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Comparison of the Morphology of the Inner Ear between Newts and Frogs in Relation to their Locomotory Capability

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ABSTRACT—The ultrastructural differences between the inner ears of Japanese red-bellied newts (*Cynops pyrrhogaster*) and black-spotted pond frogs (*Rana nigromaculata*) were investigated. Scanning electron microscopic observations showed apparent morphological differences in the shape of the ampulla cristae and the localization of the striola in the saccular macula. There were differences in the length of the kinocilia of the sensory hairs in each sensory region. In addition, the diameters of the bundles of stereocilia differed between the two species: the bundles of stereocilia in the semicircular cristae were thicker in frogs than in newts, while those of the utricular and lagenal maculae were thicker in newts than in frogs.

Key words: frog, newt, sensory polarity, vestibular organs, lagena

INTRODUCTION

The vertebrate inner ear shares basic structural patterns in different species (Harada, 1988). However, each class of vertebrates has developed a phylogenetically specific morphology that appears to be a reflection of its habitat. The inner ear of vertebrates other than birds and mammals consists of three semicircular canals with the associated ampullae, and the vestibulum containing the utricle and the saccule (Retzius, 1881; Werner, 1960). In addition, vertebrates ranging from cartilaginous fishes to birds possess the lagena, which is often referred to as the third otolithic organ (Lewis and Nemanic, 1972; Platt, 1977; Popper, 1977; Barber and Emerson, 1980; Ishiyama, 1995). Reptiles and birds have a basilar papilla in the basal part of the lagena (Bagger-Sjoback, 1974; White, 1986). In birds, the lagena extends to the outside of the membranous labyrinth, which forms the cochlear duct (Rosenhall, 1970; Ishiyama, 1995). Thus, the lagena of birds is seen as an auxiliary organ attached to the apical part of the cochlear ducts. The lagena is not present in mammals, in which the cochlear duct develops into refined spiral structures instead.

The inner ears of fishes, amphibians, and reptiles contain balance-controlling structures and function as the organ responsible for maintaining balance rather than as the organ for hearing, which is the major function of the inner ear in "more evolved" animals: birds, and mammals (Harada, 1988). Animals have evolved different locomotory capabilities depending on their habitat. Newts and frogs belong to the same taxonomic class, Amphibia, but their locomotory capabilities differ. Newts live either in water or on land and do not have the ability to jump. By contrast, frogs live mainly on land after metamorphosis and generally have the ability to jump. Therefore, these two animal groups have likely developed different balance organs. Although Lewis and Nemanic (1972) and Lewis and Li (1973) reported morphological observations of the amphibian inner ear, the physiological functions of the amphibian inner ear are poorly understood. Only a few reports have described the detailed morphological and physiological characteristics of the amphibian balance organ (Harada and Musso, 1971; Harada, 1971, 1972a).

Several studies have characterized anatomical and physiological aspects of amphibian vestibular organs (Harada, 1971, 1972a). The morphology of vestibular organs and the polarization of sensory cell hair bundles in amphibians have been described for various regions of the vestibular organs, and compared with those of other vertebrates (Harada, 1988). Recently, Harada *et al*. (2001) described the morphological and ultrastructural characteristics of the lagena of vertebrates, including amphibians.

In this study, we examined the morphology of the

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ampulla cristae of the semicircular canal and the maculae of the utricle, saccule, and lagena of Japanese red-bellied newts and black-spotted pond frogs by scanning electron microscopy, and compared the morphological features of the two kinds of animals. We discuss the relationship between morphology and locomotory capability based on the results presented here.

MATERIALS AND METHODS

Japanese red-bellied newts, *Cynops pyrrhogaster*, and black-spotted pond frogs, *Rana nigromaculata*, were obtained from the Laboratory for Amphibian Biology of Hiroshima University. The heads of these animals were used to prepare specimens for light microscopic and scanning electron microscopic observations.

In this study, we observed the semicircular canals and utricles from the right inner ears, and the saccules and lagenae from the left inner ears.

Light microscopy

The heads of the animals were fixed in Bouin's fixative for 7 days, and embedded in paraffin in the usual manner. Horizontal serial sections of 15-μm thickness were stained with hematoxylin-eosin.

