly to F-cell dendrites. Their bodies are very narrow – length is four times width. They have spines and dendrites similar to those seen on F cells. Outline sketches of Golgi silver

nitrate-impregnated sections did not allow the authors to conduct detailed studies of the characteristics of the axon systems of the nucleus [96].

Lübke studied the neuronal organization of the RNT throughout its rostrocaudal extent in rats, rabbits, and cats, and was unable to identify the structural characteristics of the dendrites of the neurons in this nucleus. The author indicated that neurons in the caudal and intermediate parts of the nucleus were extended in shape in all the animal species studied and were multipolar only in the rostral area. Large cells similar to R and F cells were described [72].

The studies of Pinault et al. [83] answered many questions about the neuronal organization of the RNT which had long been unsolved. Having identified RNT neurons on the basis of their characteristic responses to electrical stimulation using microelectrode methods, these authors filled them with biocytin or neurobiotin and studied then using light and electron microscopy. They showed that of 111 tracer-filled neurons, 12 had axons giving rise to collaterals within the RNT or close-lying thalamic nuclei. This provides grounds for suggesting that these cells may be short-axon neurons. They also observed that the axons of RNT neurons could run from the cell body (in 54 of 115 cells), from the proximal part of the dendrite (57 neurons), and the distal parts of dendrites (four cells).

**Neurogenesis of RNT Structures.** The formation of the RNT during individual development has received insufficient study. Investigation of the neurogenesis of thalamic structures (epithalamus, dorsal and ventral) in rats showed that the major processes develop from day 13 to day 19 of intrauterine development [75]. Neurogenesis is accompanied by the simultaneous presence of caudorostral, lateromedial, and ventrodorsal gradients of proliferation of the developing sectors.

Rat embryos and fetuses, as well as neonatal pups, have been studied using a $^3$H-thymidine method [11, 12]. Working from chrono-architectonic data, the author identified a series of neuron proliferation sectors – central, medial, and lateral. In the first-forming central sector (subnucleus), 50% of neurons appear on day 13 of intrauterine development; in the others, 40% develop on day 14. The peak of neuron proliferation occurs on day 14. On day 15, the medial sector develops 30% of its neurons and the lateral sector 12% of its neurons.

Studies of the rate of maturation of the GABAergic network of the RNT in the early postnatal period revealed GABA in the bodies, dendrites, growth cones, and synaptic terminals of neurons [21]. However, GABA-containing terminals were not numerous immediately after birth; numbers increased only after the end of the second week of development.

The mechanisms of ontogenetic development of the glia in the RNT in weasels and their expression of chondroitin sulfate-proteoglycans have been discussed in a report by Mitrofanis et al. [78]. Glia were identified using antibodies to vimentin and glial fibrillar acidic protein (GFAP). These studies showed that this protein is expressed in the RNT at a limited stage of the prenatal and postnatal periods (day 30 of intrauterine development to day one of postnatal life), forming a band of GFAP-expressing cells; this occurs earlier than in other thalamic nuclei.

**Neurochemical Characteristics of the RNT.** Results obtained from immunocytochemical studies of the rat RNT using light and electron microscopy using anti-GABA antibodies showed this nucleus to contain a homogeneous population of GABAergic neurons [23, 96].

Studies of the possible simultaneous location of amino acids (glutamate and aspartate) and GABA in the RNT demonstrated that most of its neurons are immunoreactive for GABA and that glutamate (and/or aspartate) is present simultaneously with GABA in most of these cells [42].

The RNT contains AMPA (α-amino-3-hydroxy-5-methyl-4-isoxazole propionic acid) and NMDA (N-methyl-D-aspartate) receptors [67]. Cox and Sherman [34] reported the existence of many subtypes of glutamate receptors on RNT neurons and identified a number of mechanisms by which they are involved in cell membrane excitability.

Mineff and Weinberg [77] supported data obtained by Lui [67] and showed that glutamate (GluR) and AMPA receptors are important for corticothalamic connections. The RNT was found to contain significantly more GluR4 and AMPA receptors than the posterior ventral nucleus [55]. The rat RNT contained glutamatergic afferent fibers from the limbic and motor centers of cortical formations, i.e., collaterals of the corticothalamic pathways [37, 53, 55].

