# **Review**

# Intrathalamic sensory connections mediated by the thalamic reticular nucleus

### J. W. Crabtree

Department of Anatomy, School of Medical Sciences, University of Bristol, Bristol BS8 1TD (UK), Fax +44 117 929 1687, e-mail: J.W.Crabtree@bristol.ac.uk

Received 11 May 1999; received after revision 15 July 1999; accepted 21 July 1999

Abstract. The thalamus and cerebral cortex are linked together to form a vast network of interconnections. Different modes of interactions among the cells in this network underlie different states of consciousness, such as wakefulness and sleep. Interposed between the dorsal thalamus and cortex are the GABAergic neurons of the thalamic reticular nucleus (TRN), which play a pivotal role not only in switching between the awake and sleep states but also in sensory processing during the awake state. The visual, somatosensory,

and auditory sectors of TRN share many of the same organizational features. Each of these sectors contains maps, which are related to its inputs and outputs, and organizational components called 'slabs.' It is proposed that, during wakefulness, TRN is crucially involved in resetting the activity levels in sensory nuclei of the dorsal thalamus, which allows the cortex to actively and periodically compare its ongoing sensory processing with the available sensory information.

**Key words.** Sensory processing; GABAergic neurons; reticular sectors; cortical projections; intrathalamic projections; organizational components; sensory maps; reticular discontinuities.

# Introduction

In mammals, neurons in the thalamus and cerebral cortex form a vast network of interconnections [1–7]. Different modes of interactions within this network underlie different states of consciousness, such as wakefulness and sleep [1, 4, 8–11]. The neural mechanisms that give rise to changes from one conscious state to another operate in the thalamus [1, 3, 4, 6, 8–17]. During wakefulness, sensory information gains access to the cortex only after considerable processing in the thalamus and, when falling asleep, the thalamus functionally disengages the cortex from ascending sensory inputs. A key player involved in these mechanisms is the thalamic reticular nucleus (TRN), which in carnivores includes the perigeniculate nucleus (PGN). The crucial role that TRN plays in promoting sleep- and wake-

related thalamic activity is well established [1, 4, 8–11, 14, 18; see also 3, 6, 13, 15–17, 19, 20]. However, the function of this nucleus in thalamic sensory processing during wakefulness is still far from clear. Thus, the purpose of this review is to inquire into the role(s) that TRN might play in sensory processing in relation to our current understanding of the anatomical connectivity of this nucleus.

# The thalamic reticular nucleus

A derivative of the ventral thalamus [21], TRN is a sheet of cells that surrounds much of the dorsal thalamus and lies between the dorsal thalamus and the cortex (fig. 1). The nucleus is bordered medially by the external medullary lamina (EML) and laterally by the

internal capsule (IC). Because of its anatomical position, TRN is traversed across its thickness by virtually all axons passing between the dorsal thalamus and cortex, giving the nucleus its reticulated appearance and name. As these thalamocortical and corticothalamic axons pass through TRN, many of them give off collaterals [22-24], providing the nucleus with both dorsal thalamic [24] and cortical [24, 25] sources of innervation (fig. 1). These collaterals extend from their parent axons at approximately right angles and thus are generally oriented parallel to the reticular plane [26–32]. Furthermore, the cortical afferents to TRN are specifically from layer VI [30, 31]. TRN also receives afferents from a variety of nonthalamic subcortical structures, such as the brainstem reticular formation [33-40] and the basal forebrain [35, 36, 41-43].

The main targets of the efferents of TRN are dorsal thalamic nuclei [22–24, 44]. Some of these nuclei can be classified as 'first order' or 'higher order' [5, 6, 45] and representations of each sensory modality are presumably contained in at least one first-order nucleus and at least one higher-order nucleus. First-order thalamic nuclei receive their main driving inputs through ascending sensory pathways and transmit information about stimuli in the sensory periphery to the cortex. Higher-order thalamic nuclei are thought to receive

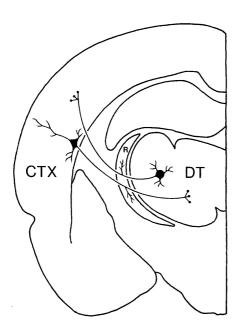


Figure 1. Schematic representation in the coronal plane of the position of the thalamic reticular nucleus (R) in relation to the dorsal thalamus (DT) and the cerebral cortex (CTX). Axons from the dorsal thalamus and cortex give off collaterals as they traverse the reticular nucleus.

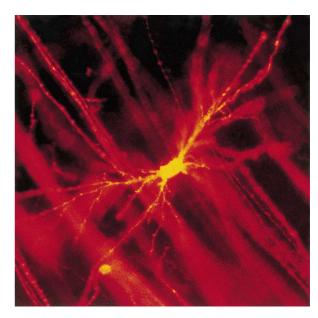


Figure 2. A labelled thalamic reticular cell and labelled thalamocortical and corticothalamic axons after a small crystal of DiI was placed into the dorsal thalamus of a rabbit. Note the extensive distribution of the reticular dendrites and their position relative to the traversing axons.

their main driving inputs through descending pathways from cortical layer V and transmit information about sensory processing in one cortical area to another cortical area.

The mammalian TRN appears to be made up entirely of  $\gamma$ -aminobutyric acid (GABA)ergic neurons [rodent: 46–49; primate: 50; carnivore: 47, 51–54; lagomorph and marsupial: 55]. The reticular somata are usually elongated parallel to the plane of TRN and the reticular dendrites extend for relatively long distances, forming disc-shaped fields that also lie parallel to the TRN plane [23, 53, 56–62]. Figure 2 shows a reticular cell in the rabbit's TRN, labelled with the fluorescent tracer DiI, and illustrates the orthogonal relationship between the dendrites of a reticular cell and traversing thalamocortical and corticothalamic axons.

# Thalamic reticular sectors

One striking organizational feature of TRN is its partition into several well-defined sectors that are distributed along the plane of the nucleus like a patchwork quilt. A TRN sector is defined as that region that (i) receives projections from a particular dorsal thalamic nucleus and the cortical area that is reciprocally connected to that nucleus and (ii) sends projections back to the

dorsal thalamic nucleus from which it receives projections [24, 25, 63-65]. The topographic organization of the reticular sectors was initially thought to reflect a general cortical organization, whereby adjacent areas along the cortical sheet would be represented by adjacent sectors along the reticular sheet. However, we now know that several functionally related cortical areas can send projections to the same reticular sector and that one reticular sector can receive projections from and send projections to several functionally related dorsal thalamic nuclei. The projections of single cells from a given reticular sector usually have restricted terminal fields within a dorsal thalamic nucleus [62] and, together with the thalamoreticular projections, these reticulothalamic projections usually form open-loop rather than closed-loop circuits [66]. In regard to the role of TRN in sensory processing during wakefulness, I will focus on what is known about the functional connectivity of the visual, somatosensory, and auditory sectors of TRN.

#### The visual reticular sector

The visual sector of the mammalian TRN occupies a discrete dorsocaudal region of the nucleus [rodent: 58, 67, 68; lagomorph: 69-71; carnivore: 72; primate: 73-76], which specifically includes PGN in carnivores [72, 77, 78]. This region lies adjacent to the dorsal lateral geniculate nucleus (dLGN), a first-order visual nucleus of the dorsal thalamus. The visual sector receives excitatory afferents from the visual cortex [52, 57, 58, 79, 80], which appear to provide predominantly 'modulatory' inputs [17, 81]. The visual sector also receives excitatory afferents from dLGN [67, 68, 70, 78, 82-85] and from higher-order visual nuclei of the dorsal thalamus, the lateral posterior nucleus (LP) and pulvinar (Pul) [84– 87]. These thalamic afferents provide 'driving' inputs [17, 52, 57, 58, 80]. In return, the visual sector sends efferents to dLGN, which make F-type synapses [76, 88-90] and which have inhibitory effects on lateral geniculate neurons [67, 91-99]. Thus, cells in dLGN and the visual sector of TRN form intrathalamic excitatory-inhibitory networks [18, 100-104]. It would appear that open-loop circuits are a more common feature of these networks than closed-loop circuits [97, 104]. The visual sector also sends efferents to LP and Pul [89, 105].

# Organizational components

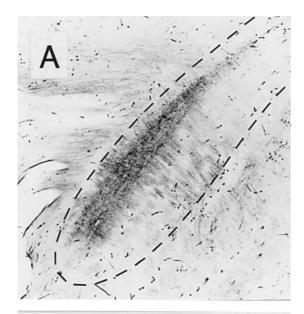
Each first-order sensory nucleus in the dorsal thalamus is a three-dimensional structure that contains a map of a peripheral receptor surface (e.g., retina, skin, or cochlea). The map of the retina and the map of the skin each occupy two dimensions within a nucleus, whereas the

map of the cochlea occupies only one nuclear dimension. The other dimension(s) of a nucleus contains organizational components, which are continuously distributed without borders and are regions of relative isorepresentation of local areas of the receptor surface. In dLGN these components are 'columns' [106, 107; see also 108] that extend along one entire dimension of the nucleus perpendicular to the dimensions that contain the retinotopic map. The columns are formed either by terminals in dLGN from focal areas of cortex or by lateral geniculate neurons that project to focal areas of cortex. Because the visual sector of TRN is also a three-dimensional structure, it should also contain organizational components and these would indicate not only the presence of a map but also its orientation. It was initially thought that each sector of TRN would reflect a cortical organization [25, 63, 64] whereby the organizational components would extend across the thickness of the nucleus. Contrary to this expectation, in the visual sector of the rabbit [71; see also 69], the bushbaby [75, 76; see also 73], and the rat [109], the organizational components are 'slabs' that are oriented parallel to the plane of TRN. As demonstrated in the rabbit's visual sector [71], figure 3 shows horizontal sections through both a slab of terminal labelling (fig. 3A), which resulted from an injection of horseradish peroxidase (HRP) into visual cortical area 1 (V1), and a slab of labelled TRN cells (fig. 3B), which resulted from an injection of HRP into dLGN. However, the organizational components in the carnivore PGN presumably extend across the thickness of this nucleus perpendicular to the retinotopic map (see below).

# Topographic organization of inputs and outputs

The visual sector receives afferents from several, if not all, visual areas of the cortex [72, 74]. The terminal distributions of these afferents provide a major clue as to the organization of the efferents of the visual sector (cf. figs. 3A and B). In this sector, inputs from V1 (area 17) and from higher-order visual areas terminate, respectively, in an outer zone (closest to IC) and an inner zone (closest to EML) in the rabbit [69, 71], the bushbaby [75, 76], and the rat [109, 110]. Furthermore, in the outer V1/area 17-related zone, there is a well-organized retinotopic map of cortical inputs that is oriented perpendicular to the plane of TRN and to the organizational components of the map (see fig. 3A) [69, 71, 75, 109]. However, in the cat, inputs from area 17 terminate in the inner-lying PGN [32] and the map of cortical inputs in this nucleus is presumably oriented parallel to its plane [72].