Scanning electron microscopy

The heads of the animals were removed and dissected in the sagittal plane. After the brain was removed, the whole labyrinth was fixed in 2% glutaraldehyde in Milloling's phosphate buffer, pH 7.4, for 2 hr at 4°C and rinsed several times in buffer. The membranous labyrinth was dissected free from cartilage and connective tissue under an anatomic microscope. Tissues from the ampullae of the three semicircular canals, *i.e.*, the utricle, saccule, and lagena, were individually separated and post-fixed in 1% osmium tetroxide in Milloling's phosphate buffer for 1–2 hr at 4°C. The specimens were dried with a critical point drier, coated with carbon/gold, and viewed through a Hitachi S-800 scanning electron microscope.

RESULTS

Morphology of the Labyrinth

Newts (Fig. 1): In gross specimens of the labyrinth, the vertical canal consisted of the anterior and posterior canals, both of which opened into the utricle (Figs. 1A and 1B). The former bent anterodorsally, and the latter posterodorsally, from the upper surface of the utricle.

Light microscopic observation of serial sections of the head located the cristae of the three canals at different heights within the head (Figs. 1C–E). The anterior crista was located most dorsally, the posterior crista was located most ventrally, and the horizontal crista was located in between. The ampulla of the anterior canal was located in the curved region of the anterior canal, and the corresponding crista

