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Cerebellar connections to the rostral reticular nucleus of the thalamus in the rat

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Abstract

We studied the cerebellar connections to the reticular nucleus thalamus (RNT) by means of retrograde axonal transport of horseradish peroxidase (HRP) in the rat. Specific HRP pressure injections to the rostral RNT (1.6–1.8 mm caudal to bregma) resulted in retrograde labelling of neurones in the cerebellar nuclei. The rostral RNT showed specific topographical organization of its cerebellar connections. Microinjections into the rostral RNT, 1.6 mm caudal to bregma, produced numerous HRP-labelled neurones within the anterior interposed (emboliform nucleus) and scarce HRP-labelled neurones within the lateral (dentate nucleus) cerebellar nuclei, whereas injections into the rostral RNT, 1.8 mm caudal to bregma, produced numerous HRP-labelled neurones within the posterior interposed (globose nucleus) and scarce lightly HRP-labelled neurones within the lateral (dentate nucleus) cerebellar nuclei. Cerebellar connections with the rostral RNT were exclusively ipsilateral to the injection site. No HRP-labelled cells were detected in the medial (fastigial nucleus) cerebellar nucleus. The cerebellar connections reach the RNT via the superior cerebellar peduncle. By contrast, HRP injections into the anterior, posterior interposed and lateral cerebellar nuclei produced no labelled cells within the RNT. This study demonstrates the existence of direct cerebello-RNT but not RNT-cerebellar connections. The presence of the cerebello-RNT connections introduces a new route through which the cerebellum may influence RNT and thus cerebral cortical activity.

Key words cerebellum; connections; nucleus reticularis thalami; rat.

Introduction

The reticular nucleus of the thalamus (RNT) lies between the external medullary lamina and the internal capsule and forms a sheet of GABAergic cells that surrounds most of the lateral, dorsolateral and anterior aspect of the thalamus. The RNT lies in a key position to influence many aspects of forebrain. Early investigations demonstrated direct projections from the RNT to the cortex and suggested that the RNT was the final common pathway of the reticular formation for cortical activation (Rose, 1952).

The majority of the inputs to the RNT are from collaterals of thalamocortical and corticothalamic axons and most of the outputs of the RNT are to the dorsal thalamus (Jones, 1975; Ohara & Lieberman, 1985; Yen et al. 1985; De Biasi et al. 1986). In addition to thalamic and cortical afferents, thalamic reticular cells also receive afferents from various brainstem centres and from the basal forebrain (Steriade et al. 1984a; Cornwall et al. 1990; Reardon & Mitrofanis, 2000). Studies have shown that RNT connections with the thalamus and cortex are organized in a topographic manner (Carman & Powell, 1964; Jones, 1975). The caudal regions of the RNT are associated with the visual cortex and dorsal lateral geniculate nucleus dorsally, and with auditory cortex and medial geniculate nucleus ventrally (Jones, 1975; Ohara et al. 1980; Conley & Diamond, 1990; Conley et al. 1991). The somatosensory cortex and the thalamic ventrobasal complex have connections within the intermediate part of the RNT, whereas various motor and limbic centres connect within the rostral part of the RNT.

The neurones of the RNT utilize the inhibitory transmitter GABA, whereas most of the neurones in the

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other thalamic nuclei utilize the excitatory transmitter glutamate. In a number of electrophysiological studies it was established that inputs to RNT from both dorsal thalamus and cortex are excitatory and the neurones of the RNT exert a powerful inhibition on transmission through dorsal thalamic neurones (Steriade & Wyzinski, 1972).

Despite these data, the precise role of the RNT is still debated. Crick (1984) postulated that the RNT acts to mediate selective attention in particular, to specifically gate dorsal thalamic input to the cerebral cortex. It has also been suggested that the RNT is involved in modulation of thalamic and/or cortical neuronal firing patterns (Steriade & Deschenes, 1984b; Steriade et al. 1986). There is also evidence that the RNT is involved in generation of oscillatory activity responsible for cortical spindle activity during the early stage of sleep (Steriade & Deschenes, 1984b; Steriade et al. 1987). The principal system involved in the control of thalamic and cortical neurones originates from the rostral midbrain reticular formation, locus ceruleus and raphe nuclei.

