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The Origin of Efferent Labyrinthine Fibers: A Comparative Study in Vertebrates* **

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Summary. Parent cells of efferent acoustic and efferent vestibular fibers were determined anatomically in all classes of vertebrates by use of retrograde axonal transport of horseradish peroxidase. These neurons were found in the brainstem, in particular in the reticular formation. In the goldfish, efferent labyrinthine neurons could be demonstrated in a medial position (lateral to the fasciculus longitudinalis medialis). In the frog, efferent neurons appeared more lateral, dorsomedial to the facial motor nucleus. In reptiles and birds, efferent acoustic neurons separate from efferent vestibular neurons. In mammals, efferent vestibular neurons are located more dorsally, lateral to the genu of the facial nerve. Efferent acoustic neurons take their origin from the superior olivary complex.

Key words: Efferent vestibular neurons – Efferent acoustic neurons – Tracer method – Fish – Amphibian – Reptile – Avian – Mammal

One of the most fascinating features of the auditory and vestibular pathway is the centrifugal projection from the brainstem to the inner ear. These efferent fibers leading from the superior olivary complex (SOC) to the cochlea were described 36 years ago by Rasmussen. These fibers are known as the olivocochlear bundle (OCB). In addition, Rasmussen and Gacek (1958) were able discover an efferent innervation to the vestibular end organ.

Electron- microscopical investigations of the receptor cell layer in the organ of Corti or vestibular apparatus revealed afferent and efferent axonal terminals synapsing on the hair cells (Wersäll and Bagger-Sjöbäck 1974). This means that there is a dual innervation of all sensory receptors in the inner ear.

Although progress has been made in specifing the distribution and development of innervation pattern in the organ of Corti (Pujol et al. 1978;

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Spoendlin 1969), methodical limitations have impeded efforts to determine the cells of origin of efferent labyrinthine fibers in the brainstem. Using the Marchi method, Rasmussen (1946) confined the origin of the crossed OCB to an area situated medial to the accessory olive and dorsal to the nucleus of the trapezoid body. The uncrossed OCB originates from the S-shaped lateral olivary nucleus (Rasmussen 1960). The discovery of acetylcholinesterase (AChE) in efferent fibers and neurons has led many investigators to believe that certain AChE-stained neurons in the brainstem project to the inner ear. However, contradictionary results were obtained by different scientists (Rossi and Cortesina 1962; Ross 1969; Osen and Roth 1969). Although retrograde cell changes of brainstem neurons have been reported as a result of cutting the octavus nerve, Gacek (1966) failled to find unequivocal cell changes in the brainstem following labyrinthectomy. However, with the method of retrograde axonal transport of protein tracers like horseradish peroxidase it is now possible to label these neurons (Gacek and Lyon 1974; Goldberg and Fernandez 1980; Schwarz et al. 1981; Strutz et al. 1980; Strutz and Spatz 1980; Strutz 1981; Strutz and Schmidt 1982; Warr 1975).

In our comparative study, in all classes of vertebrates we determined anatomically the cells of origin of efferent acoustic and vestibular fibers. In the lowest vertebrates, the fishes, we investigated the goldfish, in the amphibians the green tree frog, in the reptiles the Caiman, in the avian forms the chicken, and in mammals the guinea pig and monkey. An aqueous solution of 30%–50% horseradish peroxidase (HRP) was applited to the inner ear. In the goldfish, the tracer was injected into the ampulla of the horizontal semicircular canal. In the frog, the tracer was applited to the severed octavus nerve. In reptiles, birds, and mammals, HRP was injected both into the ampullae of the horizontal and anterior semicircular canals to determine efferent vestibular neurons and into the cochlear duct to determine efferent acoustic neurons. After 1–2 days survival, the animals were perfused transcardially with 1% paraformaldehyde and 1.5% glutaraldehyde. Frozen frontal sections of the brains were reacted for the demonstration of HRP according to the tetramethylbenzidine technique of Mesulam (1978).

In the goldfish (*Carassius auratus*), parent cells of the efferent innervation to the inner ear were located in the ipsilateral reticular formation, that is the nucleus motorius tegmenti. These neurons were fusiform with one or two dendrites.

In the green tree frog (*Hyla cinerea*), efferent labyrinthine neurons could be demonstrated again in the reticular formation. In this amphibian, the parent cells were located dorsomedial to the facial motor nucleus and dorsal to the SOC, exclusively ipsilateral to the injection site. Labeled neurons were small with a widespread dendritic ramification.

In reptiles we investigated *Caiman crocodilus*. It is in this evolutionary stage that a separation of efferent acoustic and efferent vestibular neurons could be demonstrated. Moreover, a bilateral distribution of efferent cells in the reticular formation was discernible. Efferent vestibular neurons were found in the medial reticular nucleus, between the intramedullary portion of the abducens and facial nerve. These labeled cells were fusiform in shape with one or two dendrites.