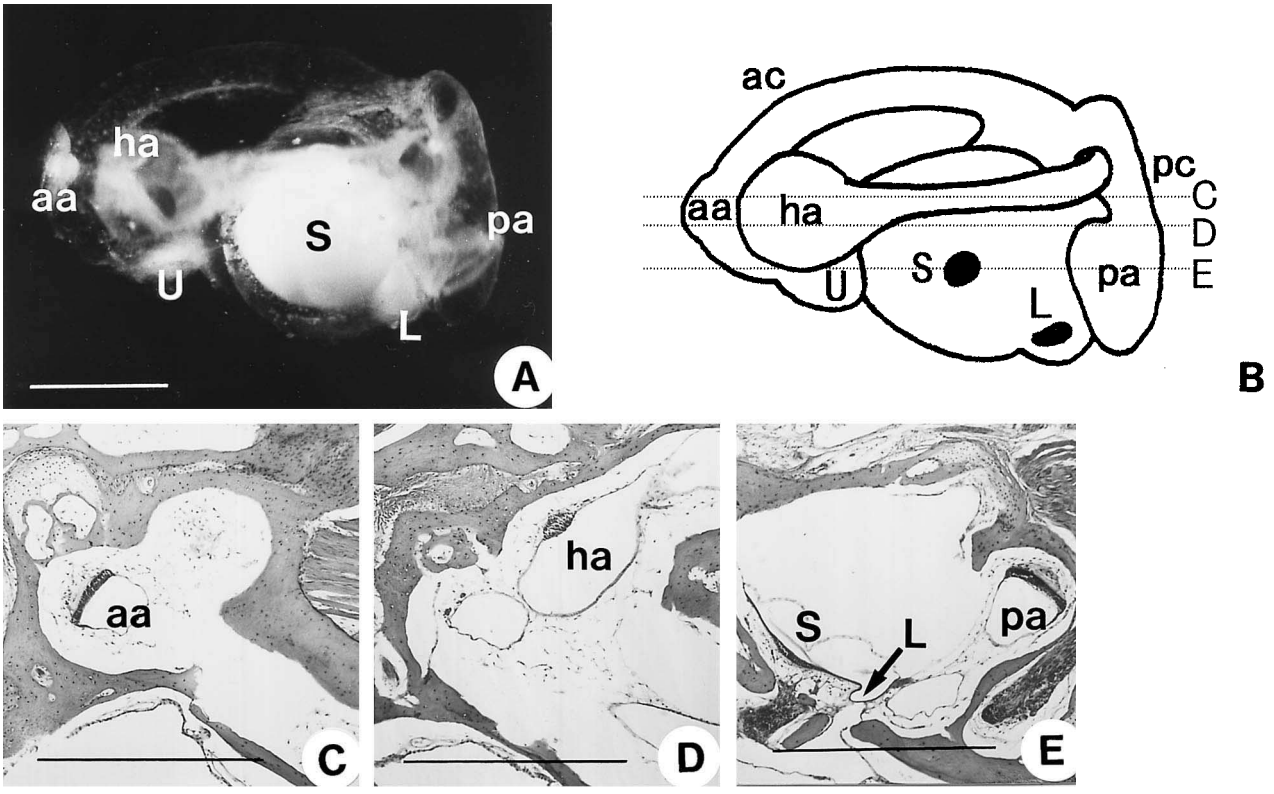

Fig. 1. Morphology of the newt membranous labyrinth. A. A gross view of the newt labyrinth. Bar, 10 mm. B. Schema of Fig. 1A. C and D. Light microscopic views of horizontalplanes through the three ampullae, the anterior ampulla (C), posterior ampulla (D), and horizontal ampulla (E). The saccular macula and lagena are also seen in E. aa: anterior ampulla, ac: anterior canal, ha: horizontal ampulla, pa: posterior ampulla, pc: posterior canal, U: utricle, S: saccule, L: lagena. Dotted lines marked "C", "D", and "E" in Fig. 1B indicate the planes corresponding to Figs. 1C, 1D, and 1E. Bar, 1 mm.