The role of the cerebellum in the regulation of somatic motor activity is also well established (Anderson et al. 1987). The cerebral cortex is directly influenced by the output of the cerebellum via the thalamus to multiple cortical areas including frontal eye fields, premotor, prefrontal, primary motor, supplementary motor, frontal association and parietal cortices (Hendry et al. 1979; Yamamoto et al. 1992; Lynch et al. 1994; Middleton & Strick, 1994; Rouiller et al. 1994). Additionally, investigations have demonstrated involvement of the cerebellum in visceral, cognitive, behavioural functions and memory (Whiteside & Snider, 1953; Albe-Fessard et al. 1985; Gonzalo & Leichnetz, 1990; Nixon & Passingham, 1990; Schmahmann & Pandya, 1997; Middleton & Strick, 2000).

Neuroanatomical studies have shown reciprocally organized direct and indirect connections between cerebellum and hippocampus and various hypothalamic, amygdaloid and brainstem nuclei (Whiteside & Snider, 1953; Somana & Walberg, 1979; Haines et al. 1990; Çavdar et al. 2001a,b).

The cerebellar inputs are relayed via the thalamus to the appropriate cortical area (Hendry et al. 1979; Yamamoto et al. 1992; Lynch et al. 1994; Middleton & Strick, 1994; Rouiller et al. 1994). However, cerebellar connections with the RNT have received little attention.

In this study we investigated the connections of the deep cerebellar nuclei to the RNT in the rat using the horseradish peroxidase (HRP) tracing technique. These connections are discussed with relation to the cerebellar influence on the functional role of the RNT.

Materials and methods

Sixteen Wistar albino rats weighing 250–400 g were fed with a standard laboratory rat chow and tap water *ad libitum*, and housed in Plexiglass cages with a 12-h light/dark cycle in a temperature-controlled room (20 ± 3 °C). The Institutional Animal Care and Use Committee of Marmara University approved all procedures, which followed the New York Academy of Sciences' guidelines for the use of animals in research, testing and education.

Rats were anaesthetized with ketamine (50 mg kg^{-1}, intraperitoneally (i.p.)) and chlorpromazine (1 mg kg^{-1}, i.p.). The head of each animal was placed in a stereotaxic frame (Stoelting Model 51600, USA), the scalp incised longitudinally, and the skull was exposed between lambda and bregma. A small hole was drilled in the skull at a position appropriate for the unilateral injection of HRP in the RNT (1.4–3.1 mm caudal to bregma, 2.2–2.6 mm lateral to midline, and 5.4–6.6 mm ventral to the surface of the skull) (Fig. 1) or the cerebellar nuclei (Lateral cerebellar nucleus, 11.3 mm posterior, 2.2 mm lateral, 5.9 mm ventral; Anterior interposed nucleus, 11.3 mm posterior, 3.4 mm lateral, 6.0 mm ventral; Posterior interposed nucleus, 11.6 mm posterior, 2.4 mm lateral, 6.0 mm ventral to the surface of the skull). Co-ordinates for the RNT injection sites between 1.4 and 1.8 mm caudal to bregma were regarded as rostral RNT according to the rat brain atlas of Paxinos & Watson (1998). A glass micropipette (10–18 μm) containing the HRP solution was lowered into the target region. The tip of the micropipette was filled with air (20 nL) to avoid diffusion of HRP to unwanted areas of the brain during the lowering procedure of the pipette to the RNT. A volume of 60 nL of HRP was applied during 20 s by pressure injection via a Hamilton microsyringe through the cannula connected to an infusion pump (Kd Scientific, USA). Following the injection, the pipette remained in the target location for 1.5 h to avoid loss of tracer during the removal of the pipette.