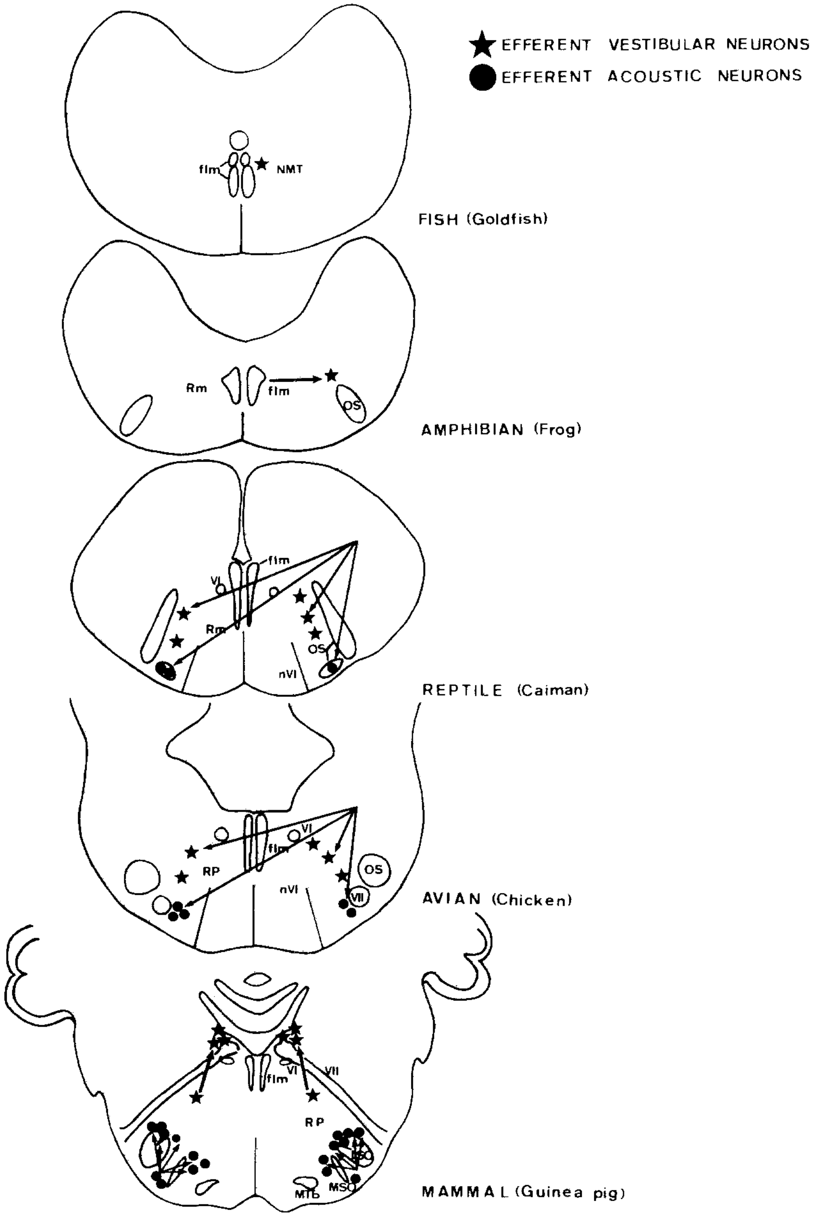

Fig. 1. Schematic representation of the origin of efferent acoustic and efferent vestibular fibers in vertebrates. *Arrow* indicates shift of efferent neurons. Abbreviations: *flm,* fasciculus longitudinalis medialis; *LSO, MSO, MTB,* nuclei of the superior olivary complex; *NMT,* nucleus motorius tegmenti; *OS,* oliva superior; *RP,* nucleus reticularis pontis caudalis; *Rm,* nucleus reticularis medius; *VI,* abducens nucleus; *nVI,* abducens nerve; *VII,* facial nucleus

There were more neurons ipsilateral to the injection. Efferent acoustic neurons were located inside or close to the rostroventral division of the SOC. These neurons were small and polygonal. Labeled acoustic neurons spread out into the dorsal adjacent medial reticular nucleus, possibly because of tracer involvement of the lagena. More labeled efferent acoustic neurons occured contralateral to the injection site.

In avians we investigated the chicken (*Gallus domesticus*). A similar finding as in the *Caiman* could be demonstrated. This data is evidence, that the brain of Crocodilia greatly resembles that of avian forms. Efferent vestibular neurons, fusiform in shape, were found bilaterally in the medial reticular nucleus, while efferent acoustic neurons could be demonstrated in the ventral reticular formation, medial to the ventral division of the facial nucleus.

In mammals, we investigated the guinea pig and the marmoset (*Callithrix jacchus*). In the guinea pig, efferent vestibular neurons were found lateral to the genu of the facial nerve bilaterally. Moreover, efferent vestibular neurons could also be demonstrated more ventrally in the medial reticular nucleus. Efferent acoustic neurons appeared bilaterally in the SOC with more labeled neurons ipsilateral to the injection site. A similar finding of parent cells of efferent labyrinthine fibers could be demonstrated in the brainstem of the monkey.

The reticular formation in vertebrates has been shown repeatedly to be the origin of efferent fibers to the inner ear. When one compares the origin of efferent vestibular and acoustic fibers, there seems to be a shift (Fig. 1) from a medial position at the border of the fasciculus longitudinalis medialis in the fish to a more lateral position, dorsal to the SOC in the amphibians. In reptiles and birds, these neurons turn ventrally in the direction of the SOC to form an elongated row of neurons. It is in this evolutionary stage that efferent acoustic neurons separate from the efferent vestibular neurons. In mammals, efferent vestibular neurons shift to a dorsal position at the floor of the IVth ventricles. However, some efferent vestibular neurons still remain in the (phylogentically older) ventral position. The distribution of efferent cochlear neurons is more expansive throughout the SOC. Moreover, Warr and Guinan (1979) recently presented evidence for a further specialization of efferent cochlear neurons, that is, two olivocochlear systems: a lateral uncrossed system with small neurons leading to the inner hair cells in the organ of Corti and a medial crossed system with medium-sized neurons leading to the outer hair cells.

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