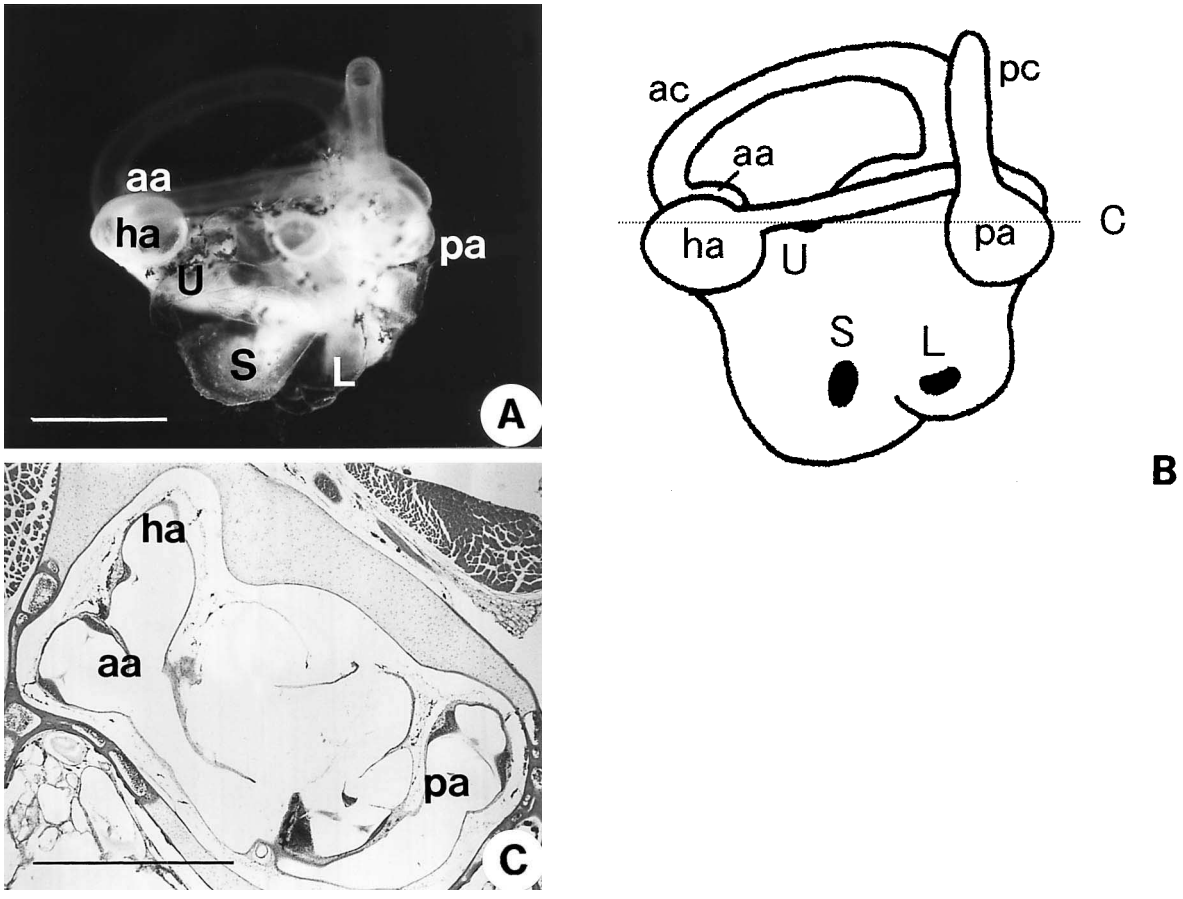

Fig. 2. Morphology of the frog membranous labyrinth. A. A gross view of the frog labyrinth. Bar, 0.6 mm. B. Schema of Fig. 2A. C. A microscopic view of horizontal planes through the three ampullae. The three ampullae are located on the same plane. aa: anterior ampulla, ac: anterior canal, ha: horizontal ampulla, pa: posterior ampulla, pc: posterior canal, U: utricle, S: saccule, L: lagena. The dotted line marked "C" in Fig. 2B indicates the plane corresponding to Fig. 2C. Bar, 1 mm.

protruded posterovertically (Fig. 1C). The horizontal canal extended laterally from the utricle, and its crista protruded posterointernally (Fig. 1D). The ampulla of the posterior canal was located adjacent to its basal region, and the corresponding crista protruded anteroventrally (Fig. 1E). The long axis of the crista of the anterior canal paralleled that of the posterior canal. However, the long axis of the crista of the horizontal canal was perpendicular to those of the other cristae.

The utricle was situated more ventrally than the other cristae (Figs. 1A and 1B). The utricular macula was in the horizontal plane and was covered by the otoconial membrane. The saccule was larger than the utricle and was recognized as a white mass, as it was covered by numerous otoconiae. The lagena was found in the posteroventral region of the utricle and contained the otolith (Fig. 1A).

Frogs (Fig. 2): The gross morphology of the labyrinth was the same as that of (Figs. 2A and 2B). In contrast to newts, the three cristae were located in the same plane (Fig. 2C). The long axes of the anterior and horizontal cristae were almost perpendicular to each other, as they were in newts. The anterior ampulla was located in the basal region of the canal, and its crista protruded in a dorsal direction (Fig. 2C). The posterior ampulla was located in the basal part of the canal, and its crista protruded anterodorsally. The utricle was situated more ventrally than the three canals, and its macula was seen in the horizontal plane (Fig. 2A). Otoconiae covered the otolithic membrane of the macula. The saccule was larger than the utricle. The lagena was present in the posteroventral side of the saccule (Figs. 2A and 2B).

Crista ampullaris

Newts (Fig. 3): The crista of the anterior vertical canal was saddle-shaped. Its central part was slightly swollen, but it did not develop like an eminentia cruciata (Fig. 3A). The cristae of the horizontal canal developed dorsally as a semilunar plane on the side facing the anterior canal ampulla, but not on the opposite side (Fig. 3B). The cristae of the posterior canal were saddle-shaped and had no eminentia (Fig. 3C).

Sensory cells were scarce in the central region of the anterior and posterior canals, but became dense towards the ends (Figs. 3A and 3C). In the horizontal canal, the number of sensory cells gradually increased from the central region to the semilunar plane (Fig. 3B). The sensory hairs