The visual sector sends efferents to both first-order and higher-order dorsal thalamic nuclei and the thalamic projections of single neurons from this sector have restricted terminal fields [62, 90, 111, 112]. Figure 4 shows the axonal distribution of an HRP-labelled PGN cell within dLGN of the cat [111]. The outputs from the visual sector to dLGN and to LP and/or Pul arise from outer and inner zones, respectively, in the rabbit [71], the bushbaby [75, 76], and the rat [109, 110; see also 84,



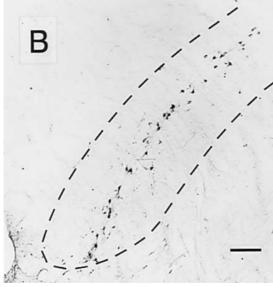


Figure 3. Horizontal sections through the thalamic reticular nucleus of the rabbit. Rostral is at the top and medial is to the right. Scale bar =  $200 \, \mu m$ . Reprinted with permission from Crabtree and Killackey [71], © 1999 Blackwell Science Ltd, Oxford. (A) Labelled terminals after an injection of horseradish peroxidase (HRP) into visual cortical area 1. The borders of the nucleus are indicated by the dashed line. (B) Labelled cells after an injection of HRP into the dorsal lateral geniculate nucleus. The borders of the reticular nucleus are indicated by the dashed line.

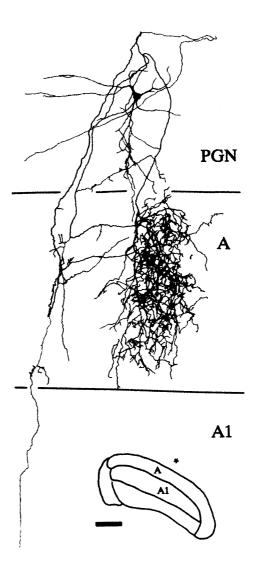


Figure 4. Reconstruction of an HRP-labelled cell in the perigeniculate nucleus (PGN) showing a dense axonal arbor that is restricted to lamina A of the dorsal lateral geniculate nucleus. Dorsal is at the top and medial is to the left (scale bar =  $100~\mu m$ ). Below is shown a lower-power outline of the dorsal lateral geniculate nucleus and the location of the labelled perigeniculate soma (asterisk) (scale bar = 1.0~mm). Reprinted with permission from Uhlrich et al. [111] T,  $\odot$  1999 The American Physiological Society, Bethseda, MD.

85]. Furthermore, the reticular cells projecting to dLGN form a well-organized retinotopic map [71, 75]. This map is oriented perpendicular to the plane of TRN and to the organizational components of the map (see fig. 3B) and is in register with the map formed by V1/area 17 inputs. Presumably, the dLGN-related map in the carnivore PGN is oriented parallel to the plane of this nucleus. However, the reticular cells projecting to LP and/or Pul do not appear to form a map [75, 86, 87].

The visual sector also receives afferents from first-order and higher-order nuclei of the dorsal thalamus [24, 26, 68, 86, 87]. In the rabbit [71] and the bushbaby [75], there appears to be a well-organized retinotopic map of lateral geniculate inputs in the visual sector, which is in register with the maps formed by V1/area 17 inputs and by reticular cells that project to dLGN. However, in the cat, inputs in the visual sector from cells in the LP-Pul complex do not appear to form a map [86].

# Receptive fields

Compared to the receptive fields of neurons in dLGN, the receptive fields of neurons in the visual sector of TRN, including PGN in carnivores, differ substantially [68, 77, 78, 81, 113]. They are noticeably larger, exhibit both on- and off-center responses, and are binocular. Nevertheless, there is evidence for a well-organized retinotopic map in the rat's TRN [68] and the cat's PGN [77]. The map in the cat's PGN is unique in that it reflects a direct spatial continuation of the organizational components in a first-order dorsal thalamic nucleus (i.e., dLGN).

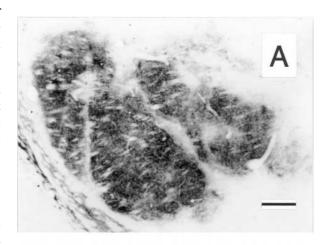
# The somatosensory reticular sector

In the mammalian TRN, the somatosensory sector occupies a discrete centroventral region of the nucleus [rodent: 58, 114–117; primate: 118; carnivore: 53, 118– 120; lagomorph: 121]. This region lies adjacent to the first-order somatosensory nuclei of the dorsal thalamus, the ventrobasal complex (VB). The somatosensory sector receives excitatory afferents from the somatosensory cortex [122, 123], which presumably provide modulatory inputs. The somatosensory sector also receives excitatory afferents from VB [53, 114, 118, 123-126] and from the medial part of the posterior complex (POm) [127], which is a higher-order somatosensory nucleus of the dorsal thalamus. These thalamic afferents provide driving inputs. In return, the somatosensory sector sends efferents to VB, which make F-type synapses [122, 128, 129] and which have inhibitory effects on ventrobasal neurons [93, 125, 126, 130–136]. These intrathalamic connections allow cells in VB and the somatosensory sector of TRN to form excitatory-inhibitory networks [137], which appear to be largely made up of open-loop circuits [125; see also 131]. The somatosensory sector also sends efferents to POm [53, 127, 138].

# Organizational components

Organizational components in VB are composed of elongated clusters of neurons that form 'barreloids' in

the rodent [139, 140] or 'rods' in the primate [141, 142]. These components in VB extend along one dimension of the complex at right angles to the dimensions that contain the somatotopic map. In the cat, the nuclei themselves that make up VB provide a rather striking example of large-scale organizational components. Figure 5A shows an oblique coronal section through the cat's VB following staining with monoclonal antibody Cat-301 [143]. The staining pattern exactly corresponds not only to the nuclei of VB, the ventroposterior medial



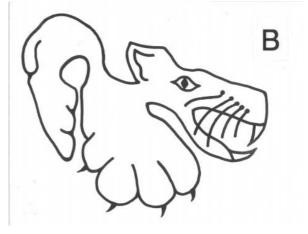
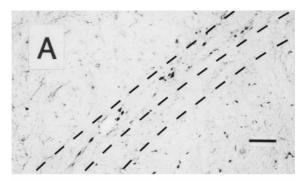


Figure 5. (A) Oblique coronal section through the ventrobasal complex of a cat showing immunoreactivity to monoclonal antibody Cat-301. Dorsal is at the top and medial is to the right. The Cat-301-stained tissue is divided into three compartments corresponding medially to laterally with the ventroposterior medial, the medial part of the ventroposterior lateral, and the lateral part of the ventroposterior lateral nuclei. Scale bar = 500 μm. Reprinted with permission from Crabtree and Kind [143], © 1999 Kluwer Academic Publishers, Dordrecht. (B) Schematic representation of an oblique coronal section through the cat's ventrobasal complex. The somatotopic map as determined by evoked potentials to peripheral stimulation is shown. Adapted from Mountcastle and Henneman [144] and Rose and Mountcastle [145].



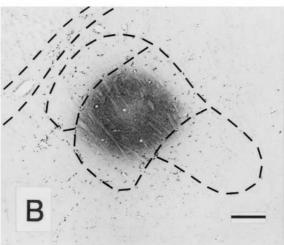


Figure 6. Horizontal sections through the somatosensory thalamus of the cat. Rostral is at the top and medial is to the right. Reprinted with permission from Crabtree [120], © 1999 John Wiley & Sons, Inc., New York. (A) Labelled cells in the thalamic reticular nucleus after the injection of wheatgerm agglutinin (WGA)-HRP shown in B. The dashed lines indicate the rostrolateral border of the ventrobasal complex (lower right dashed line) and the inner and outer borders of the reticular nucleus (central pair of dashed lines). Scale bar = 200 μm. (B) Reaction product after an injection of WGA-HRP in the medial part of the ventroposterior lateral nucleus. The dashed lines indicate the borders of the nuclei of the ventrobasal complex (center) and the thalamic reticular nucleus (upper left-hand corner). Scale bar = 500 μm.

nucleus and the medial and lateral divisions of the ventroposterior lateral nucleus, but also to the somatotopic map in VB (fig. 5B) as determined electrophysiologically [144, 145]. The somatosensory sector of TRN should also contain organizational components, indicating the presence and orientation of a map. Again, the organizational components in this sector are 'slabs,' formed either by terminals from focal areas of cortex or by reticular cells that project to the dorsal thalamus, and these slabs lie parallel to the plane of TRN [cat: 119, 120; rabbit: 121; rat: 138; see also 117]. As demon-

strated in the cat's somatosensory sector [120], figure 6 shows a horizontal section through a slab of labelled cells in TRN (fig. 6A) and a horizontal section through an injection site in VB (fig. 6B). The labelled cells in TRN (fig. 6A) resulted from a large injection of wheatgerm agglutinin (WGA)-HRP in the forelimb representation of VB (fig. 6B).

# Topographic organization of inputs and outputs

The somatosensory sector receives afferents from some, if not all, somatosensory areas of the cortex. Again, the terminal distributions of these afferents provide a major clue to the organization of the efferents of the somatosensory sector. In this sector in the mouse [117], the cat [119], and the rabbit [121], inputs from somatosensory area 1 (S1) terminate across the entire thickness of TRN. In the cat [119], these S1-related inputs are overlapped by those from somatosensory area 2. Moreover, there is a well-organized somatotopic map of S1 inputs that is oriented perpendicular to the plane of TRN and to the organizational components of the map [117, 119, 120].

The somatosensory sector sends efferents to both firstorder and higher-order dorsal thalamic nuclei. The overall impression is that the thalamic projections of single neurons from this sector have relatively restricted terminal fields [53, 138, 146]. For the rat, figure 7 shows the axonal distribution of a biocytin-labelled TRN cell within VB [146] and figure 8 shows the axonal distribution of a biocytin-labelled TRN cell within POm [138]. Whereas in the rat the outputs from the somatosensory sector to VB and to POm tend to arise mainly from outer and inner zones, respectively [127, 138], in the cat these outputs arise from overlapping zones across the thickness of the sector [120]. Furthermore, well over half of the cells in the cat's somatosensory sector projects to both VB and POm. In addition, the reticular cells projecting to VB form a well-organized somatotopic map [120, 138]. This map is oriented perpendicular to the plane of TRN and to the organizational components of the map (see fig. 5A) and is in register with the map formed by S1 inputs. However, the reticular cells projecting to POm do not appear to form a map [120, 138].

The somatosensory sector also receives afferents from first-order and higher-order nuclei of the dorsal thalamus [24, 27, 28]. In the cat [120], there appears to be a well-organized somatotopic map of ventrobasal inputs in the somatosensory sector, which is in register with the maps formed by S1 inputs and by reticular cells that project to VB. However, inputs in the somatosensory sector from cells in POm do not appear to form a map [120].

# Receptive fields

Neurons in the somatosensory sector of TRN have response properties that differ substantially from those of VB neurons. In the cat [53, 118] and the macaque monkey [118], neurons in the somatosensory sector have quite large receptive fields. Although neurons in the somatosensory sector of the rat have small receptive fields [124, 126], such neurons lack direction selectivity, which is a property of VB neurons. There is evidence for a well-organized somatotopic map in the rat's TRN [115] and some evidence for such a map in TRN of the cat and the macaque monkey [118].