The calcium-binding protein parvalbumin has been found in neuron bodies in the rat RNT, as well as in their dendrites and rare axonal terminals, simultaneously with GABA [13, 22, 25]. Two classes of relay neurons could be identified on the basis of their stainability using reactions for calbindin and parvalbumin [55]. Calbindin was located in the thalamus, without nuclear margins, while parvalbumin was concentrated in defined nuclei.

Neuropeptides observed in this nucleus can modulate the effects of neurotransmitters. Thus, in 1985, Kaneko et al. [57] reported the presence of vasoactive intestinal peptide (VIP) in RNT neurons throughout the nucleus, with the exception of its rostral part. In situ hybridization reactions showed that the rat RNT contains neurons expressing not only VIP, but also thyrotropin-releasing factor [18, 23].

Studies of the RNT in cats and weasels using antibodies to GABA, somatostatin, and parvalbumin showed that the main body of the RNT contains neurons immunoreactive to all the antibodies tested. In the parvocellular subnucleus, seen only in cats, neurons gave negative reactions for GABA and only a small group of these cells in the caudal part of this subnucleus gave positive reactions for parvalbumin [31].

In situ hybridization demonstrated neurons expressing preproenkephalin mRNA in the rostral part of the RNT in

adult rats. The rostral part of the RNT is regarded as a source of enkephalin-containing pathways to the nuclei of the dorsal thalamus. These data show that GABA and enkephalin can be colocated in neurons [49].

RNT neurons have been found to have receptors for opioid peptides, particularly type μ [26]. The functional heterogeneity of RNT neurons was identified using agonists of these receptors combined with microelectrode techniques in living slices. Studies of 28 neurons revealed two types of neuron in this nucleus, giving different reactions for agonists (D-Ala2, N-Me-Phe4, glycinol-5-enkephalin), the effects of which are mediated via calcium channels. Attempts to use δ and χ receptor agonists were unsuccessful. These data on opioid peptides are interesting because they suggest an involvement in the pathogenesis of absence epilepsy [63–65].

Tyrosine hydroxylase expression was seen throughout the RNT in the Syrian hamster by in situ hybridization [17]. The authors' finding of tyrosine hydroxylase mRNA led them to suggest that catecholaminergic neurons are present in this nucleus.

The RNT contain dopamine $D_1$ receptors [51]. These are located on spines, postsynaptic dendrites, and axon terminals. The high density of these receptors in the limbic areas and RNT led the authors to suggest that that they were involved in learning processes and the mechanisms of memory and recognition. RNT neurons were also found to bear $D_2$ and $D_4$ receptors, though there were no type $D_3$ receptors [58].

In addition, the nucleus may receive afferent fibers, both noradrenergic and serotoninergic, running from the basal ganglia, substantia nigra (pars reticulata), locus coeruleus, and various brainstem areas [16, 46, 56].

Studies of the RNT in the human brain demonstrated the presence of NADPH-diaphorase (NADPH-d)-positive cells, which produce nitric oxide using NADPH-diaphorase [2]. This method also allowed visualization of the structural details of neurons, which showed them to be reticular and short-axon neurons.

Immunocytochemical methods were used to detect glycosaminoglycans in the rat RNT [102], located on the surfaces of calretinin-expressing neurons.

Data on the presence of neurons immunoreactive to the enzyme cytochrome aromatase P450 in the RNT of rats aged 30–60 days are of interest; this enzyme catalyzes the formation of estrogens and is a marker for brain structures involved in its sexual differentiation [93]. The authors suggested that the RNT, like other brain areas containing this enzyme, may be involved in modulating the neuroendocrine system.

The interaction of corticothalamic relay cells is mediated by NMDA, AMPA, and glutamate receptors, while the interaction of neurons in the reticular and relay nuclei of the thalamus is mediated by $GABA_A$ and $GABA_B$ receptors [55].