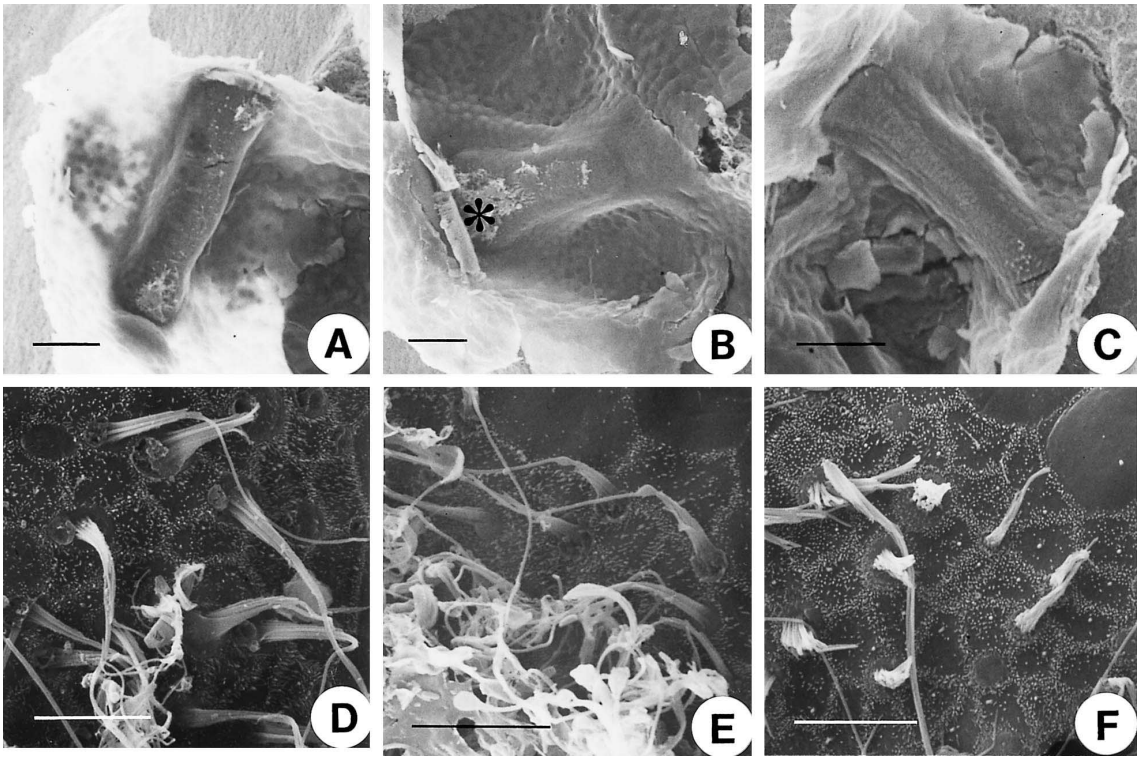

Fig. 3. Scanning electron microscopic views of newt cristae. A, B, and C represent anterior, horizontal, and posterior cristae, respectively. The horizontal crista contains a semilunar plane (indicated by the asterisk in B). Bar, 100 μm. D, E, and F show sensory cells of the anterior, horizontal, and posterior cristae, respectively. Bar, 10 μm.