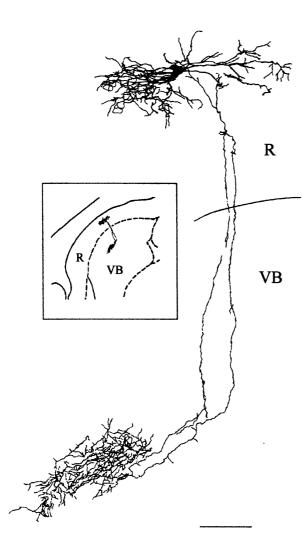


Figure 7. Reconstruction of a biocytin-labelled cell in the thalamic reticular nucleus (R) showing a dense axonal arbor within the ventrobasal complex (VB). Rostral is at the top and medial is to the right. The inset shows a lower-power outline of the section, indicating the location of the labelled thalamic reticular soma. Scale bar = 100  $\mu m$ . Reprinted with permission from Cox et al. [146], © 1999 John Wiley & Sons, Inc., New York.

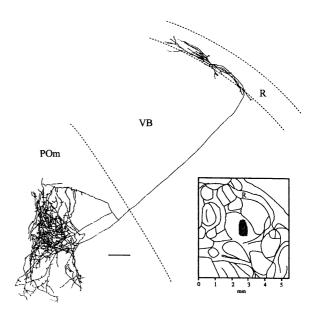


Figure 8. Reconstruction of a biocytin-labelled cell in the thalamic reticular nucleus (R) showing a dense axonal arbor within the medial part of the posterior complex (POm). The reticular axon traverses the ventrobasal complex (VB) to reach the posterior complex. Rostral is at the top and medial is to the left. The inset shows a lower-power outline of the section, indicating the location (stippling) of the labelled axonal arbor. Scale bar = 200  $\mu m$ . Reprinted with permission from Pinault et al. [138], © 1999 Blackwell Science Ltd, Oxford.

# The auditory reticular sector

The auditory sector of the mammalian TRN occupies a discrete ventrocaudal region of the nucleus [rodent: 58, 147; carnivore: 148–151; primate: 152]. This region lies adjacent to the medial geniculate complex (MG), which contains first-order and higher-order nuclei of the dorsal thalamus. The auditory sector presumably receives excitatory modulatory afferents from the auditory cortex [29]. The auditory sector also receives excitatory afferents from MG [147], which provide driving inputs. In return, the auditory sector sends efferents to MG, which make F-type synapses [153] and which have inhibitory effects on medial geniculate neurons [93, 147, 154]. Presumably, as in the visual and somatosensory thalamus, cells in MG and the auditory sector of TRN form intrathalamic excitatory-inhibitory networks.

# Organizational components

In the ventral nucleus of MG (MGv), a first-order dorsal thalamic nucleus, organizational components are 'lamellae' of somata, dendrites, and afferent fibers [155; see also 156–158]. These components in MGv extend

690

along two dimensions of the nucleus perpendicular to the dimension that contains the one-dimensional cochleotopic map. The auditory sector of TRN should also contain organizational components and these would indicate not only the presence of a map but also its orientation. Once again, the organizational components in this sector are 'slabs,' formed by reticular cells that project to the dorsal thalamus, and these slabs are also oriented parallel to the plane of TRN [151; see also 152]. As demonstrated in the cat's auditory sector [151], figure 9 shows horizontal sections through slabs of labelled TRN cells following an injection of WGA-HRP in the middle- to high-frequency representation in MGv (fig. 9A) and in the middle- to low-frequency representation in MGv (fig. 9B).



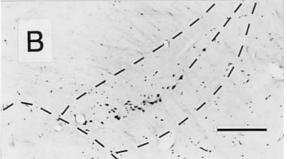


Figure 9. Horizontal sections through the thalamic reticular nucleus (TRN) of a cat. Rostral is at the top and medial is to the right. The lower left dashed line indicates the borders of the optic tract and the ventral lateral geniculate nucleus, the lower right dashed line indicates the inner border of the dorsal part of the zona incerta, and the central pair of dashed lines indicates the inner and outer borders of TRN. Reprinted with permission from Crabtree [151], © 1999 John Wiley & Sons, Inc., New York. (A) Labelled cells after an injection of WGA-HRP in the medial part of the ventral nucleus of the medial geniculate complex. (B) Labelled cells after an injection of WGA-HRP in the lateral part of the ventral nucleus of the medial geniculate complex. Scale bar = 500 µm.

# Topographic organization of inputs and outputs

The auditory sector receives afferents from some, if not all, auditory areas of the cortex [152]. As in the visual and somatosensory sectors of TRN, the terminal distributions of these afferents may have an organization similar to that of the efferents of the auditory sector. In the auditory sector of the bushbaby, inputs from auditory areas 1 and 2 terminate across most or all of the entire thickness of TRN [152]. Whether there are cochlectopic maps of inputs from these cortical areas remains to be determined.

The auditory sector sends efferents to both first-order and higher-order dorsal thalamic nuclei. In the cat, the outputs from the auditory sector to the medial part of MGv (MGvm) and to the lateral part of MGv (MGvl) arise from outer and inner zones, respectively [151; see also 152]. Thus, the reticular neurons projecting to MGv appear to form a well-organized cochleotopic map. This map is oriented perpendicular to the plane of TRN and to the organizational components of the map (see fig. 9). Furthermore, the outputs from the auditory sector to the medial nucleus of MG (MGm) and to the dorsal nucleus of MG (MGd) also arise from outer and inner zones, respectively [151; see also 152]. Thus, outputs to MGvm and MGm arise from overlapping zones, as do outputs to MGvl and MGd. In addition, many cells in the cat's auditory sector project either to both MGvm and MGm or to both MGvl and MGd [151]. MGm and MGd are presumably higher-order nuclei. The auditory sector also receives afferents from first-order and higher-order nuclei of the dorsal thalamus [24, 151]. There appears to be a well-organized map of ventral medial geniculate inputs in the auditory sector [151; see also 152], which is in register with the map formed by reticular cells that project to MGv.

# Receptive fields

Compared to receptive fields of neurons in MG, the receptive fields of neurons in the auditory sector of TRN differ substantially [149, 150]. They have much more complex discharge properties and exhibit broader frequency tuning. In the cat there is some evidence for a cochleotopic map in the TRN [150].

# Overview of sensory thalamic reticular sectors

The visual, somatosensory, and auditory sectors of TRN have many similar organizational features. Each of these sectors occupies a discrete region of TRN and receives excitatory afferents from a particular set of functionally related areas of the cerebral cortex and nuclei of the dorsal thalamus. Afferents from the dorsal thalamus provide driving inputs and afferents while

those from the cortex appear to provide mainly modulatory inputs. Furthermore, each sector contains zones, or compartments, that are related to different cortical areas and to different dorsal thalamic nuclei. However, differences can be seen among the sensory sectors in the degree to which these compartments overlap or, conversely, in the degree to which they are segregated. In addition, each sector receives convergent inputs from both the cortex and dorsal thalamus, which is particularly evident from the receptive field properties of sensory TRN cells. Thus, the receptive fields of these cells would have components that reflect the properties of different sources of inputs. Moreover, each sensory sector sends inhibitory efferents back to the functionally related dorsal thalamic nuclei from which it receives inputs. Overall, these outputs have relatively restricted terminal fields and there is good evidence that sensory TRN neurons can project to more than one dorsal thalamic nucleus. The outputs from the sensory sectors complete intrathalamic circuits, which appear to be predominantly composed of open loops rather than closed loops. Thus, sensory cells in the dorsal thalamus and TRN form a network of excitatory-inhibitory interconnections.

The sensory sectors of TRN each contain organizational components. These have been identified as either slabs of cortical terminals or slabs of cells projecting to the dorsal thalamus. Contrary to an early expectation, in which the components were thought to reflect a cortical organization and to extend across the thickness of TRN (fig. 10 top), the slabs of cortical terminals, for example, are oriented parallel to the plane of TRN (fig. 10 bottom). Consequently, these slabs are discretely aligned with the dendrites of cells that occupy the same zone within the thickness of TRN (fig. 10 bottom) rather than with the dendrites of cells that occupy the same region across the thickness of the nucleus (fig. 10 top). Terminals from the dorsal thalamus are also aligned with the reticular dendrites. This remarkable spatial alignment of cortical and dorsal thalamic terminals and reticular dendrites accounts for the similar orientation between slabs of terminals and slabs of cells that project to the dorsal thalamus (cf. fig. 3A with figs 3B, 6A, 9). Furthermore, the sensory sectors contain maps that are related to inputs from primary, or firstorder, cortical areas, reticular cells projecting to a firstorder dorsal thalamic nucleus, and inputs from a first-order dorsal thalamic nucleus. These maps lie perpendicular to the plane of TRN and to the organizational components and, where information is available, all of the input and output maps are in register. However, the orientation of the organizational components and map in the carnivore PGN appears to be exactly orthogonal to the orientation of those in the carnivore TRN and in TRN of other mammalian species. In

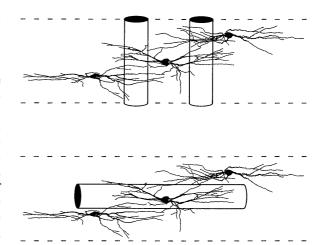


Figure 10. Schematic representations of possible orientations of organizational components in the sensory sectors of the thalamic reticular nucleus. These components are shown as cylinders and the inner and outer borders of the reticular nucleus are indicated by the dashed lines. Note the very different relationship between the components and the dendrites of the reticular neurons in each scheme. The scheme at the top represents the traditional view of the organization reticular nucleus [25, 63, 64]. That at the bottom represents the current view of the organization in the sensory reticular sectors. The exception to this current view is the organization in the perigeniculate nucleus (part of the visual reticular sector in carnivores), which presumably reflects the organizational scheme shown at the top. The reconstructed cells are reprinted with permission from Lübke [60], © 1999 John Wiley & Sons, Inc., New York.

addition, sensory TRN cells that project to a higher-order dorsal thalamic nucleus or the thalamoreticular inputs from such a nucleus appear not to be mapped. Whether there are topographic projections from higherorder cortical areas to the sensory TRN sectors remains to be determined.

Each sensory sector of TRN has an organization that mimics rather than mirrors the organization in the functionally related first-order nucleus of the dorsal thalamus. Such mimicry is seen not only in the orientation of the reticular organizational components but also in the positioning of the axes (visual and somatosensory sectors) or axis (auditory sector) of the reticular maps. Because these maps, except the one in PGN, lie perpendicular to the plane of TRN, continuous mapping of cortical inputs, dorsal thalamic inputs, or outputs to the dorsal thalamus is constrained by the inner and outer borders of the nucleus. Such constraints create significant discontinuities, or breaks, between sensory sectors relative to their cortical or thalamic connections. For example, when mapped inputs from one cortical area (or dorsal thalamic nucleus) reach an inner or outer border of TRN, then inputs from an adjacent cortical area (or dorsal thalamic nucleus) must project onto a different sector or onto the same sector that receives inputs from the first cortical area (or dorsal thalamic nucleus). Similarly, when mapped outputs to one dorsal thalamic nucleus reach an inner or outer border of TRN, then outputs to an adjacent dorsal thalamic nucleus must arise from a different sector or from the same sector that sends outputs to the first dorsal thalamic nucleus. Developmentally, these discontinuities may provide a mechanism whereby each sensory sector of TRN can group together its connections with a particular set of functionally related cortical areas and dorsal thalamic nuclei.