**Characteristics of RNT Ultrastructure.** Electron microscopic studies of the RNT in cats demonstrated axons with intranuclear collaterals within its territory [108]. The immunocytochemical reaction for glutamic acid decarboxylase showed that axon collaterals and presynaptic dendrites were GABAergic [23]. It was also established that the GABA-immunoreactive bodies and presynaptic dendrites of RNT cells bear synapses of at least three different types of GABA-immunoreactive terminals.

Combined studies (electron microscopy, immunocytochemistry, HRP tracer methods, and degeneration studies) of the RNT demonstrated three morphological types of terminals: L, D, and F [82]. D (dark) terminals were characterized by their small size and content of densely located 42-nm spherical vesicles; these were of cortical origin. L (light) terminals were lighter and larger, with loosely distributed 46-nm spherical vesicles; these came from cells in the dorsal thalamus. F (flattened synaptic vesicles) terminals contained flattened synaptic vesicles, an electron-dense matrix, and may have been collaterals from the axons of neurons in the reticular nucleus itself. L and D terminals formed Grey type I synapses (asymmetrical) on the spines and main stems of dendrites and, more rarely, on the bodies of neurons and axon hillocks. F terminals formed Grey type II synapses (symmetrical).

Data were obtained in 1988 showing that the RNT contains ChAT (choline acetyltransferase)-immunoreactive synaptic axon terminals, whose neurons were located in the basal nucleus of Meynert, as well as in the nucleus pedunculopontinus and nucleus tegmentalis in the brainstem [45]. These brain centers are the most important sources of the cholinergic innervation of the RNT [99]. Studies using antibodies to the neurotrophin p75 receptor (p75NTR), which is synthesized only in neurons in the basal nuclei, described the characteristics of axons entering the rostral part of the RNT in three-week-old rats [81].

Noradrenergic terminals enter the RNT from the locus coeruleus and are collaterals of axons in the dorsal thalamus [16].

Administration of label into the somatosensory cortex revealed the monosynaptic connections of this area with RNT neurons [106]. Two classes of presynaptic terminals were seen, forming asymmetrical contacts on small dendrites. Presynaptic dendrites of the first class were less frequent than those of the second. They contained densely distributed vesicles and small mitochondria. Presynaptic terminals of the second class were characterized by sparsely distributed vesicles and several mitochondria, and accounted for one third of all labeled contacts. These data supported previous results [82].

Studies of the ultrastructure of the RNT in the monkey *Macaca fascicularis* combined with immunocytochemical detection of GABA-containing structures showed that most synaptic contacts (87.5%) in the anterior and posterior parts of this nucleus were formed by axon terminals lacking GABA [105]. These were asymmetrical and were located on dendrites and cell bodies. Some 6.4% of synapses were

with GABAergic presynaptic terminals, which formed symmetrical synapses with the dendrites of reticular neurons.

Studies of RNT ultrastructure in WAG/Rij rats revealed dark and light neurons, whose characteristic shape depended on the characteristics of their functional state. Data were first obtained on the ultrastructure of small RNT neurons which, based on their characteristics, were regarded by the authors as short-axon neurons [9]. Studies of the ultrastructure of interneuronal interactions demonstrated the presence of various types of synapses, including dendrosomatic, axoaxonal, and dendrodendritic, most of which were chemical synapses. Electrical synapses were first discovered among groups of neurons formed by a dendrite and a neuron body, these being located alongside an axosomatic asymmetrical synapse whose presynaptic component was an F-type terminal [9, 24].

Data on intercellular non-synaptic contacts in the RNT are presented in a study on WAG/Rij rats [7]. These could be desmosome-like, dense, fused-membrane, and septated contacts. RNT neurons may also interact by ephaptic transmission and ionic interactions, occurring on accumulation of $K^+$ ions in the intercellular space after increased activity in the nerve endings and in neighboring neurons.

Studies of the projections from the limbic area of the cortex using tracer methods (horseradish peroxidase, biocytin, neurobiotin, fluorescent dextran) showed that terminals arriving in the RNT were type D; these formed asymmetrical synapses on dendrites [70]. It was also shown that the terminals of fibers arriving in the RNT from the anterior medial and ventral nuclei of the thalamus contain densely located synaptic vesicles and form asymmetrical synapses on the bodies of reticular neurons and their dendrites [71].