After 2–3 days survival, the animals were deeply anaesthetized with ether and perfused transcardially with 500 mL of saline solution, and 1% paraformaldehyde and 1.25% glutaraldehdyde in 0.05 M phosphate

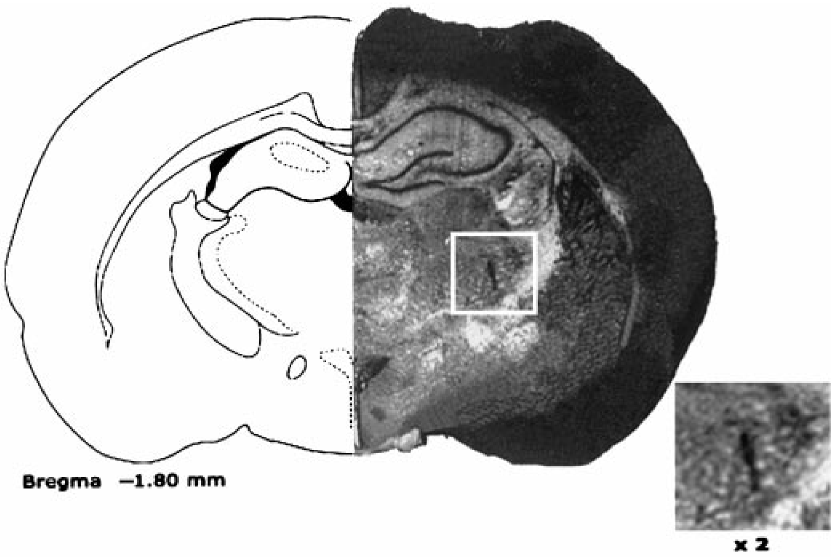

Fig. 1 Photomicrograph combined with a schematic drawing of the coronal section (bregma −1.80 mm) of the brain with a high power view to show the injection site of the HRP into the RNT in the rat.

buffer (500 mL). The brains were removed and post-fixed for 24 h at 4 °C. Coronal sections (30–50 μm) were cut using a cryostat (Microtom, Germany). Sections were collected in phosphate buffer (pH 7.7). The sections were treated with tetramethylbenzidine as described by Mesulam (1978). The HRP injection sites were stained and examined microscopically to verify the location. Only proper placements were included in the study.

The HRP injection site consisted of a central core (black zone) which is considered to be an effective site for uptake of the transported tracer.

HRP-labelled neurone counts

Of the 16 animals, eight with proper injections were included in the study. The HRP-labelled neurones in each cerebellar nuclei were counted at ×400 magnification. An eyepiece graticule (covering 0.0785 mm^2) was used to define the counting area. At least 15 such areas in each nucleus were surveyed for HRP-labelled neurones and the average number of HRP-labelled neurones were calculated for each eight animal. The standard deviations were calculated from the average number of HRP-labelled neurones for each animal.

Results

The RNT lies between the coordinates 1.4 and 3.1 mm caudal to bregma according the rat brain atlas of Paxinos & Watson (1998). Injections of HRP to various sites of RNT showed that it is connected to various cortical, subcortical and brainstem structures but only the rostral RNT was connected to the cerebellum. Cerebellar labelling was undetectable after injections into other areas of the RNT.

Microinjections into the rostral RNT of the rat produced varied labelling among the cerebellar nuclei depending on the position of the injection. Injections into the rostral RNT, 1.6 mm caudal to bregma, produced numerous HRP-labelled neurones within the anterior interposed (emboliform) nucleus and fewer labelled cells in the lateral (dentate) cerebellar nucleus (Fig. 2), whereas injections administered into the rostral RNT, 1.8 mm caudal to bregma, produced numerous HRP-labelled neurones within the posterior interposed and scarce lightly HRP-labelled neurones

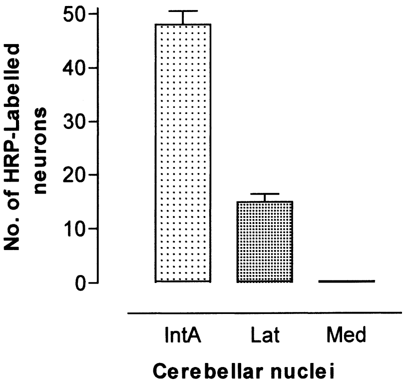

Fig. 2 Number of HRP-labelled neurones per unit area (0.0785 mm^2) in the cerebellar nuclei, subsequent to HRP injections into the RNT 1.6 mm caudal to bregma. The error bars on the graph give the SD, which was calculated from the average numbers of HRP-labelled neurones for each animal.