# Thalamic reticular-mediated connections between dorsal thalamic nuclei

Until recently, intrathalamic interactions were thought of as mediated by reciprocal connections between a given dorsal thalamic nucleus and its functionally related sector of TRN. However, in the cat's somatosensory [120] and auditory [151] sectors of TRN, cells projecting to different modality-related nuclei of the dorsal thalamus occupy overlapping territories. Furthermore, many of these cells project to at least two dorsal thalamic nuclei. These findings suggested that reticular cells with outputs to one nucleus could receive inputs from another nucleus and vice versa. These connections would allow interactions between modality-related nuclei in the dorsal thalamus through a disynaptic pathway mediated by TRN. To test this possibility, an in vitro slice preparation was developed [127]. Horizontally sectioned slices through the somatosensory thalamus were prepared from adolescent rats, allowing whole-cell voltage-clamp recordings to be made from neurons in POm (or VB) while stimulating neurons in VB (or POm) with pressure pulses of glutamate. Figure 11 shows the slice preparation and the positioning of a stimulating pipette in VB and a recording pipette in

Robust inhibitory postsynaptic currents (IPSCs) were recorded in POm (or VB) cells in response to glutamate stimulation in VB (or POm) [127]. The traces in figure 12 at the top show examples of such IPSCs, which represent typical extremes in a wide range of responses. In part, this variability in evoked IPSCs from one recording to the next reflected differences in the final concentration of glutamate that reached appropriately connected cells and in the number of such cells that were activated. The evoked IPSCs can be entirely accounted for by the activation of a disynaptic pathway mediated by the GABAergic neurons of TRN. Furthermore, the locations of a stimulation site in VB (or POm) and a responsive neuron in POm (or VB) were in

somatotopic register, which could provide a major clue as to the function of these novel circuits. A schematic representation of the circuits that link together VB, a first-order nucleus (FO), and POm, a higher-order nucleus (HO), is shown in figure 12 at the bottom. Clearly, these circuits point the way toward a greater complexity in intrathalamic connectivity than previously thought. Moreover, it is to be expected that reticular-mediated disynaptic circuits that link together modality-related first-order and higher-order nuclei are also present in the visual and auditory parts of the thalamus.

### Function of intrathalamic connections

From the outset of this review, the ultimate concern has been the role(s) TRN might play in thalamic sensory processing during wakefulness. A variety of functions has been attributed to TRN, such as (i) modulator of sensory transmission through the dorsal thalamus [3, 12, 159], (ii) enhancer of selected sensory transmission through the dorsal thalamus [13, 135, 160–164], and (iii) regulator of receptive field properties of dorsal thalamic neurons [95, 132, 133, 150, 165]. These proposed functions are not mutually exclusive and each of them relies on the inhibitory, or hyperpolarizing, effects exerted by reticular cells on thalamocortcial relay cells. Clearly, such effects will affect on-going temporal and spatial integration of diverse afferents by dorsal thala-

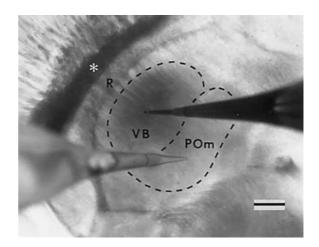


Figure 11. The thalamic slice preparation as it appears in the recording chamber. Transilluminating the slice clearly reveals the thalamic reticular nucleus (R), the ventrobasal complex (VB), the medial part of the posterior complex (POm), and the internal capsule (asterisk). A glutamate-filled stimulating pipette is positioned in VB and a recording electrode is positioned in POm. The dashed lines indicate the borders of VB and POm. Scale bar = 500 μm. Reprinted with permission from Crabtree et al. [127], © 1999 Nature America, Inc., New York.

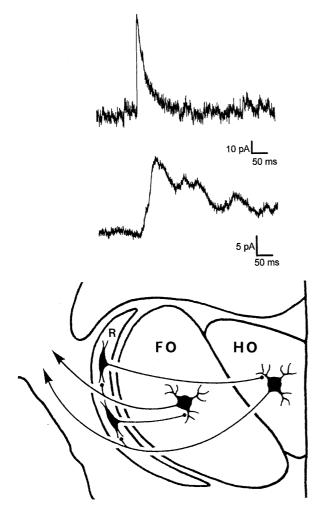


Figure 12. At the top, examples of inhibitory postsynaptic currents (IPSCs) recorded from a POm cell (top trace) and a VB cell (bottom trace) in response to glutamate stimulation in VB or POm, respectively. These IPSCs are not typical of the responses recorded from VB or POm cells but represent the extremes in a range of responses that is typical of both VB and POm cells. At the bottom, a schematic representation of a coronal section through the thalamus showing intrathalamic pathways linking VB, a first-order nucleus (FO), and POm, a higher-order nucleus (HO). These are disynaptic pathways mediated by the thalamic reticular nucleus (R). The cells in the first-order and higher-order nuclei project to the cortex (arrows).

mic cells [3, 6, 9, 12, 14–17, 20, 132, 133, 135], which will affect, in turn, the transmission of sensory information by these cells to the cerebral cortex. However, a rigorous assessment of any proposed function for TRN also relies on detailed knowledge of the connectivity of this nucleus.

One striking attribute now recognized to be shared by the different sensory sectors of TRN is the topographic organization of the projections of reticular cells to firstorder dorsal thalamic nuclei, in conjunction with topographically organized inputs from a first-order cortical area and a first-order dorsal thalamic nucleus. Thus, these reticular projections would exert local rather than global effects on the cells in such nuclei. Before considering what these local effects might achieve, it would be worthwhile to inquire as to whether dorsal thalamic interneurons (i.e., local circuit neurons) could influence these effects. Furthermore, the functional behavior of thalamic neurons must also be taken into account. In addition to thalamocortical relay cells, dorsal thalamic sensory nuclei also contain interneurons [2]. The proportion of these interneurons varies widely across different sensory nuclei and mammalian species [166]. For example, interneurons account for about 25% of the neurons in the cat dLGN [51, 167, 168], whereas interneurons are very scarce in the rat VB [48, 169]. Interneurons in thalamic sensory nuclei receive F-type terminals [129, 170-173], but whether the source of these terminals is TRN (or PGN), the interneurons themselves [172, 174], or pretectal cells [175-177] is unclear. What is known is that the projections of TRN/ PGN cells preferentially target thalamocortical cells in the sensory nuclei [89, 129, 172, 175; see also 100]. Without a direct demonstration of a physiologically active pathway from TRN/PGN to dorsal thalamic interneurons, there is no compelling reason to believe that these interneurons play a significant role in intrathalamic sensory processes mediated by TRN/PGN. Neurons in both the dorsal thalamus and TRN/PGN exhibit two main patterns of firing, tonic and burst [178–188]. Each of these firing modes is triggered by depolarizing input and the cells switch between the modes in response to sustained changes in membrane potential. Figure 13 shows the tonic (upper trace) and the burst (lower trace) firing modes for a typical thalamic neuron that was recorded intracellularly and held at different membrane potentials. With regard to TRN/ PGN cells, modulatory glutamatergic inputs from the cortex are depolarizing [6, 9, 11] and promote the tonic firing mode in these cells, whereas modulatory cholinergic inputs from the brainstem are hyperpolarizing [189-196] and promote the burst firing mode in these cells. Either mode can be triggered by the driving and depolarizing inputs from the dorsal thalamus [9, 11, 15]. Figure 14 shows the powerful influence that burst firing in TRN/PGN (upper trace) has on a neuron in the dorsal thalamus (lower trace). Following the burst, a barrage of inhibitory, or hyperpolarizing, postsynaptic potentials was recorded in the dorsal thalamic cell,

The organization and main functional connections of TRN under consideration are summarized in figure 15, according to what we currently know about the sensory

which would effectively silence the tonic firing of the

sectors of this nucleus. In a given sensory sector of TRN (e.g., visual, somatosensory, or auditory), organizational components A, B, and C are shown, which are specifically connected to functionally related components A, B, and C in the first-order cortical area (CTX) and in the first-order dorsal thalamic nucleus (DT), respectively. The representation, or map, of the peripheral receptor sheet (e.g., retina, skin, or cochlea) lies orthogonal to components A, B, and C in each structure. It is assumed that the outputs of reticular neurons in a given component (e.g., B) engage in within-component circuits within TRN [53, 58, 62, 97, 125, 146, 197-201] and in predominantly open-loop circuits within the related component (i.e., B) in the dorsal thalamic nucleus [66, 97, 104, 125, 131]. Only inputs to and outputs from component B in TRN are shown, including inputs from the brainstem (BS). Although

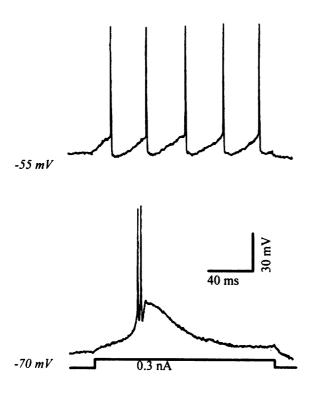


Figure 13. Different firing modes for an intracellularly recorded neuron in the cat's dorsal lateral geniculate nucleus. The tonic mode is shown in the top trace and the burst mode is shown in the bottom trace. When the cell was held at a relatively depolarized membrane potential ( $-55~\rm mV$ ), a stream of conventional action potentials was triggered by a depolarizing 0.3 nA current pulse (bottom) injected into the cell. However, when the cell was held at a relatively hyperpolarized membrane potential ( $-70~\rm mV$ ), the same depolarizing current pulse triggered a low-threshold Ca²+ spike with a burst of conventional action potentials riding on the crest of the spike. Reprinted with permission from Sherman and Guillery [6], © 1999 The American Physiological Society, Bethseda, MD.

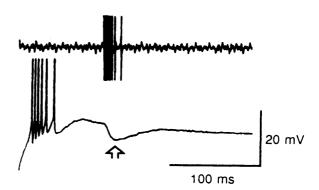


Figure 14. Effect of burst firing recorded extracellularly in the perigeniculate nucleus (part of the carnivore thalamic reticular nucleus) on an intracellularly recorded neuron in the ferret's dorsal lateral geniculate nucleus. The burst firing is shown in the top trace. The resultant barrage of inhibitory postsynaptic potentials (arrow) in the dorsal lateral geniculate neuron is shown in the bottom trace. Reprinted with permission from Bal et al. [100], © 1999 The Journal of Physiology, Cambridge.

equally applicable to components A and C, respectively, in the cortex, dorsal thalamus, and TRN, we will now consider the following possibilities related only to component B in these structures.