The localization of AMPA and NMDA receptors on synaptic elements in the RNT was first demonstrated in 1997 [67] by studies showing that these were uniformly distributed on the bodies and the proximal and distal parts of dendrites.

The RNT was found to contain dendrodendritic and dendrosomatic synapses [83]. Their postsynaptic components, described previously as axon-like processes, are derivatives of the dendrites and bodies of reticular cells.

Synapses in the rat RNT were studied in fixed brain slices after administration of the stain Lucifer yellow into cells of the reticular nucleus; the terminals of corticothalamic connections were visualized by administration of *Phaseolus vulgaris* leukoagglutinin, while GABA-containing connections were visualized immunocytochemically [68]. The authors showed that the nucleus contained three types of terminals: small (ST), large (LT), and GABA-containing; these were described on all parts of the dendrite stems. Small and large terminals formed asymmetrical synaptic contacts. On the proximal parts of dendrites, about 50% of synapses were formed by small terminals, while 30–40% were formed by large terminals and 10–25% by GABA-containing terminals.

About 30% of synapses detected around the perikarya of parvalbumin-immunopositive neurons were found to be somatodendritic. Their formation involved large dendrites of neurons in specific thalamic nuclei [36]. These synapses were GABA-containing synapses.

It is generally accepted that RNT neurons provide the inhibitory input in the relay nuclei of the thalamus and generate synchronous activity during sleep and convulsions [62]. Until recently, it was considered that RNT neurons interact via chemical synapses. However, more recent investigations performed on living slices have demonstrated that many RNT neurons, lying in rows, in rats and mice can interact via electrical synapses [62]. The authors took the view that these latter provide a mechanism allowing the nervous system to support the synchronized activity of inhibitory neurons in mammals. It has been suggested that electrical synapses in the RNT may coordinate the spindle-frequency rhythm generated by small groups of neurons bearing metabotropic glutamate receptors [69].

**Connections of the RNT.** The RNT is located at the crossroads of the ascending and descending pathways running from cortical formations to the thalamus and on to the brainstem and, conversely, from stem structures to the cerebral cortex. It is important to note that most pathways passing through the RNT give rise to collaterals within it. The dendrites of neurons in the adjacent thalamic nuclei may also extend into the RNT.

*Efferent fibers* are distributed only within the thalamus. This was first demonstrated by investigators summarizing published data on the connections of this nucleus [53]. These data were subsequently expanded in detail. RNT neurons were found to project to the opposite dorsal thalamus – to the anterior and intralaminar nuclei and to the ventromedial nucleus [85].

Experiments using tracers showed that the medial part gives rise to *commissural fibers* running to the RNT in the opposite hemisphere [30]. The authors believed these fibers to be important in supporting the generation of sleep spindles and suggested that they may also be involved in the processes synchronizing diffuse modulatory actions on the associative areas of the cortex.

This view that commissural RNT fibers are important is supported by the suggestion that the RNT, acting via bilateral (symmetrical) connections with the intralaminar nuclei of the thalamus, can affect the activity of extensive zones of the cortex and basal ganglia in both hemispheres [19, 30, 85]. These data were supplemented by other investigators, who demonstrated that the connections of the RNT with the intralaminar nuclei and midline nuclei (non-specific nuclei) were more diffuse than those with the specific dorsal nuclei [59].

Efferent fibers running from the RNT to the anterior group of thalamic nuclei were identified in rabbits [84]. These ran from GABAergic nuclei in the RNT to the anteroventral and anterodorsal nuclei of the thalamus [41],

forming F terminals in these nuclei [103]. Fibers ran from the rostral part of the RNT to the limbic sector of the thalamus, consisting of the anteroventral and anteromedial nuclei [71]. GABA-containing terminals from the RNT were present in the ventral nuclear complex of the thalamus [94, 98]. The RNT is connected with the medial geniculate body [35].

Thus, these data show that the reticular nucleus projects exclusively to the thalamus [76].

*Afferent fibers* arrive in the RNT from the thalamic nuclei, brain stem, basal nuclei, and cortical formations.

