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Cytoarchitecture of the medial nucleus of trapezoid body of three neotropical species of bats (*Noctilio leporinus, Phyllostomus hastatus, and Carollia perspicillata*) with different foraging behavior

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Abstract

The present study was taken to test the hypothesis that the medial nucleus of the trapezoid body (MNTB) of echolocating neotropical bats with different foraging behavior will exhibit morphological variations in relative size, degree of complexity and spatial distribution. The brains were collected from six male adult bats of each species: *Noctilio leporinus* (fish-eating), *Phyllostomus hastatus* (carnivorous/ omnivorous) and *Carollia perspicillata* (fruit-eating) and were double-embedded and transverse serial sections were cut and stained with cresyl fast violet. The results showed that the MNTB is well developed in all the bats in general and the mean length of the MNTB was 1160 ± 124 μm in *N. leporinus*, 400 ± 59 μm in *P. hastatus* and 320 ± 25 μm in *C. perspicillata*. The body and brain weight do not reflect proportionately on the size of the MNTB in the present study. The hearing frequency spectrum did not covary with the size of the MNTB among the bats studied. The MNTB is clearly demarcated from the ventral nucleus of the trapezoid body (VNTB) only in *P. hastatus*. The MNTB comprised mainly three types of cells in all three bats: dense-staining multipolar cells (12.5 μm and 25.0 μm diameter); light-staining multipolar cells measuring (12.5 μm and 25.0 μm diameter) and light-staining round cells (5.0 μm diameter). The large sized MNTB was observed in *N. leporinus,* which suggests that it relies heavily on echolocation whereas *P. hastatus* and *C. perspicillata* use echolocation as well but also rely on hearing, smell and vision.

Keywords: medial nucleus of trapezoid nucleus, cytoarchitecture, *Noctilio leporinus*, *Phyllostomus hastatus*, *Carollia perspicillata*.

Citoarquitetura do núcleo medial do corpo trapezoidal de três espécies neotropicais de morcegos (Noctilio leporinus, Phyllostomus hastatus e Carollia perspicillata) com diferentes comportamentos de forrageamento

Resumo

O presente estudo foi realizado para testar a hipótese de que o núcleo medial do corpo trapezoide (MNTB) de morcegos neotropicais ecolocativos com comportamento forrageiro diferente apresenta variações morfológicas no tamanho relativo, grau de complexidade e distribuição espacial. Os cérebros foram coletados de seis morcegos machos adultos de cada espécie, Noctilio leporinus (comedor de peixe), Phyllostomus hastatus (carnívoro/onívoro) e Carollia perspicillata (comedor de frutas), e foram seccionados em série e seções seriais transversais duplas e coradas com cresil violeta. Os resultados mostraram que o MNTB é bem desenvolvido em todos os morcegos em geral e que o comprimento médio do MNTB foi de 1.160 ± 124 μm em N. leporinus, 400 ± 59 μm em P. hastatus e 320 ± 25 μm em C. perspicillata. O peso corporal e cerebral não reflete proporcionalmente o tamanho do MNTB no presente estudo. O espectro da frequência auditiva não covaria com o tamanho do MNTB entre os morcegos estudados. O MNTB é claramente demarcado do núcleo ventral do corpo trapezoidal (VNTB) apenas em P. hastatus. O MNTB compreendia principalmente três tipos de células nos três morcegos: células multipolares de coloração densa (12,5 μm e 25,0 μm de diâmetro), células multipolares de coloração clara (12,5 μm e 25,0 μm de diâmetro) e células redondas manchadas de luz (5,0 μm de diâmetro). O MNTB de grande porte foi observado em N. leporinus, o que sugere que ele depende muito da ecolocalização, enquanto P. hastatus e C. perspicillata também usam a ecolocalização, mas dependem da audição, olfato e visão.

Palavras-chave: núcleo medial do núcleo trapezoidal, citoarquitetura, *Noctilio leporinus*, *Phyllostomus hastatus*, *Carollia perspicillata*.