During periods of activity of cortical and brainstem inputs, the net effect of the tonic release of glutamate and acetylcholine, respectively, on thalamic reticular neurons would favor a cortical influence [178, 179, 182–184]. This would result in a depolarizing shift in the reticular cells, priming them for the tonic firing mode. Sensory transmission through a zone of dorsal thalamic component B, en route to cortical component B, would then trigger the tonic firing mode in a zone of reticular cells in component B. The tonic firing of these cells would inhibit both the activity in an adjacent zone of dorsal thalamic component B (small peaks) and in an adjacent zone of reticular cells in component B. This latter inhibition would disinhibit the activity of the dorsal thalamic zone in componet B (large peaks) through which sensory information is being transmitted. Thus, on-going sensory transmission through the dorsal thalamic nucleus would be enhanced. This process would be entirely consistent with models suggesting that TRN enhances locally the transmission of salient sensory information through the dorsal thalamus [13, 135, 160–164].

Alternatively, during periods of activity of brainstem inputs and selective inactivity of cortical inputs from component B ( $\geq 100$  ms) [180], there would be a sufficient hyperpolarizing shift in component B reticular cells to prime them for the burst firing mode. Sensory transmission through a zone of dorsal thalamic component B would then trigger the burst firing mode in a

zone of reticular cells in component B. The burst firing of these cells would silence the activity in an adjacent zone of dorsal thalamic component B (abolition of the small peaks) and would prime and trigger the burst firing mode [202] in an adjacent zone of reticular cells in component B. Consequently, this latter burst firing would inhibit and interrupt the activity of the dorsal thalamic zone in component B through which sensory information is being transmitted (abolition of the large peaks). Thus, through TRN, the cortex could actively

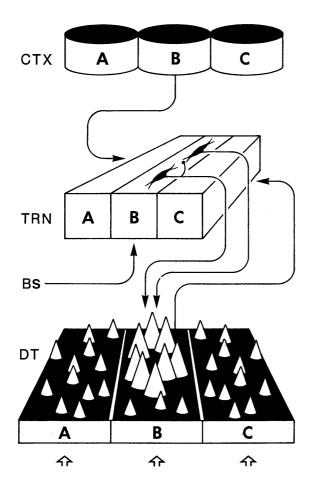


Figure 15. Schematic representation of some of the functional connections of the thalamic reticular nucleus (TRN). For a given sensory sector of the reticular nucleus, organizational components A, B, and C are shown, which are specifically connected to organizational components A, B, and C, respectively, in the functionally related cortical area (CTX) and first-order dorsal thalamic nucleus (DT) and which are connected to the brainstem (BS). Ascending sensory inputs to the dorsal thalamic nucleus (bottom arrows) are shown, as are activity levels (large and small peaks) of on-going transmission of sensory information within the dorsal thalamic nucleus. Although an axodendritic contact is shown between two cells in the reticular nucleus, there are other types of synaptic connections among the cells in this nucleus [198, 200; see also 52, 199].

and selectively reset the activity levels in a dorsal thalamic nucleus. This would enable shifts in the transmission of information over new channels through the dorsal thalamic nucleus or the re-establishment of transmission over the same channel, thereby allowing periodic and frequent comparison of on-going cortical sensory processing with available sensory information.

The above hypothetical processes will require revision as new information concerning thalamic functional connectivity becomes available. For example, glutamatergic inputs can have inhibitory effects on TRN cells [203]. Whether these inputs arise from the cortex and/or the dorsal thalamus is not yet known.

For a given sensory sector of TRN, the above processes incorporate the well-organized topographic relationship between inputs from first-order cortical areas and dorsal thalamic nuclei and outputs to first-order dorsal thalamic nuclei. However, because of the apparent lack of topography in the reciprocal projections between TRN and higher-order dorsal thalamic nuclei, it is difficult to envisage any reticular-mediated local enhancement of transmission [13, 162-164] through higher-order nuclei of the thalamus. Nevertheless, it is still possible for TRN to mediate in a global fashion the resetting of the activity level in higher-order nuclei. Furthermore, reticular-mediated thalamic processing is not simply limited to the interactions between a given sensory sector of TRN and a single nucleus of the dorsal thalamus. Rather, in conjunction with the interplay of inputs from the cortex and brainstem, modalityrelated first-order and higher-order dorsal thalamic nuclei could influence each other's sensory processing through intrathalamic pathways mediated by TRN [127]. The current evidence suggests that these pathways would mediate local effects.

Acknowledgements. I thank The Wellcome Trust and the UK Medical Research Council for their generous support.

- 1 Steriade M. and Deschênes M. (1984) The thalamus as a neuronal oscillator. Brain Res. Rev. 8: 1-63
- 2 Jones E. G. (1985) The Thalamus. Plenum, New York
- 3 Sherman S. M. and Koch C. (1986) The control of retinogeniculate transmission in the mammalian lateral geniculate nucleus. Exp. Brain Res. 63: 1-20
- 4 Steriade M. and Llinás R. (1988) The functional states of the thalamus and the associated neuronal interplay. Physiol. Rev. **68**: 649–742
- 5 Guillery R. W. (1995) Anatomical evidence concerning the role of the thalamus in corticocortical communication: a brief review. J. Anat. 187: 583-592
- 6 Sherman S. M. and Guillery R. W. (1996) Functional organization of thalamocortical relays. J. Neurophysiol. 76: 1367–1395
- 7 Jones E. G. (1998) Viewpoint: the core and matrix of thalamic organization. Neuroscience 85: 331–345
- 8 Steriade M., Jones E. G. and Llinás R. R. (1990) Thalamic Oscillations and Signalling. Wiley, New York

- 9 McCormick D. A. (1992) Neurotransmitter actions in the thalamus and cerebral cortex and their role in neuromodulation of thalamocortical activity. Prog. Neurobiol. 39: 337– 388
- 10 Steriade M., McCormick D. A. and Sejnowski T. J. (1993) Thalamocortical oscillations in the sleeping and aroused brain. Science 262: 679–685
- 11 McCormick D. A. and Bal T. (1997) Sleep and arousal: thalamocortical mechanisms. Annu. Rev. Neurosci. 20: 185– 215
- 12 Singer W. (1977) Control of thalamic transmission by corticofugal and ascending reticular pathways in the visual system. Physiol. Rev. 57: 386–420
- 13 Crick F. (1984) Function of the thalamic reticular complex: the searchlight hypothesis. Proc. Natl. Acad. Sci. USA 81: 4586–4590
- 14 McCormick D. A. and Bal T. (1994) Sensory gating mechanisms of the thalamus. Curr. Opin. Neurobiol. 4: 550–556
- 15 Salt T. E. and Eaton S. A. (1996) Functions of ionotropic and metabotropic glutamate receptors in sensory transmission in the mammalian thalamus. Prog. Neurobiol. 48: 55– 72
- 16 Sherman S. M. (1996) Dual response mode in lateral geniculate neurons: mechanisms and functions. Vis. Neurosci. 13: 205–213
- 17 Sherman S. M. and Guillery R. W. (1998) On the actions that one nerve cell can have on another: distinguishing 'drivers' from 'modulators'. Proc. Natl. Acad. Sci. USA 95: 7121-7126
- 18 Krosigk M. von, Bal T. and McCormick D. A. (1993) Cellular mechanisms of a synchronized oscillation in the thalamus. Science 261: 361–364
- 19 Crunelli V. and Leresche N. (1991) A role for GABA<sub>B</sub> receptors in excitation and inhibition of thalamocortical cells, Trends Neurosci. 14: 16–21
- 20 Sillito A. M. (1992) GABA mediated inhibitory processes in the function of the geniculo-striate system. Prog. Brain Res. 90: 349–384
- 21 Rose J. E. (1942) The ontogenetic development of the rabbit's diencephalon. J. Comp. Neurol. 7: 61–129
- 22 Ramón y Cajal S. (1911) Histologie du Système Nerveux de l'Homme et des Vertébrés, vol. II, translated by L. Azoulay. Maloine, Paris
- 23 Scheibel M. E. and Scheibel A. B. (1966) The organization of the nucleus reticularis thalami: a Golgi study. Brain Res. 1: 43–62
- 24 Jones E. G. (1975) Some aspects of the organization of the thalamic reticular complex. J. Comp. Neurol. 162: 285–308
- 25 Carman J. B., Cowan W. M. and Powell T. P. S. (1964) Cortical connexions of the thalamic reticular nucleus. J. Anat. (Lond.) 98: 587–598
- 26 Friedlander M. J., Lin C.-S., Stanford L. R. and Sherman S. M. (1981) Morphology of functionally identified neurons in lateral geniculate nucleus of the cat. J. Neurophysiol. 46: 80-129
- 27 Yen C.-T., Conley M. and Jones E. G. (1985) Morphological and functional types of neurons in cat ventral posterior thalamic nucleus. J. Neurosci. 5: 1316-1338
- 28 Harris R. M. (1987) Axon collaterals in the thalamic reticular nucleus from thalamocortical neurons of the rat ventrobasal thalamus. J. Comp. Neurol. 258: 397–406
- 29 Rouiller E. M. and Ribaupierre F. de (1990) Arborization of corticothalamic axons in the auditory thalamus of the cat: a PHA-L tracing study. Neurosci. Lett. 108: 29–35
- 30 Bourassa J. and Deschênes M. (1995) Corticothalamic projections from the primary visual cortex in rats: a single fiber study using biocytin as an anterograde tracer. Neuroscience 66: 253–263
- 31 Bourassa J., Pinault D. and Deschênes M. (1995) Corticothalamic projections from the cortical barrel field to the somatosensory thalamus in rats: a single-fibre study using biocytin as an anterograde tracer. Eur. J. Neurosci. 7: 19–30