Axon collaterals from nuclei in the ventrobasal nucleus of the thalamus are directed to the RNT [47]. Subsequent studies showed that the axons of neurons in the ventral posterior parvocellular nucleus of the thalamus [98], as well as its mediodorsal and paraventricular nuclei, enter the territory of the RNT [32]. Connections of the RNT via the paraventricular nucleus of the thalamus with the basal ganglia of the brain show that the RNT may be involved in the mechanisms of Parkinson's disease. There are also data on afferent fibers arriving from the lateral geniculate body [71].

Connections between the reticular formation of the brainstem and the RNT have been demonstrated [20]. These data were made more precise by subsequent studies, which revealed afferent fibers running from the gigantocellular nucleus of the reticular formation of the medulla oblongata to the mediobasal nucleus and the RNT [101].

In amphibia (*Rana esculenta*), injection of leukoagglutinin into the lateral vestibular nucleus demonstrated that the projections of the RNT to the midbrain were similar to those in mammals [74]. Studies in recent years have demonstrated ipsilateral connections of the nucleus emboliformis and the nucleus dentatus of the cerebellum with the rostral part of the RNT [29].

There are connections between groupings of neurons located around the central aqueduct of the brain and the adjacent parts of the reticular formation (nucleus tegmentalis, nucleus pedunculopontinus, area tegmentalis ventralis, and pretectum medialis) with the RNT [32]. The source of connections with the RNT is the substantia nigra, which projects to the ventral part of this nucleus [40, 60]. The axons of neurons in the nucleus pedunculopontinus and nucleus tegmentalis laterodorsalis, running on to the intralaminar nuclei, give rise to collaterals which reach the rostral part of the RNT. Conversely, axons running from midbrain centers and the pons to the sensorimotor nuclei of the thalamus give rise to collaterals in the caudal part of the RNT [97].

Some brainstem nuclei give rise to projections to the RNT directly and via the dorsal thalamus, and have influences on thalamocortical interactions [60, 61]. Fibers from the medial part of the pons and midbrain components of the reticular formation arrive in the ventral part of the RNT [14].

Afferent fibers running from the basal nucleus of Meynert are the most important source of the cholinergic innervation of the RNT [53, 92]. Connections are also known between the RNT and the medial part of the globus pallidus [32, 40]. The courses of fibers from the medial and olfactory nuclei of the amygdaloid body running to RNT neurons have been characterized [87].

The most powerful afferent connections of the RNT are with cortical formations. A number of tracer labels were administered into the somatosensory area of the cortex to identify their projections to the RNT [70].

Anterograde and retrograde tracer studies with lectin showed that the projections from the cingulate, orbital, and infralimbic cortex run from layer VI to the lateral, intermediate, and medial parts of the nucleus [32]. This was subsequently supported by Levesque et al. [66], who found that the secondary somatosensory area of the cortex in rats contained neurons in layer VI whose axons were directed to the thalamic nuclei, giving rise to collaterals to the RNT.

Afferent fibers from layer IV of the somatosensory cortex (the barrel field) run to projection neurons [104, 107].

Pathways from the auditory cortex have been studied. These investigations demonstrated that fibers from the primary auditory cortex pass through the internal capsule and then through the caudate nucleus and putamen, crossing the reticular nucleus. Some of these give rise to collaterals on RNT territory, branching in the auditory sector [88, 92]. It is also known that descending fibers from the auditory field of the neocortex to the medial geniculate body pass through the RNT, generating axon collaterals [48]. It is possible that connections exist between the auditory cortex and the dorsolateral, posterolateral, and subgeniculate nuclei of the thalamus [15, 27].

## CONCLUSIONS

The RNT occupies a special place among the thalamic nuclei. It is a grouping of neurons which is penetrated by corticopetal (ascending from the brainstem) and corticofugal (descending from the cortex) fibers. Most of the axons passing through RNT give rise to collaterals within its territory [1]. Afferent fibers arriving in the RNT from the cortex are glutamatergic and have excitatory influences. RNT neurons contain GABA and its influences on the structures connected to it are inhibitory. The function as a unique regulator of the state of neurons connected to the RNT is mediated in this nucleus on the background of integration of information arriving within it from specific and non-specific brain systems.

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