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1. Introduction

The medial nucleus of the trapezoid body (MNTB) is a major auditory nucleus in the brainstem located in the hind brain next to superior olive. It consists of several type of neurons and the calyces of Held, the large synaptic endings of certain auditory neurons of the anterior ventral cochlear nucleus (AVCN). It involved in the sound source localization pathway, as well as in a number of other auditory circuits (Grothe et al., 2010; Ashida and Carr, 2011; Borst and Soria van Hoeve, 2012). The principal neurons of the MNTB receive their main excitatory input from the globular bushy cells (GBCs) of the contralateral AVCN. The large diameter axons of GBCs pass in the acoustic stria and decussate at the midline within the trapezoid body (Smith et al., 1991) and terminate on principal neurons of the MNTB via a type of giant calyceal axo-somatic terminal, calyx of Held (Morest, 1968; Held, 1893) The MNTB is a major source of glycinergic inhibition to the ipsilateral medial and lateral superior olivary nuclei (MSO, LSO, respectively), the ventral and dorsal nuclei of the lateral lemniscus (VNLL, DNLL, respectively), and other targets (Harrison and Warr, 1962; Elverland, 1978; Spangler et al., 1985). The inhibition is projected chiefly to the ipsilateral lateral superior olive (LSO), which also receives excitatory input from spherical bushy cells (SBCs) of the ipsilateral cochlear nucleus. Many LSO cells, then, are excited by stimulation of the ipsilateral ear and inhibited by stimulation of the contralateral ear. As a consequence, they become the initial point at which sensitivity to interaural level disparities is processed (Smith et al., 1998). Three types of neurons viz., stellate, elongate and principal cells were identified in the MNTB of cats and rats (Morest, 1968) with a majority (82%) of principal cells in rats (Casey and Feldman, 1985).

The auditory nuclei in general were well developed in animals with an excellent sense of hearing and echolocating capacity (Prado Reis and Abrantes Erhart, 1979). Many bats use echolocation for orientation in space and for detecting and capturing prey in total darkness (Neuweiler and Covey, 2000; Fenzl and Schuller, 2005). Echolocating bats have evolved widely diverse foraging behaviors, echolocation sound designs, and sensory/neural adaptations for the processing of echoes. The ability to locate the source of a sound is critical in echolocation and hearing in bats as it is vital for the survival of the species. Since the different bats forage different environment, it is assumed that different foraging strategies reflect on morphology of the MNTB, an important nucleus in sound localization pathway. Though few studies were done on comparative cytoarchitecture of the various auditory nuclei of echolocating bats with different foraging strategies (Gibbons et al., 2013a, b, 2019; Adogwa et al., 2014), the MNTB was not studied.

The *Noctilio leporinus* Linnaeus 1758, *Phyllostomus hastatus* Pallas 1767 and *Carollia perspicillata* Linnaeus 1758 are the three neotropical species of bats used in the present study based on their differing foraging behavior. The *N. leporinus* bats are carnivorous/piscivorous,

eat small fish in both fresh and salt water and forage near streams, coastal marine habitats, major river basins, or other moist places (Schnitzler et al., 1994). *P. hastatus* bats are omnivorous, feeding on flowers, pollen, insects and small vertebrates, and forage on open and forested regions (Koay et al., 2002). *C. perspicillata* bats are mainly frugivorous. However, they may feed on insects and sometimes pollen which forage on moist evergreen and dry deciduous forests (Koay et al., 2003). The present study is aimed to document the structure of the MNTB of these three species of bats and correlate the findings with their foraging behavior.
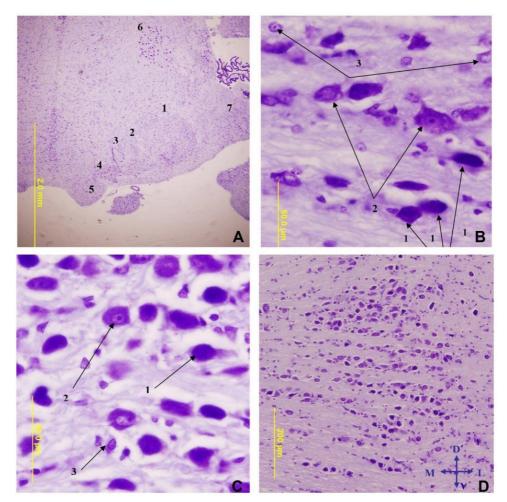
2. Material and Methods