- 32 Murphy P. C. and Sillito A. M. (1996) Functional morphology of the feedback pathway from area 17 of the cat visual cortex to the lateral geniculate nucleus. J. Neurosci. 16: 1180–1192
- 33 Ahlsén G. and Lo F.-S. (1982) Projection of brain stem neurons to the perigeniculate nucleus and the lateral geniculate nucleus in the cat. Brain Res. 238: 433–438
- 34 Mackay-Sim A., Sefton A. J. and Martin P. R. (1983) Subcortical projections to lateral geniculate and thalamic reticular nuclei in the hooded rat. J. Comp. Neurol. 213: 24–35
- 35 Hallanger A. E., Levey A. I., Lee H. J., Rye D. B. and Wainer B. H. (1987) The origins of cholinergic and other subcortical afferents to the thalamus in the rat. J. Comp. Neurol. **262**: 105–124
- 36 Levey A. I., Hallanger A. E. and Wainer B. H. (1987) Cholinergic nucleus basalis neurons may influence the cortex via the thalamus. Neurosci. Lett. 74: 7–13
- 37 Paré D., Smith Y., Parent A. and Steriade M. (1988) Projections of brainstem core cholinergic and non-cholinergic neurons of cat to intralaminar and reticular thalamic nuclei. Neuroscience 25: 69–86
- 38 Smith Y., Paré D., Deschênes M., Parent A. and Steriade M. (1988) Cholinergic and non-cholinergic projections from the upper brainstem core to the visual thalamus in the cat. Exp. Brain Res. **70:** 166–180
- 39 Uhlrich D. J., Cucchiaro J. B. and Sherman S. M. (1988) The projection of individual axons from the parabrachial region of the brain stem to the dorsal lateral geniculate nucleus in the cat. J. Neurosci. 8: 4565–4575
- 40 Cornwall J., Cooper J. D. and Phillipson O. T. (1990) Afferent and efferent connections of the laterodorsal tegmental nucleus in the rat. Brain Res. Bull. 25: 271–284
- 41 Steriade M., Parent A., Paré D. and Smith Y. (1987) Cholinergic and non-cholinergic neurons of cat basal forebrain project to reticular and mediodorsal thalamic nuclei. Brain Res. 408: 372–376
- 42 Chen S. and Bentivoglio M. (1993) Nerve growth factor receptor-containing cholinergic neurons of the basal fore-brain project to the thalamic reticular nucleus in the rat. Brain Res. **606**: 207–212
- 43 Bickford M. E., Günlük A. E., Van Horn S. C. and Sherman S. M. (1994) GABAergic projection from the basal forebrain to the visual sector of the thalamic reticular nucleus in the cat. J. Comp. Neurol. 348: 481–510
- 44 Minderhoud J. M. (1971) An anatomical study of the efferent connections of the thalamic reticular nucleus. Exp. Brain Res. 12: 435–446
- 45 Guillery R. W., Feig S. L. and Lozsádi D. A. (1998) Paying attention to the thalamic reticular nucleus. Trends Neurosci. 21: 28-32
- 46 Houser C. R., Vaughn J. E., Barber R. P. and Roberts E. (1980) GABA neurons are the major cell type of the nucleus reticularis thalami. Brain Res. 200: 341–354
- 47 Oertel W. H., Graybiel A. M., Mugnaini E., Elde R. P., Schmechel D. E. and Kopin I. J. (1983) Coexistence of glutamic acid decarboxylase- and somatostatin-like immunoreactivity in neurons of the feline nucleus reticularis thalami. J. Neurosci. 3: 1322–1332
- 48 Barbaresi P., Spreafico R., Frassoni C. and Rustioni A. (1986) GABAergic neurons are present in the dorsal column nuclei but not in the ventroposterior complex of rats. Brain Res. 382: 305–326
- 49 De Biasi S., Frassoni C. and Spreafico R. (1986) GABA immunoreactivity in the thalamic reticular nucleus of the rat: a light and electron microscopical study. Brain Res. 399: 143–147
- 50 Hendrickson A. E., Ogren M. P., Vaughn J. E., Barber R. P. and Wu J.-Y. (1983) Light and electron microscopic immunocytochemical localization of glutamic acid decarboxylase in monkey geniculate complex: evidence for GABAergic neurons and synapses. J. Neurosci. 3: 1245–1262

- 51 Fitzpatrick D, Penny G. R. and Schmechel D. E. (1984) Glutamic acid decarboxylase immunoreactive neurons and terminals in the lateral geniculate nucleus of the cat. J. Neurosci. 4: 1809–1829
- 52 Montero V. M. and Singer W. (1984) Ultrastructure and synaptic relations of neural elements containing glutamic acid decarboxylase (GAD) in the perigeniculate nucleus of the cat. Exp. Brain Res. **56**: 115–125
- 53 Yen C.-T., Conley M., Hendry S. H. C. and Jones E. G. (1985) The morphology of physiologically identified GABAergic neurons in the somatic sensory part of the thalamic reticular nucleus in the cat. J. Neurosci. 5: 2254–2268
- 54 Clemence A. E. and Mitrofanis J. (1992) Cytoarchitectonic heterogeneities in the thalamic reticular nucleus of cats and ferrets. J. Comp. Neurol. 322: 167–180
- 55 Penny G. R., Conley M., Schmechel D. E. and Diamond I. T. (1984) The distribution of glutamic acid decarboxylase immunoreactivity in the diencephalon of the opossum and rabbit. J. Comp. Neurol. 228: 38–56
- 56 Scheibel M. E. and Scheibel A. B. (1972) Specialized organizational patterns within the nucleus reticularis thalami of the cat. Exp. Neurol. 34: 316–322
- 57 Ide L. S. (1982) The fine structure of the perigeniculate nucleus in the cat. J. Comp. Neurol. 210: 317-334
- 58 Ohara P. T. and Lieberman A. R. (1985) The thalamic reticular nucleus of the adult rat: experimental anatomical studies. J. Neurocytol. 14: 365–411
- 59 Spreafico R., Battaglia G. and Frassoni C. (1991) The reticular thalamic nucleus (RTN) of the rat: cytoarchitectural, Golgi, immunocytochemical, and horseradish peroxidase study. J. Comp. Neurol. 304: 478–490
- 60 Lübke J. (1993) Morphology of neurons in the thalamic reticular nucleus (TRN) of mammals as revealed by intracellular injections into fixed brain slices. J. Comp. Neurol. 329: 458–471
- 61 Ohara P. T. and Havton L. A. (1996) Dendritic arbors of neurons from different regions of the rat thalamic reticular nucleus share a similar orientation. Brain Res. 731: 236–240
- 62 Pinault D. and Deschênes M. (1998) Projection and innervation patterns of individual thalamic reticular axons in the thalamus of the adult rat: a three-dimensional, graphic, and morphometric analysis. J. Comp. Neurol. 391: 180–203
- 63 Chow K. L. (1952) Regional degeneration of the thalamic reticular nucleus following cortical ablations in monkeys. J. Comp. Neurol. 97: 37-60
- 64 Rose J. E. (1952) The cortical connections of the reticular complex of the thalamus. Res. Publ. Assoc. Res. Nerv. Ment. Dis. 30: 454–479
- 65 Steriade M., Parent A. and Hada J. (1984) Thalamic projections of nucleus reticularis thalami of cat: a study using retrograde transport of horseradish peroxidase and fluorescent tracers. J. Comp. Neurol. 229: 531–547
- 66 Pinault D. and Deschênes M. (1998) Anatomical evidence for a mechanism of lateral inhibition in the rat thalamus. Eur. J. Neurosci. 10: 3462–3469
- 67 Sumitomo I., Nakamura M. and Iwama K. (1976) Location and function of the so-called interneurons of rat lateral geniculate body. Exp. Neurol. **51**: 110–123
- 68 Hale P. T., Sefton A. J., Baur L. A. and Cottee L. J. (1982) Interrelations of the rat's thalamic reticular and dorsal lateral geniculate nuclei. Exp. Brain Res. 45: 217–229
- 69 Montero V. M., Guillery R. W. and Woolsey C. N. (1977) Retinotopic organization within the thalamic reticular nucleus demonstrated by a double label autoradiographic technique. Brain Res. 138: 407–421
- 70 Lo F.-S. and Xie G.-Y. (1987) Location of interneurones in the recurrent inhibitory circuit of the rabbit lateral geniculate nucleus. Exp. Brain Res. 66: 83–89
- 71 Crabtree J. W. and Killackey H. P. (1989) The topographic organization and axis of projection within the visual sector of the rabbit's thalamic reticular nucleus. Eur. J. Neurosci. 1: 94–109

- 72 Updyke B. V. (1977) Topographic organization of the projections from cortical areas 17, 18, and 19 onto the thalamus, pretectum and superior colliculus in the cat. J. Comp. Neurol. 173: 81–122
- 73 Symonds L. L. and Kaas J. H. (1978) Connections of striate cortex in the prosimian, *Galago senegalensis*. J. Comp. Neurol. 181: 477–512
- 74 Graham J., Lin C.-S. and Kaas J. H. (1979) Subcortical projections of six visual cortical areas in the owl monkey, *Aotus trivirgatus*. J. Comp. Neurol. 187: 557–580
- 75 Conley M. and Diamond I. T. (1990) Organization of the visual sector of the thalamic reticular nucleus in *Galago*: evidence that the dorsal lateral geniculate and pulvinar nuclei occupy separate parallel tiers. Eur. J. Neurosci. 2: 211– 226
- 76 Harting J. K., Van Lieshout D. P. and Feig S. (1991) Connectional studies of the primate lateral geniculate nucleus: distribution of axons arising from the thalamic reticular nucleus of *Galago crassicaudatus*. J. Comp. Neurol. 310: 411–427
- 77 Sanderson K. J. (1971) The projection of the visual field to the lateral geniculate and medial interlaminar nuclei in the cat. J. Comp. Neurol. 143: 101-118
- 78 Dubin M. W. and Cleland B. G. (1977) Organization of visual inputs to interneurons of lateral geniculate nucleus of the cat. J. Neurophysiol. 40: 410-427
- 79 Ohara P. T. and Lieberman A. R. (1981) Thalamic reticular nucleus: anatomical evidence that cortico-reticular axons establish monosynaptic contact with reticulo-geniculate projection cells. Brain Res. 207: 153–156
- 80 Montero V. M. (1989) Ultrastructural identification of synaptic terminals from cortical axons and from collateral axons of geniculo-cortical relay cells in the perigeniculate nucleus of the cat. Exp. Brain Res. 75: 65–72
- 81 Xue J. T., Carney T., Ramoa A. S. and Freeman R. D. (1988) Binocular interaction in the perigeniculate nucleus of the cat. Exp. Brain Res. 69: 497–508
- 82 Ahlsén G. and Lindström S. (1982) Excitation of perigeniculate neurones via axon collaterals of principal cells. Brain Res. 236: 477–481
- 83 Ahlsén G., Lindström S. and Lo F.-S. (1982) Functional distinction of perigeniculate and thalamic reticular neurons in the cat. Exp. Brain Res. **46**: 118–126
- 84 Sumitomo I., Hsiao C.-F. and Fukuda Y. (1988) Two types of thalamic reticular cells in relation to the two visual thalamocortical systems in the rat. Brain Res. 446: 354–362
- 85 Zhu J. J. and Lo F.-S. (1997) Recurrent inhibitory interneurons of the rabbit's lateral posterior pulvinar complex. J. Neurophysiol. 78: 3117–3124
- 86 FitzGibbon T. (1994) Rostral reticular nucleus of the thalamus sends a patchy projection to the pulvinar lateralis-posterior complex of the cat. Exp. Neurol. 129: 266–278
- 87 FitzGibbon T., Tevah L. V. and Sefton A. J. (1995) Connections between the reticular nucleus of the thalamus and pulvinar-lateralis posterior complex: A WGA-HRP study. J. Comp. Neurol. 363: 489–504
- 88 Ohara P. T., Sefton A. J. and Lieberman A. R. (1980) Mode of termination of afferents from the thalamic reticular nucleus in the dorsal lateral geniculate nucleus of the rat. Brain Res. 197: 503–506
- 89 Montero V. M. and Scott G. L. (1981) Synaptic terminals in the dorsal lateral geniculate nucleus from neurons of the thalamic reticular nucleus: a light and electron microscope autoradiographic study. Neuroscience 6: 2561–2577
- 90 Cucchiaro J. B., Uhlrich D. J. and Sherman S. M. (1991) Electron-microscopic analysis of synaptic input from the perigeniculate nucleus to the A-laminae of the lateral geniculate nucleus in cats. J. Comp. Neurol. 310: 316–336
- 91 Burke W. and Sefton A. J. (1966) Recovery of responsiveness of cells of lateral geniculate nucleus of rat. J. Physiol. 187: 213–229
- 92 Burke W. and Sefton A. J. (1966) Inhibitory mechanisms in lateral geniculate nucleus of rat. J. Physiol. **187:** 231–246