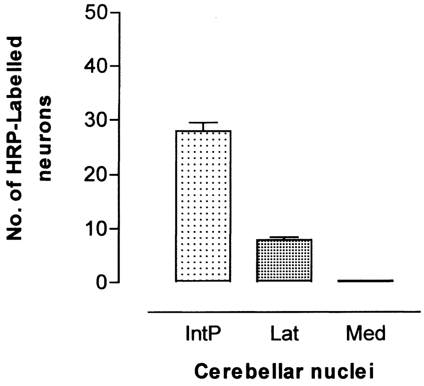

Fig. 3 Number of HRP-labelled neurones per unit area in the cerebellar nuclei, subsequent to HRP injections into the RNT 1.8 mm caudal to bregma. The error bars on the graph give the SD, which was calculated from the average numbers of HRP-labelled neurones for each animal.

within the lateral (dentate) cerebellar nucleus (Fig. 3). Cerebellar connections with the rostral RNT were all exclusively ipsilateral to the injection site. No HRP-labelled cells were detected in the medial cerebellar nucleus. The presence of labelled fibres showed that cerebellar connections reach the RNT via the superior cerebellar peduncle.

The HRP-labelled cells were distributed randomly throughout the anterior interposed nucleus of the cerebellum and were almost all small neurones (Fig. 4). The HRP-labelled neurones in the posterior interposed cerebellar nucleus were mainly localized in the ventral part of the nucleus close to the 4th ventricle. The shape and dendritic pattern of the cells revealed two populations: multipolar and fusiform (Fig. 5). The fusiform neurones were significantly less than multipolar neurones. HRP-labelled neurones in the lateral cerebellar nucleus were observed after injections both 1.6 and 1.8 mm caudal to bregma. These neurones were mostly localized to the ventral aspect of the nucleus.

No labelled neurones were detected within the RNT after HRP injections into the lateral cerebellar, anterior or posterior interposed cerebellar nuclei.

Discussion

The cerebellum has long been regarded as being involved in the control of movement, primarily through its connections with the cerebral cortex. It is well known that cortical afferents to the cerebellum arise from multiple areas of the cerebral cortex including frontal, parietal and temporal lobes (Schmahmann & Pandy, 1997; Glickstein et al. 1985). However, the thalamic relays of cerebellar efferents reaching the cortex are not clearly defined in various species. The output of the cerebellar nuclei was thought to terminate in a single region of ventrolateral thalamus (Kemp & Powell, 1971; Asanuma et al. 1983). This thalamic region was believed to project exclusively upon a single cortical area, the primary motor cortex. It is now apparent that cerebellar projections to the thalamus are not limited to a single region of ventrolateral thalamus, but target other thalamic nuclei as well (Yamamoto et al. 1992;

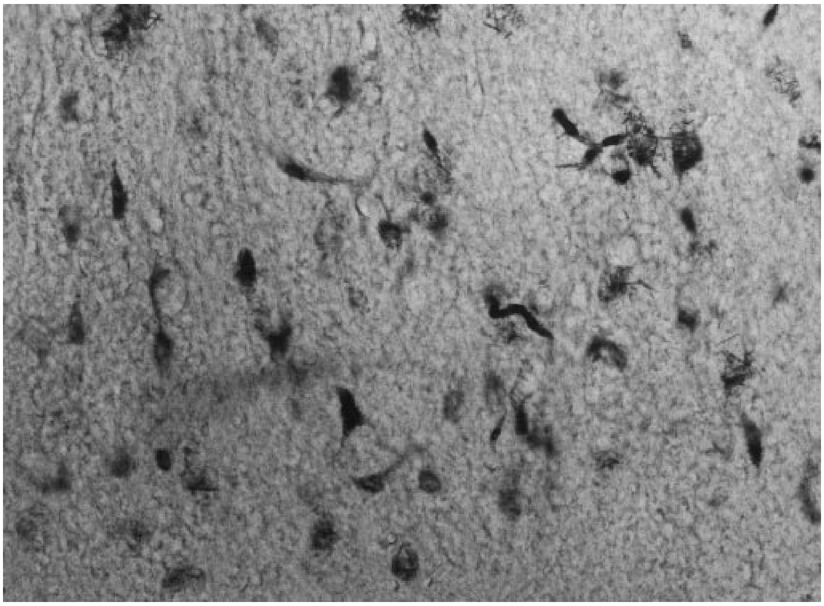

Fig. 4 Photomicrograph showing randomly distributed HRP-labelled neurones within the anterior interposed nucleus of cerebellum subsequent to HRP injections into RNT 1.6 mm caudal to bregma (×200).