A total of 18 bats, six for each bat species *N. leporinus, P. hastatus* and *C. perspicillata* were collected for the present study. The bats used in this study were shared in collaboration with a group involved in the study of leptospirosis surveillance in bats. All animal procedures were approved by the University of the West Indies Animal Care and Use Committee, and were conducted in accordance with National Institutes of Health standards on humane treatment of laboratory animals. Each bat was anaesthetized by using xylazine (2 mg/kg body weight) and ketamine (10 mg/kg body weight) intramuscularly and weighed. Then each bat was euthanized by natrium pentobarbital (1ml of 20% solution/kg body weight) and the brain stem of the bats were dissected out, weighed and placed in 10% buffered formalin. The brain stem samples were manually processed and double embedded (Gibbons et al., 2013 a, b). The tissues were then blocked and transverse serial sections at 10 μm thickness were made by using the rotary microtome MT 960. Every fourth section were stained with cresyl fast violet and analyzed with the aid of Olympus BX51 System Microscope and the digital images were taken with the help of Olympus DP71 microscope digital camera. The MNTB in all bats were identified as the group of neurons located medial and ventral to the medial superior olive (MSO) based on the approximate region on the brain stem, location relative to other major nuclei, axonal bundles and neuronal morphology in the other species including bats. Descriptive statistics on the body weight, brain weight, length, height and width, cell size of the MNTB were calculated and presented as mean ± standard deviation.

3. Results

3.1. Medial nucleus of trapezoid body of the Noctilio leporinus bat

The mean body and brain weight of *N. leporinus* bat weighed as 48.1 ± 3.5 g and 6.93 ± 0.47 g respectively. The MNTB was located ventral and medial to the MSO (see Figure 1A). It extended slightly more rostral and ventral than the latter but not quite as far dorsal in the brain stem. The dorsomedial peri-olivary nucleus was located dorsal to the MNTB. The MNTB extended caudo-cranially from

Figure 1. The MNTB of the Noctilio leporinus Bat. (A) A transverse section of the brainstem at the level of the motor nucleus of the trigeminal nerve of the N. leporinus bat. 1. Superior olivary nucleus 2. Superior paraolivary nucleus 3. Accessory superior olivary nucleus 4. Medial nucleus of the trapezoid body 5. Pyramid 6. Motor nucleus of the trigeminal nerve 7. Superior cerebellar peduncle; (B) Cells in the medial nucleus of the trapezoid body (MNTB) at the level of the motor nucleus of the trigeminal nerve of the N. leporinus bat. 1. Dense-staining, multipolar cells (12.5 to 25.0 µm diameter) 2. Light-staining, multipolar cells (12.5 to 25.0 µm in diameter) 3. Light-staining, round cells (5.0 µm in diameter); (C) Relatively more dark staining cells in the middle third of the MNTB at the level of the trigeminal nerve of the Noctilio leporinus bat. 1. Dense-staining, multipolar cells (12.5 to 25.0 µm diameter) 2. Light-staining, multipolar cells (12.5 to 25.0 µm in diameter) 3. Light-staining, round cells (5.0 µm in diameter); (D) Extensive fibres of the trapezoid body (TB) throughout the MNTB of the N. leporinus bat, at the level of the commissure of the inferior colliculus (IC). The large, light staining cells were seen predominantly (D-Dorsal, M-Medial, L-Lateral, V-Ventral).

the level of the motor nucleus of the trigeminal nerve to the caudal end of the inferior colliculus in the brain stem with a mean length of 1160 ± 124 µm. It measured 389 ± 34 µm in height and 412 ± 55 µm in width at the caudal third (at the level of the trigeminal nucleus) and increased in size at the middle third with 400 ± 35 µm in height and 500 ± 67 µm in width and diminished in size at the cranial third (ventrolateral to the medial lemniscus) to 480 ± 29 µm in height and 450 ± 34 µm in width.

Three types of cells viz., the dense staining multipolar cells, light staining multipolar cells and light staining round cells were observed in the MNTB of *N. leporinus*
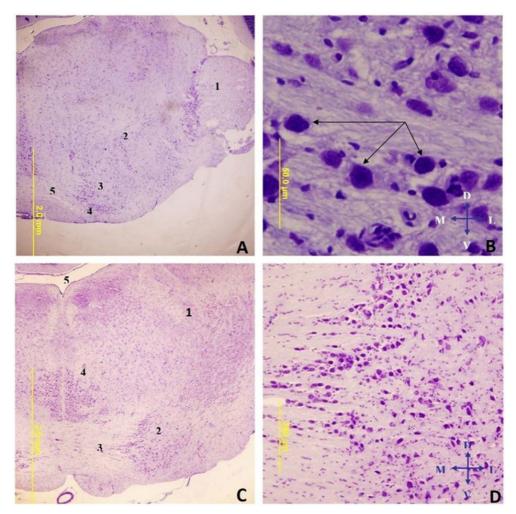
(see Figure 1B). These cells were scattered between the large diameter axons of the TB (see Figure 1C). The cell bodies of dense staining multipolar cells exhibited various shapes like round/ globular/ multipolar with a range of 12.5 to 25.0 µm diameter (see Figure 1B, C). These cells exhibit eccentric, heterochromatic nuclei with densely scattered Nissl substance throughout the cytoplasm. These cells were predominantly scattered throughout the MNTB in the *N. leporinus* bats and considered as the principal cells. The second type of cells were the light staining multipolar cells. These cells were of same size of the dense staining multipolar cells. The cell body of the cells