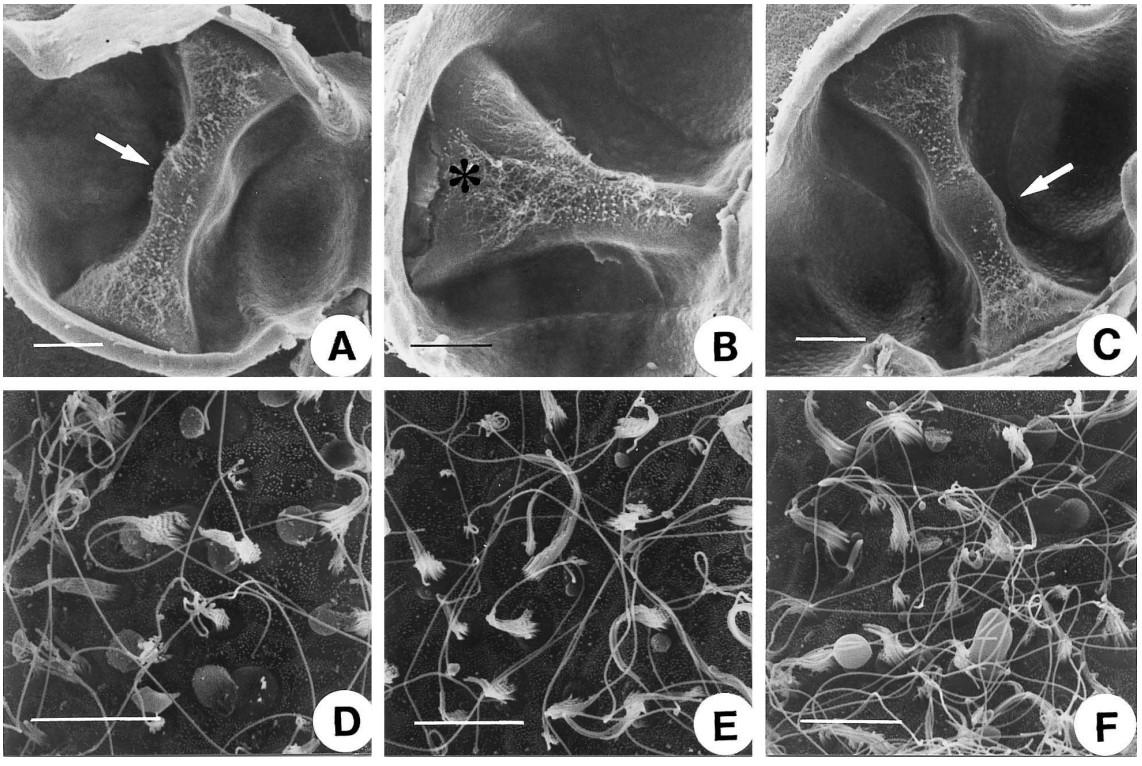

Fig. 4. Scanning electron microscopic views of frog cristae. A, B, and C show anterior, horizontal, and posterior cristae, respectively. Eminentia cruciata (indicated by arrows) are seen on the center of the anterior and posterior cristae. The horizontal crista contains a semilunar plane (indicated by the asterisk in B). Bar, 100 μm. D, E, and F represent sensory cells of the anterior, horizontal, and posterior cristae, respectively. Bar, 10 μm.

of the sensory cells in the three semicircular canals were ultrastructurally similar by electron microscopy. A single bundle of stereocilia was thin, with a diameter of 2 μm, and the longest cilia were 8–10 μm. The diameter of each stereocilium was 0.1–0.15 μm. The kinocilia were heterogeneous in length and were 16–40 μm long and 0.2 μm in diameter (Figs. 3D-3F). The kinocilia were polarized anteriorly and posteriorly in the anterior and posterior cristae, respectively (Figs. 3D and 3F). Those in the horizontal crista were polarized toward the utricle (Fig. 3E).

Frogs (Fig. 4): In frogs, apparent differences from newts were noted in the anterior and posterior cristae. Both had eminentia cruciata in their central regions, in contrast to newts (Figs. 4A and 4C). Sensory cells were scarce in the eminentia cruciata. The shape and distribution pattern of sensory hairs in the horizontal crista were similar to that of newts (Figs. 4A–4F).

Sensory hairs consisted of a kinocilium and stereocilia. The single tuft of stereocilia was thin, with a diameter of 3–4 μm, and the cilia were 3–6 μm long. The kinocilia were 10–35 μm long. The diameter of each stereocilium and kinocilium was 0.1–0.15 μm and 0.2 μm, respectively. The polarization of the kinocilia of frogs was the same as that of newts (Figs. 4D–4F).

Utricular maculae

Newts (Fig. 5): The utricular macula was located in the horizontal plane of the head and was shell-shaped (Fig. 5A). The striola was seen near its frontal margin, and the kinocilia faced each other with the striola in between them (Figs. 5B and 5C). Sensory hairs were ultrastructurally similar everywhere in the macula. A single bundle of stereocilia was 1–2 μm in diameter, and contained cilia that were at most 1.5–2 μm long and kinocilia that were about 6 μm long. The diameter of a single stereocilium was 0.1–0.15 μm, and that of a single kinocilium was 0.2 μm.