- 93 Yingling C. D. and Skinner J. E. (1976) Selective regulation of thalamic sensory relay nuclei by nucleus reticularis thalami. Electroenceph. Clin. Neurophysiol. 41: 476–482
- 94 Lindström S. (1982) Synaptic organization of inhibitory pathways to principal cells in the lateral geniculate nucleus of the cat. Brain Res. 234: 447–453
- 95 Sillito A. M. and Kemp J. A. (1983) The influence of GABAergic inhibitory processes on the receptive field structure of X and Y cells in cat dorsal lateral geniculate nucleus (dLGN). Brain Res. 277: 63–77
- 96 French C. R., Sefton A. J. and Mackay-Sim A. (1985) The inhibitory role of the visually responsive region of the thalamic reticular nucleus in the rat. Exp. Brain Res. 57: 471–479
- 97 Lo F.-S. and Sherman S. M. (1994) Feedback inhibition in the cat's lateral geniculate nucleus. Exp. Brain Res. 100: 365–368
- 98 Kim U., Sanchez-Vives M. V. and McCormick D. A. (1997) Functional dynamics of GABAergic inhibition in the thalamus. Science 278: 130–134
- 99 Sanchez-Vives M. V. and McCormick D. A. (1997) Functional properties of perigeniculate inhibition of dorsal lateral geniculate nucleus thalamocortical neurons in vitro. J. Neurosci. 17: 8880–8893
- 100 Bal T., Krosigk M. von and McCormick D. A. (1995) Synaptic and membrane mechanisms underlying synchronized oscillations in the ferret lateral geniculate nucleus in vitro. J. Physiol. 483: 641–663
- 101 Bal T., Krosigk M. von and McCormick D. A. (1995) Role of the ferret perigeniculate nucleus in the generation of synchronized oscillations in vitro. J. Physiol. 483: 665–685
- 102 Kim U., Bal T. and McCormick D. A. (1995) Spindle waves are propagating synchronized oscillations in the ferret LGNd in vitro. J. Neurophysiol. 74: 1301-1323
- 103 Kim U., Sanchez-Vives M. V. and McCormick D. A. (1997) Functional dynamics of GABAergic inhibition in the thalamus. Science 278: 130–134
- 104 Kim U. and McCormick D. A. (1998) The functional influence of burst and tonic firing mode on synaptic interactions in the thalamus. J. Neurosci. 18: 9500–9516
- 105 Rodrigo-Angulo M. L. and Reinoso-Suárez F. (1988) Connections to the lateral posterior-pulvinar thalamic complex from the reticular and ventral lateral geniculate thalamic nuclei: a topographical study in the cat. Neuroscience 26: 449-459
- 106 Rose J. E. and Malis L. I. (1965) Geniculo-striate connections in the rabbit. II. Cytoarchitectonic structure of the striate region and of the dorsal lateral geniculate body: organization of the geniculo-striate projections. J. Comp. Neurol. 125: 121–140
- 107 Sanderson K. J. (1971) Visual field projection columns and magnification factors in the lateral geniculate nucleus of the cat. Exp. Brain Res. 13: 159-177
- 108 Bishop P. O., Kozak W., Levick W. R. and Vakkur G. J. (1962) The determination of the projection of the visual field on to the lateral geniculate nucleus in the cat. J. Physiol 163: 503-539
- 109 Lozsádi D. A., Gonzalez-Soriano J. and Guillery R. W. (1996) The course and termination of corticothalamic fibres arising in the visual cortex of the rat. Eur. J. Neurosci. 8: 2416–2427
- 110 Coleman K. A. and Mitrofanis J (1996) Organization of the visual reticular thalamic nucleus of the rat. Eur. J. Neurosci. 8: 388-404
- 111 Uhlrich D. J., Cucchiaro J. B., Humphrey A. L. and Sherman S. M. (1991) Morphology and axonal projection patterns of individual neurons in the cat perigeniculate nucleus. J. Neurophysiol. 65: 1528–1541
- 112 Pinault D., Bourassa J. and Deschênes M. (1995) Thalamic reticular input to the rat visual thalamus: a single fiber study using biocytin as an anterograde tracer. Brain Res. 670: 147–152
- 113 So Y. T. and Shapley R. (1981) Spatial tuning of cells in and around lateral geniculate nucleus of the cat: X and Y relay

- cells and perigeniculate interneurons. J. Neurophysiol. **45**: 107-120
- 114 Sugitani M. (1979) Electrophysiological and sensory properties of the thalamic reticular neurones related to somatic sensation in rats. J. Physiol. 290: 79–95
- 115 Shosaku A., Kayama Y. and Sumitomo I. (1984) Somatotopic organization in the rat thalamic reticular nucleus. Brain Res. 311: 57-63
- 116 Bernardo K. L. and Woolsey T. A. (1987) Axonal trajectories between mouse somatosensory thalamus and cortex. J. Comp. Neurol. 258: 542–564
- 117 Hoogland P. V., Welker E. and Van der Loos H. (1987) Organization of the projections from barrel cortex to thalamus in mice studied with *Phaseolus vulgaris*-leucoagglutinin and HRP. Exp. Brain Res. 68: 73–87
- 118 Pollin B. and Rokyta R. (1982) Somatotopic organization of nucleus reticularis thalami in chronic awake cats and monkeys. Brain Res. 250: 211–221
- 119 Crabtree J. W. (1992) The somatotopic organization within the cat's thalamic reticular nucleus. Eur. J. Neurosci. 4: 1352-1361
- 120 Crabtree J. W. (1996) Organization in the somatosensory sector of the cat's thalamic reticular nucleus. J. Comp. Neurol. 366: 207–222
- 121 Crabtree J. W. (1992) The somatotopic organization within the rabbit's thalamic reticular nucleus. Eur. J. Neurosci. 4: 1343–1351
- 122 De Biasi S., Frassoni C. and Spreafico R. (1988) The intrinsic organization of the ventroposterolateral nucleus and related reticular thalamic nucleus of the rat: a double-labeling ultrastructural investigation with γ-aminobutyric acid immunogold staining and lectin-conjugated horseradish peroxidase. Somatosens. Res. 5: 187–203
- 123 Curtis M. de, Spreafico R. and Avanzini G. (1989) Excitatory amino acids mediate responses elicited in vitro by stimulation of cortical afferents to reticularis thalami neurons of the rat. Neuroscience 33: 275–283
- 124 Shosaku A. (1985) A comparison of receptive field properties of vibrissa neurons between the rat thalamic reticular and ventro-basal nuclei. Brain Res. 347: 36–40
- 125 Shosaku A. (1986) Cross-correlation analysis of a recurrent inhibitory circuit in the rat thalamus. J. Neurophysiol. 55: 1030-1043
- 126 Sumitomo I. and Iwama K. (1987) Neuronal organization of rat thalamus for processing information of vibrissal movements. Brain Res. 415: 389–392
- 127 Crabtree J. W., Collingridge G. L. and Isaac J. T. R. (1998) A new intrathalamic pathway linking modality-related nuclei in the dorsal thalamus. Nat. Neurosci. 1: 389–394
- 128 Peschanski M., Ralston H. J. and Roudier F. (1983) Reticularis thalami afferents to the ventrobasal complex of the rat thalamus: an electron microscope study. Brain Res. 270: 325-329
- 129 Liu X.-B., Warren R. A. and Jones E. G. (1995) Synaptic distribution of afferents from reticular nucleus in ventroposterior nucleus of cat thalamus. J. Comp. Neurol. 352: 187– 202
- 130 Andersen P., Eccles J. C. and Sears T. A. (1964) The ventro-basal complex of the thalamus: types of cells, their responses and their functional organization. J. Physiol. 174: 370-399
- 131 Salt T. E. (1989) Gamma-aminobutyric acid and afferent inhibition in the cat and rat ventrobasal thalamus. Neuroscience 28: 17–26
- 132 Lee S. M., Friedberg M. H. and Ebner F. F. (1994) The role of GABA-mediated inhibition in the rat ventral posterior medial thalamus. I. Assessment of receptive field changes following thalamic reticular nucleus lesions. J. Neurophysiol. 71: 1702–1715
- 133 Lee S. M., Friedberg M. H. and Ebner F. F. (1994) The role of GABA-mediated inhibition in the rat ventral posterior medial thalamus. II. Differential effects of GABA<sub>A</sub> and GABA<sub>B</sub> receptor antagonists on responses of VPM neurons. J. Neurophysiol. 71: 1716–1726

699

- 134 Huguenard J. R. and Prince D. A. (1994) Clonazepam suppresses GABA<sub>B</sub>-mediated inhibition in thalamic relay neurons through effects in nucleus reticularis. J. Neurophysiol. **71**: 2576–2581
- 135 Warren R. A. and Jones E. G. (1994) Glutamate activation of cat thalamic reticular nucleus: effects on response properties of ventroposterior neurons. Exp. Brain Res. 100: 215-
- 136 Cox C. L., Huguenard J. R. and Prince D. A. (1997) Nucleus reticularis neurons mediate diverse inhibitory effects in thalamus. Proc. Natl. Acad. Sci. USA 94: 8854-8859
- 137 Warren R. A., Agmon A. and Jones E. G. (1994) Oscillatory synaptic interactions between ventroposterior and reticular neurons in mouse thalamus in vitro. J. Neurophysiol. 72: 1993-2003
- 138 Pinault D., Bourassa J. and Deschênes M. (1995) The axonal arborization of single thalamic reticular neurons in the somatosensory thalamus of the rat. Eur. J. Neurosci. 7: 31-40
- Van der Loos H. (1976) Barreloids in mouse somatosensory thalamus. Neurosci. Lett. 2: 1-6
- Belford G. R. and Killackey H. P. (1979) The development of vibrissae representation in subcortical trigeminal centers of the neonatal rat. J. Comp. Neurol. 188: 63-74
- Jones E. G. and Friedman D. P. (1982) Projection pattern of functional components of thalamic ventrobasal complex on monkey somatosensory cortex. J. Neurophysiol 48: 521-544
- 142 Jones E. G., Friedman D. P. and Hendry S. H. C. (1982) Thalamic basis of place- and modality-specific columns in monkey somatosensory cortex: a correlative anatomical and
- physiological study. J. Neurophysiol. **48**: 545–568 143 Crabtree J. W. and Kind P. C. (1993) Monoclonal antibody Cat-301 selectively identifies a subset of nuclei in the cat's somatosensory thalamus. J. Neurocytol. 22: 903-912
- 144 Mountcastle V. and Henneman E. (1949) Pattern of tactile representation in thalamus of cat. J. Neurophysiol. 12: 85-
- 145 Rose J. E. and Mountcastle V. B. (1952) The thalamic tactile region in rabbit and cat. J. Comp. Neurol. 97: 441-489
- Cox C. L., Huguenard J. R. and Prince D. A. (1996) Heterogeneous axonal arborizations of rat thalamic reticular neurons in the ventrobasal nucleus. J. Comp. Neurol. 366: 416 - 430
- 147 Shosaku A. and Sumitomo I. (1983) Auditory neurons in the rat thalamic reticular nucleus. Exp. Brain Res. 49: 432-442
- 148 Rouiller E. M., Colomb E., Capt M. and De Ribaupierre F. (1985) Projections of the reticular complex of the thalamus onto physiologically characterized regions of the medial geniculate body. Neurosci. Lett. 53: 227-232
- Simm G. M., De Ribaupierre F., De Ribaupierre Y. and Rouiller E. M. (1990) Discharge properties of single units in auditory part of reticular nucleus of thalamus in cat. J. Neurophysiol. 63: 1010-1021
- Villa A. E. P. (1990) Physiological differentiation within the auditory part of the thalamic reticular nucleus of the cat. Brain Res. Rev. 15: 25-40
- Crabtree J. W. (1998) Organization in the auditory sector of the cat's thalamic reticular nucleus. J. Comp. Neurol. 390: 167 - 182
- 152 Conley M., Kupersmith A. C. and Diamond I. T. (1991) The organization of projections from subdivisions of the auditory cortex and thalamus to the auditory sector of the thalamic reticular nucleus in Galago. Eur. J. Neurosci. 3: 1089-1103
- 153 Montero V. M. (1983) Ultrastructural identification of axon terminals from the thalamic reticular nucleus in the medial geniculate body in the rat: an EM autoradiographic study. Exp. Brain Res. 51: 338-342
- 154 Bartlett E. L. and Smith P. H. (1999) Anatomic, intrinsic, and synaptic properties of dorsal and ventral division neurons in rat medial geniculate body. J. Neurophysiol. 81: 1999-2016
- 155 Morest D. K. (1965) The laminar structure of the medial geniculate body of the cat. J. Anat. (Lond.) 99: 143–160