exhibited more centrally placed, euchromatic nucleus with finely distributed Nissl substance throughout the cytoplasm. These cells were found more at the level of the commissure of the inferior colliculi. The third type of cells were light staining round/oval cells with 5.0 μm average diameter. They exhibited centrally placed euchromatic nuclei with eosinophilic cytoplasm. These cells were few in number and scattered throughout the MNTB between the other types of cells. The trapezoid body (TB) fibres were extensively ramified throughout the MNTB of the *N. leporinus* bat (see Figure 1D).

3.2. Medial nucleus of trapezoid body of the Phyllostomus hastatus bat

The mean body and brain weight of *P. hastatus* bat weighed as 73.24 ± 7.25 g and 8.57 ± 0.67 g respectively.

The MNTB was located as in the *N. leporinus* bats but in addition, a distinct nucleus made up of heterogenous cells was found ventrolateral to the MNTB and ventral superior olive (VSO) and forms the medial olivocochlear bundle (MOC) and identified as ventral nucleus of MNTB (VNTB) (see Figure 2A). The MNTB extended caudo-cranially from the level of middle cerebellar peduncle to the middle third of the lateral lemnisci with a mean length of 400 ± 59 μm. It measured 500 ± 43 μm height and 460 ± 33 μm width at the caudal third and appeared to be divided into dorsal MNTB and ventral VNTB at the level of middle cerebellar peduncle and increased in size slightly at the middle third (at the level of caudal third lateral lemniscus) with the measurements of 520 ± 54 μm height and 480 ± 23 μm width and it became larger and denser at the rostral

Figure 2. The MNTB of Phyllostomus hastatus bat. (A) A transverse section of the brainstem at the level of the middle cerebellar peduncle of the P. hastatus bat. 1. Middle cerebellar peduncle 2. Superior paraolivary nucleus 3. Medial nucleus of the trapezoid body 4. Ventral nucleus of the trapezoid body 5. Fibres of the trapezoid body; (B) Medium-sized, dark-staining, round/ oval cells (12.5 to 17.5 μm diameter) in the caudal third of the MNTB of the P hastatus bat; (C) A transverse section at the rostral third of the MNTB of the P. hastatus bat. 1. Inferior colliculus 2. Medial nucleus of the trapezoid body 3. Fibres of the trapezoid body 4. Medial lemniscus 5. Fourth ventricle; (D) The fibres and cells of the rostral third of the MNTB of the P. hastatus bat (D-Dorsal, M-Medial, L-Lateral, V-Ventral).
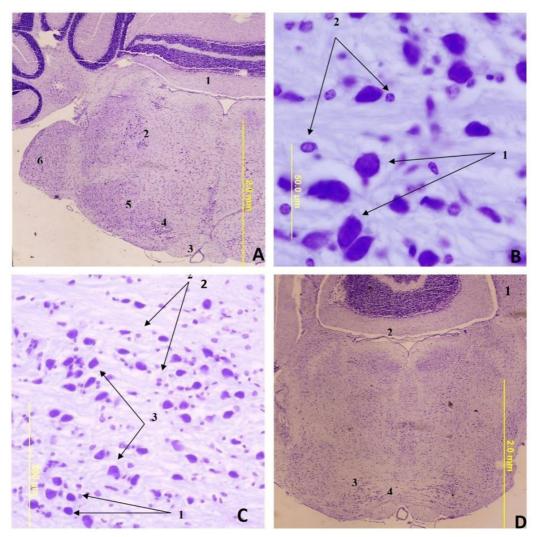
third (at the level of middle third of lateral lemniscus) and measured 560 ± 54 μm height and 505 ± 40 μm width.