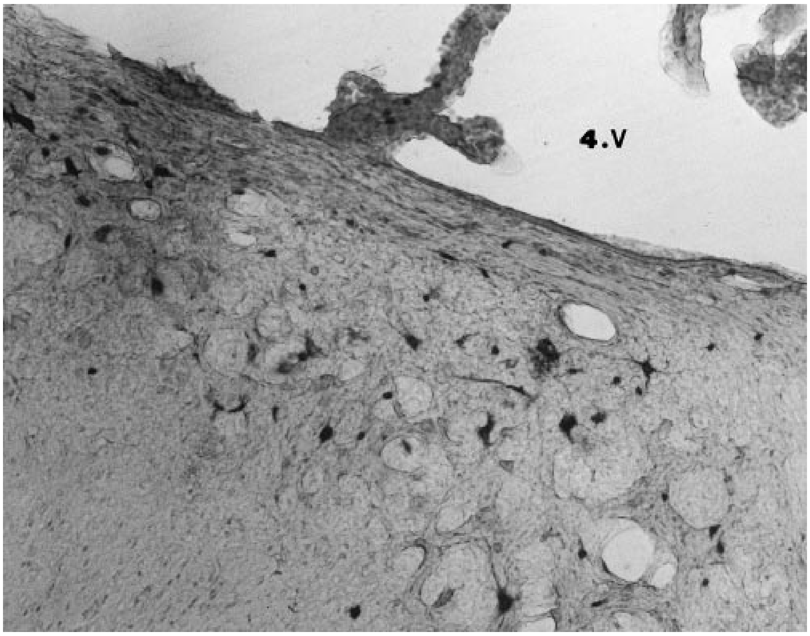

Fig. 5 Photomicrograph showing dark HRP-labelled multipolar and fusiform neurones within the posterior interposed nucleus of cerebellum localized close to the fourth ventricle (×100).

Hendry et al. 1979). Yamamoto et al. (1992) performed a double staining technique to reveal thalamic connections of deep cerebellar nuclei on monkey and showed that ventral thalamic nuclei, nucleus X and the ventrolateral part of mediodorsal thalamic nucleus are thalamic relays of cerebellocortical circuit. Liu et al. (1993) demonstrated possible pathways from cerebellum via parafasciular nucleus of the thalamus in modulating noxious inputs.

Studies have shown that the cerebellum via the thalamus is connected to wide areas of the cortex (frontal eye field, oculomotor nucleus, supplementary motor area, frontal association cortex, primary motor, premotor, prefrontal and parietal cortices) (Hendry et al. 1979; Lynch et al. 1994; Middleton & Strick, 1994; Rouiller et al. 1994). Additionally, the cerebellum is also connected to subcortical structures such as the basal ganglia, hypothalamus, amygdala and hippocampus (Cornwall et al. 1990; Haines et al. 1990; Çavdar et al. 2001a,b).

If the cerebellum is to influence cognition, visceral control, behavioural function and memory as well as motor control, it must do so through projections from deep cerebellar nuclei to thalamocortical circuits concerned with these functions.

Our results show that the anterior, posterior and lateral but not medial cerebellar nuclei have connections with specific regions of the RNT in varying density. Experimental studies have reported the involvement of the medial cerebellar nucleus in cardiovascular and behavioural responses (Miura & Reis, 1969; Chida et al. 1986; Omura et al. 1989). In contrast to the involvement of the medial cerebellar nucleus in cardiovascular responses, stimulation of the anterior interposed, lateral and posterior interposed nuclei of the cerebellum results in no such responses (Achari et al. 1973). These results may indicate that the medial cerebellar nucleus is more related to visceral functions, whereas the other cerebellar nuclei have regulatory effects on somatosensory systems.