- 156 Aitkin L. M. and Webster W. R. (1972) Medial geniculate body of the cat: organization and responses to tonal stimuli of neurons in ventral division. J. Neurophysiol. 35: 365-380
- Calford M. B. and Webster W. R. (1981) Auditory representation within principal division of cat medial geniculate body: an electrophysiological study. J. Neurophysiol. 45: 1013-1028
- 158 Imig T. J. and Morel A. (1985) Tonotopic organization in ventral nucleus of medial geniculate body in the cat. J. Neurophysiol. **53**: 309-340
- Scheibel M. E. and Scheibel A. B. (1967) Structural organization of nonspecific thalamic nuclei and their projection toward cortex. Brain Res. 6: 60-94
- Skinner J. E. and Yingling C. D. (1977) Central gating mechanisms that regulate event-related potentials and behavior: a neural model for attention. Prog. Clin. Neurophysiol. 1. 30-69
- 161 Scheibel A. B. (1981) The problem of selective attention: a possible structural substrate. In: Brain Mechanisms of Perceptual Awareness, pp 319-326, Pompeiano O. and Ajmone-Marsan C. (eds), Raven, New York
- LaBerge D., Carter M. and Brown V. (1992) A network simulation of thalamic circuit operations in selective attention. Neural Comp. 4: 318-331
- Vidal de Carvalho L. A. (1994) Modeling the thalamocortical loop. Int. J. Bio-Med. Comp. 35: 267-296
- Taylor J. G. and Alavi F. N. (1995) A global competitive neural network. Biol. Cybern. 72: 233-248
- Villa A. E. P., Rouiller E. M., Simm G. M., Zurita P., De Ribaupierre Y. and De Ribaupierre F. (1991) Corticofugal modulation of the information processing in the auditory thalamus of the cat. Exp. Brain Res. 86: 506-517
- Spreafico R., Fressoni C., Regondi M. C., Arcelli P. and De Biasi S. (1993) Interneurons in the mammalian thalamus. In: Thalamic Networks for Relay and Modulation, pp 17-28, Minciacchi D., Molinari M., Macchi G. and Jones E. G. (eds), Pergamon, Oxford
- LeVay S. and Ferster D. (1979) Proportion of interneurons in the cat's lateral geniculate nucleus. Brain Res. 164: 304-
- Montero V. M. and Zempel J. (1985) Evidence for two types of GABA-containing interneurons in the A-laminae of the cat lateral geniculate nucleus: a double-label HRP and GABA-immunocytochemical study. Exp. Brain Res. 60: 603-609
- Harris R. M. and Hendrickson A. E. (1987) Local circuit neurons in the rat ventrobasal thalamus: a GABA immunocytochemical study. Neuroscience 21: 229–236
- Montero V. M. and Singer W. (1985) Ultrastructural identification of somata and neural processes immunoreactive to antibodies against glutamic acid decarboxylase (GAD) in the dorsal lateral geniculate nucleus of the cat. Exp. Brain Res. **59:** 151–165
- Montero V. M. (1991) A quantitative study of synaptic contacts on interneurons and relay cells of the cat lateral geniculate nucleus. Exp. Brain Res. 86: 257-270
- Takács J., Hámori J. and Silakov V. (1991) GABA-containing neuronal processes in normal and cortically deafferented dorsal lateral geniculate nucleus of the cat: an immunogold and quantitative EM study. Exp. Brain Res. 83: 562-574
- Erişir A., Van Horn S. C. and Sherman S. M. (1998) Distribution of synapses in the lateral geniculate nucleus of the cat: differences between laminae A and A1 and between relay cells and interneurons. J. Comp. Neurol. 390: 247-255
- 174 Montero V. M. (1987) Ultrastructural identification of synaptic terminals from the axon of type 3 interneurons in the cat lateral geniculate nucleus. J. Comp. Neurol. 264: 268 - 283
- Cucchiaro J. B., Bickford M. E. and Sherman S. M. (1991) A GABAergic projection from the pretectum to the dorsal lateral geniculate nucleus in the cat. Neuroscience 41: 213-226

- 176 Cucchiaro J. B., Uhlrich D. J. and Sherman S. M. (1993) Ultrastructure of synapses from the pretectum in the A-laminae of the cat's lateral geniculate nucleus. J. Comp. Neurol. 334: 618–630
- 177 Wahle P., Stuphorn V., Schmidt M. and Hoffmann K.-P. (1994) LGN-projecting neurons of the cat's pretectum express glutamic acid decarboxylase mRNA. Eur. J. Neurosci. 6: 454–460
- 178 Mukhametov L. M., Rizzolatti G. and Tradardi V. (1970) Spontaneous activity of neurones of nucleus reticularis thalami in freely moving cats. J. Physiol. 210: 651–667
- 179 Deschênes M., Paradis M., Roy J. P. and Steriade M. (1984) Electrophysiology of neurons of lateral thalamic nuclei in cat: resting properties and burst discharges. J. Neurophysiol. 51: 1196–1219
- 180 Jahnsen H. and Llinás R. (1984) Electrophysiological properties of guinea-pig thalamic neurones: an in vitro study. J. Physiol. 349: 205–226
- 181 Jahnsen H. and Llinás R. (1984) Ionic basis for the electroresponsiveness and oscillatory properties of guinea-pig thalamic neurones in vitro. J. Physiol. 349: 227–247
- 182 Domich L., Oakson G. and Steriade M. (1986) Thalamic burst patterns in the naturally sleeping cat: a comparison between cortically projecting and reticularis neurones. J. Physiol. 379: 429–449
- 183 Mulle C., Madariaga A. and Deschênes M. (1986) Morphology and electrophysiological properties of reticularis thalami neurons in cat: in vivo study of a thalamic pacemaker. J. Neurosci. 6: 2134–2145
- 184 Steriade M., Domich L. and Oakson G. (1986) Reticularis thalami neurons revisited: activity changes during shifts in states of vigilance. J. Neurosci. 6: 68–81
- 185 Spreafico R., Curtis M. de, Frassoni C. and Avanzini G. (1988) Electrophysiological characteristics of morphologically identified reticular thalamic neurons from rat slices. Neuroscience 27: 629-638
- 186 Avanzini G., Curtis M. de, Panzica F. and Spreafico R. (1989) Intrinsic properties of nucleus reticularis thalami neurones of the rat studied in vitro. J. Physiol. 416: 111-122
- 187 McCormick D. A. and Feeser H. R. (1990) Functional implications of burst firing and single spike activity in lateral geniculate relay neurons. Neuroscience 39: 103–113
- 188 Lo F.-S., Lu S.-M. and Sherman S. M. (1991) Intracellular and extracellular in vivo recording of different response modes for relay cells of the cat's lateral geniculate nucleus. Exp. Brain Res. 83: 317–328

- 189 Ben-Ari Y., Dingledine R., Kanazawa I. and Kelly J. S. (1976) Inhibitory effects of acetylcholine on neurons in the feline nucleus reticularis thalami. J. Physiol. (Lond.) 261: 647-671
- 190 Dingledine R. and Kelly J. S. (1977) Brain stem stimulation and the acetylcholine-evoked inhibition of neurones in the feline nucleus reticularis thalami. J. Physiol. 271: 135–154
- 191 McCormick D. A. and Prince D. A. (1986) Acetylcholine induces burst firing in thalamic reticular neurones by activating a potassium conductance. Nature 319: 402–405
- 192 Francesconi W., Müller C. M. and Singer W. (1988) Cholinergic mechanisms in the reticular control of transmission in the cat lateral geniculate nucleus. J. Neurophysiol. 59: 1690– 1718
- 193 Hu B., Steriade M. and Deschênes M. (1989) The effects of brainstem peribrachial stimulation on perigeniculate neurons: the blockage of spindle waves. Neuroscience 31: 1-12
- 194 McCormick D. A. (1989) Cholinergic and noradrenergic modulation of thalamocortical processing. Trends Neurosci. 12: 215–221
- 195 Funke K. and Eysel U. T. (1993) Modulatory effects of acetylcholine, serotonin, and noradrenaline on the activity of cat perigeniculate neurons. Exp. Brain Res. 95: 409–420
- 196 Marks G. A. and Roffwarg H. P. (1991) Cholinergic modulation of responses to glutamate in the thalamic reticular nucleus of the anesthetized rat. Brain Res. 557: 48–56
- 197 Ahlsén G. and Lindström S. (1982) Mutual inhibition between perigeniculate neurones. Brain Res. 236: 482–486
- 198 Deschenes M., Madariaga-Domich A. and Steriade M. (1985) Dendrodendritic synapses in the cat reticularis thalami nucleus: a structural basis for thalamic spindle synchronization. Brain Res. 334: 165-168
- 199 Williamson A. M., Ohara P. T., Ralston D. D., Milroy A. M. and Ralston H. J. (1994) Analysis of gamma-aminobutyric acidergic synaptic contacts in the thalamic reticular nucleus of the monkey. J. Comp. Neurol. 349: 182–192
- 200 Pinault D., Smith Y. and Deschênes M. (1997) Dendrodendritic and axoaxonic synapses in the thalamic reticular nucleus of the adult rat. J. Neurosci. 17: 3215–3233
- 201 Sanchez-Vives M. V., Bal T. and McCormick D. A. (1997) Inhibitory interactions between perigeniculate GABAergic neurons. J. Neurosci. 17: 8894–8908
- 202 Bazhenov M., Timofeev I., Steriade M. and Sejnowski T. J. (1999) Self-sustained rhythmic activity in the thalamic reticular nucleus mediated by depolarizing GABA<sub>A</sub> receptor potentials. Nat. Neurosci. 2: 168–174
- 203 Cox C. L. and Sherman S. M. (1999) Glutamate inhibits thalamic reticular neurons. J. Neurosci. 19: 6694–6699