Three types of cells viz., the dense staining multipolar cells, light staining multipolar cells and light staining round cells were observed in the MNTB of *P. hastatus* as in *N. leporinus*. (see Figure 2A). The dense staining multipolar cells (12.5 to 17.5 μm diameter) were predominantly dispersed among the trapezoidal fibres. Very few large dense staining cells (17.5 to 25 μm diameter) were also noticed at the level of caudal and middle third of the MNTB (see Figure 2B). At the rostral third, large dense-staining, multipolar cells were seen (17.5 to 25 μm diameter) mostly in the ventral portion of the MNTB (see

Figure 2C). The trapezoid fibres were predominantly seen and dense and light staining, multipolar cells measuring (12.5 to 17.5 μm diameter) were present between the fibres (see Figure 2D).

3.3. Medial nucleus of trapezoid body of the Carollia perspicillata bat

The mean body and brain weight of *C. perspicillata* bat weighed as 14.4 ± 2.1 g and 3.74 ± 0.75 g respectively. The MNTB was located as a distinct large cluster of cells, ventral and medial to the MSO (Figure 3A). It extends caudocranially from the level of facial nucleus to the level of pontine nuclei in the brain stem with a mean

Figure 3. The MNTB of Carollia perspicillata bat. (A) A transverse section of the brainstem at the level of the facial nucleus of the Carollia perspicillata bat. 1. Cerebellum 2. Facial nucleus 3. Pyramid 4. Medial nucleus of the trapezoid body 5. Superior olivary complex 6. Cochlear nucleus; (B) The predominant cells of the caudal third of the MNTB of the C. perspicillata bat. 1. Large, oval cells (12.5 to 25.0 μm in diameter) 2. Small round cells (5.0 μm diameter); (C) Three cell-types of the MNTB of the C. perspicillata bat. 1. Large, oval cells (12.5 to 25.0 μm in diameter) 2. Small round cells (5.0 μm in diameter) 3. Large multipolar cells (20.0 to 32.5 μm in diameter); (D) A transverse section of the brainstem at the level of the caudal inferior colliculus of the C. perspicillata bat. 1. Inferior colliculus 2. Cerebellum 3. Medial nucleus of the trapezoid body 4. Fibres of the trapezoid body.

length of 320 ± 25 µm. It measured 370 ± 39 µm in height and 350 ± 32 µm in width at the caudal third (at the level of facial nucleus) and increased in size up to 390 ± 46 µm in height and 360 ± 27 µm in width at the middle third (at the level of caudal end of inferior colliculus) and reduced at the rostral third (at the middle of the inferior colliculus) to 360 ± 28 µm in height and 320 ± 17 µm in width.

Three types of cells viz., the dense staining large oval/round/multipolar cells, light staining large multipolar cells and light staining small round cells were observed as in other bats. At the level of the facial nucleus, large round/oval dense-staining cells (12.5 to 25.0 µm diameter) were predominately seen. There were also a few small round cells of 5.0 µm diameter dispersed among the large cells throughout the MNTB (Figure 3B). Laterally, more large dense staining multipolar cells (20.0 to 32.5 µm diameter) were seen and ventrally, the small (5.0 µm average diameter) light staining round cells were mainly apparent. All three cell-types of cells were seen throughout the MNTB and the fibres of the TB traversed the entire MNTB (Figure 3C) at the middle third of the MNTB at the level of the most caudal end of the inferior colliculus. The medial part of the MNTB was more densely-populated than the lateral part with all three cell types (Figure 3D).

4. Discussion

The general outline of the MNTB within the superior olivary complex (SOC) in all the bats studied in the present study is similar to the other mammals. The MNTB appeared large in size, extending medially to the raphe and penetrated by most of the fibres of passage in all the bats studied. The auditory nuclei are relatively larger in echolocating animals like the marmoset (Prado Reis and Abrantes Erhart, 1979), dolphins (Thomas et al., 2004; DeLong et al., 2007) and bats (Zook and Casseday, 1982; Gibbons et al., 2013a, b, 2019; Adogwa et al., 2014; Gibbons et al., 2019) than the human and non-human primates (Neuweiler and Covey, 2000) which is similar in the present study. The very well developed MNTB in *N. leporinus* (1160 $\pm$ 124 µm in length) indicated that this bat heavily depends on the echolocation than the two other bats studied.