The cerebello-RNT connections have not been previously described in the literature. Several explanations can be suggested for this. Firstly, the intrinsic organization of the RNT and its connections with other brain regions may not be uniform among different species. It has been reported that projections from the RNT to the intralaminar nuclei of the cat are heavier than to other dorsal thalamic nuclei and further that the anterior nuclei do not receive input from RNT in this species (Steriade et al. 1984b). Moreover, reticulothalamic projections in the rat are entirely ipsilateral, whereas in the cat bilateral projections to the ventral nuclear group have been reported (Rinvik, 1984). Secondly, experimental studies using tract tracing techniques and autoradiography have shown that the RNT is organized in a topographical manner (Carman et al. 1964; Jones, 1975). Our findings confirm the former results, and indicate that only specific regions of the RNT (between 1.6 and

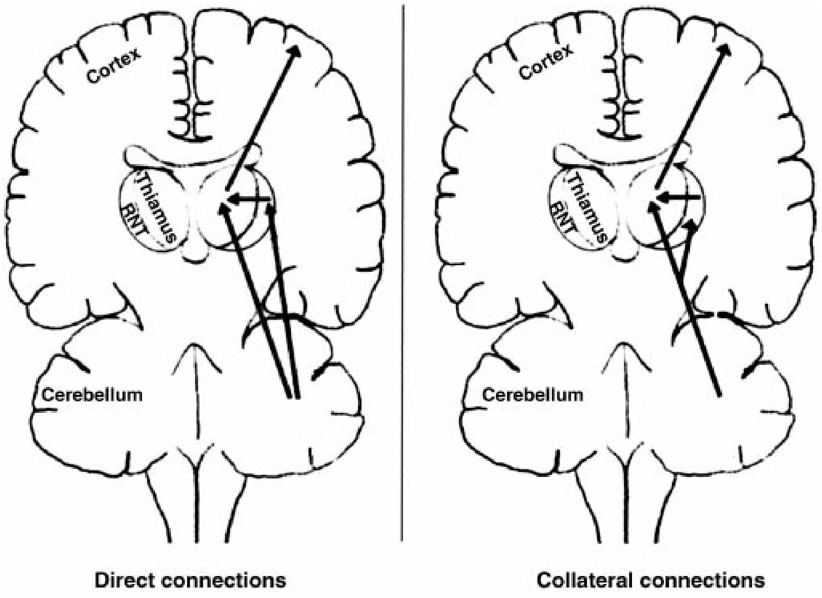

Fig. 6 Schematic drawing of the probable pathway showing the direct or indirect cerebellar influence on the thalamocortical pathways via RNT.

1.8 mm caudal to bregma) are connected to the cerebellum. These connections can be direct or/and collaterals of cerebellar fibres reaching other thalamic nuclei (Fig. 6). It is well known that neurones of the RNT are not directly connected to the cortex, rather their axons terminate on other thalamic nuclei. Therefore, the cerebellum through its RNT connections (direct or/and collaterals) may be in a position to modulate thalamic nuclei.

In summary, the present study shows that: (1) direct or/and collateral connections between cerebellar nuclei (anterior, posterior and lateral cerebellar nuclei) and RNT can be present in rat; (2) cerebello-RNT connections are not reciprocal; (3) cerebello-RNT connections were only demonstrated by HRP injections made 1.6–1.8 mm caudal to bregma, which corresponds to the rostral RNT; (4) the rostral RNT-cerebellar connections are topographically organized. The rostral RNT, 1.6 mm caudal to bregma, was connected to the anterior interposed and lateral cerebellar nuclei, whereas the rostral RNT, 1.8 mm caudal to bregma, was connected to posterior interposed and lateral cerebellar nuclei; (5) the density of projections from each cerebellar nuclei to the RNT varied.

The next step of our investigations is to determine whether cerebello-RNT connections are direct or/and collaterals of cerebellar fibres reaching thalamic nuclei.

The cerebello-RNT fibre system connecting the two parts of the central nervous system may provide a control circuit through which the cerebellum may influence cognition, visceral control, behavioural function and memory as well as motor control.

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