The insectivorous bats rely heavily on echolocation for the pursuit and capture of prey would have larger auditory nuclei than do phytophagous species (Hutcheon et al., 2002). The Phyllostomus species which also echolocate while foraging but the size of the MNTB is smaller when compare with the *N. leporinus* in the present study. The body and brain weight do not reflect proportionately on the size of the MNTB in the present study as the body and brain weight of the *P. hastatus* measured as 73.24 $\pm$ 7.25 g and 8.57 $\pm$ 0.67 g respectively which is higher than the *N. leporinus* 48.1 $\pm$ 3.5 g and 6.93 $\pm$ 0.47 g, whereas the length of the MNTB measured 400 $\pm$ 59 µm in P. hastatus and 1160 $\pm$ 124 µm in N. leporinus. The differences in length of the entire MNTB of the three bats used were attributed to the varied feeding strategies, where it is

surmised that the N. leporinus bat, with the largest MNTB, requires echolocation to a higher degree than the other two bats studied (Neuweiler, 1989; Aguirre et al., 2000; Dumont, 2007).

The *N. leporinus* emit echolocation signals that are either at constant frequency (CF), frequency-modulated (FM) or a combination of the two (CF-FM). CF-FM signals have CF followed by a FM. In an CF-FM signal, the CF are typically 8.9 ms with a frequency of 52.8-56.2 kHz while the FM ranges up to 3.9 ms with 25.9 kHz bandwidth. The best sensitivity is at the range of 32-57 KHz (Schnitzler et al., 1994). The hearing range of *P. hastatus* was 1.8 to 105 kHz with best sensitivity is at 20kHz (Koay et al., 2002) whereas the *C. perspicillata* hearing ranged from 5.2 to 150 kHz and best at 15kHz (Koay et al., 2003).The best sensitivity of the hearing range is high in *N. leporinus* which is having a well-developed MNTB than other bats in the present study. The maximum range of hearing is seen in *C. Perspicillata* followed by *P. hastatus*, however there was no hypertrophy of the MNTB observed in the present study. The present findings do not support the theory that size of MNTB covaries with the frequency spectrum across which a species can hear, especially as high frequency (and ultrasound hearing) is added by species, more MNTB neurons are needed to cover the increased tonotopic axis well.

The MNTB and VNTB were not clearly demarcated in the present study as in other bats (Grothe and Park, 2000) whereas the VNTB is well-defined in the cats (Schwartz, 1992). The VNTB appeared as cluster of cells on the ventral aspect of the MNTB in *P. hastatus* bats whereas the VNTB was not apparent in *N. leporinus* and *C. perspicillata* bats. It may be due to the looser arrangement of VNTB cells than in the *P. hastatus* bat. The VNTB is one of the major sources of glycinergic inhibitory input to the ipsilateral MNTB and able to suppress MNTB spiking when activated (Awatramani et al., 2005) which will make the bats more sensitive to the interaural level disparities. The *P. hastatus* is omnivorous, and, although it eats fruit and insects, it prefers meat, preying on small vertebrates, including other bats. Like many other bats that forage for fruit amidst leaf clutter or detect live prey against a solid surface (gleaners), it uses relatively low-intensity, brief sonar pulses when foraging (Kalko and Schnitzler, 1993; Kalko and Condon, 1998; Neuweiler, 1989). It may also listen passively for sounds generated by the movements of its prey, a behavior thought to be common in bats that take large prey from substrates (Belwood, 1986). The presence of VNTB could possibly associated with passive listening and good low-frequency sensitivity.

The cell types of the MNTB of the bats in the present study were similar to those found in other bats. The principal cells of the MNTB in all the bats studied are large, dense-staining cells (12.5 to 25.0 µm diameter) with variable shapes; round, elongated or multipolar. The other large cells with light-stained nuclei of same dimensions observed in the present study would be the same type of dark stained cells. The variation in the stainability due to the abundance

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of Nissl bodies and it indicated that the dark stained cells are metabolically active. Small light staining round cells observed in the present study also similar to the findings in other bats (Schwartz, 1992).

The principal cells of the MNTB receive excitatory input from GBCs of the contralateral AVCN by the prominent Calyces of Held. These principal cells then project to the ipsilateral LSO (LSO) to inhibit postsynaptic neurons and provide a basis for interaural level detection (ILD), required for sound localization.

5. Conclusion

The present study revealed that although the MNTB is large in all the bats generally, there appears to be differences among the species. The MNTB in all bats comprised three main cell types: dense-staining, light-staining multipolar cells and round cells. The VNTB is clearly demarcated in *P. hastatus* bat. The large size of the MNTB of the *N. leporinus* bat compared to the other two species are probably due to the fact that it relies heavily on echolocation in order to feed. The *P. hastatus* and the *C. perspicillata* use echolocation as well but also rely on hearing, vision and smell.

Acknowledgements

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