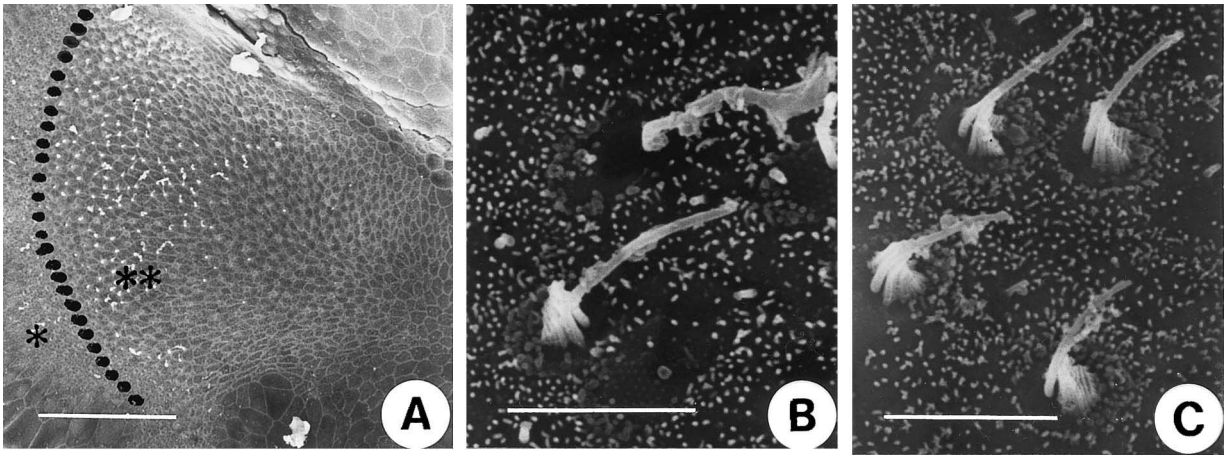

Fig. 5. Scanning electron microscopic views of newt utricular maculae. A. A view of the whole utricular macula. Bar, 100 μm. B and C represent sensory cells of the anterior and posterior regions of the utricular macula, respectively. Bar, 5 μm. The dotted line indicates the striola. B. A higher magnification view of the region indicated by the asterisk in Fig. 5A. C. A higher magnification view of the region indicated by double asterisks in Fig. 5A.

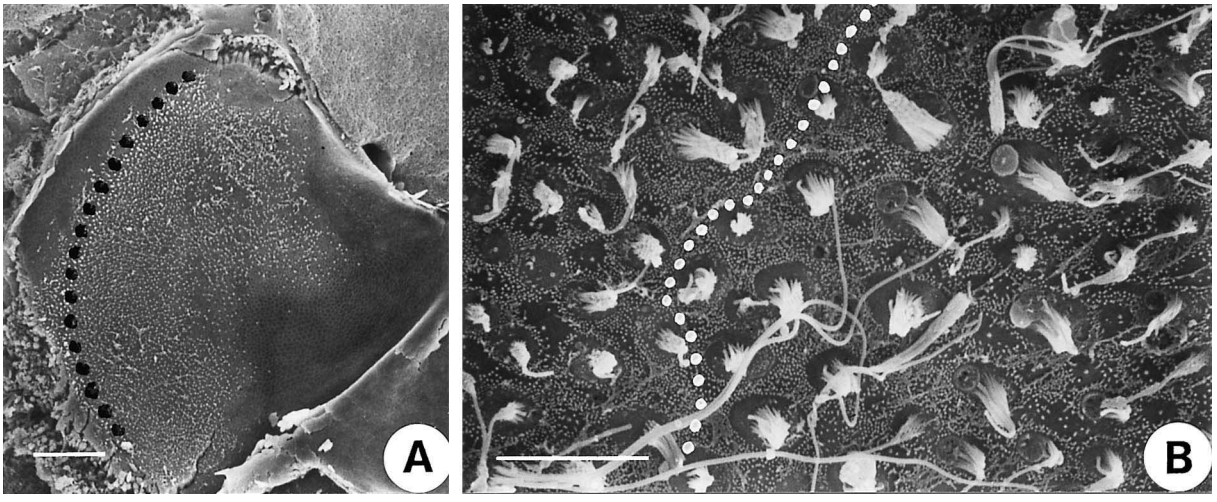

Fig. 6. Scanning electron microscopic views of frog utricular maculae. A. A view of the whole utricular macula. Bar, 100 μm. B. A higher magnification view of the striola region in Fig. 6A. Bar, 10 μm. The dotted lines are the striolae.

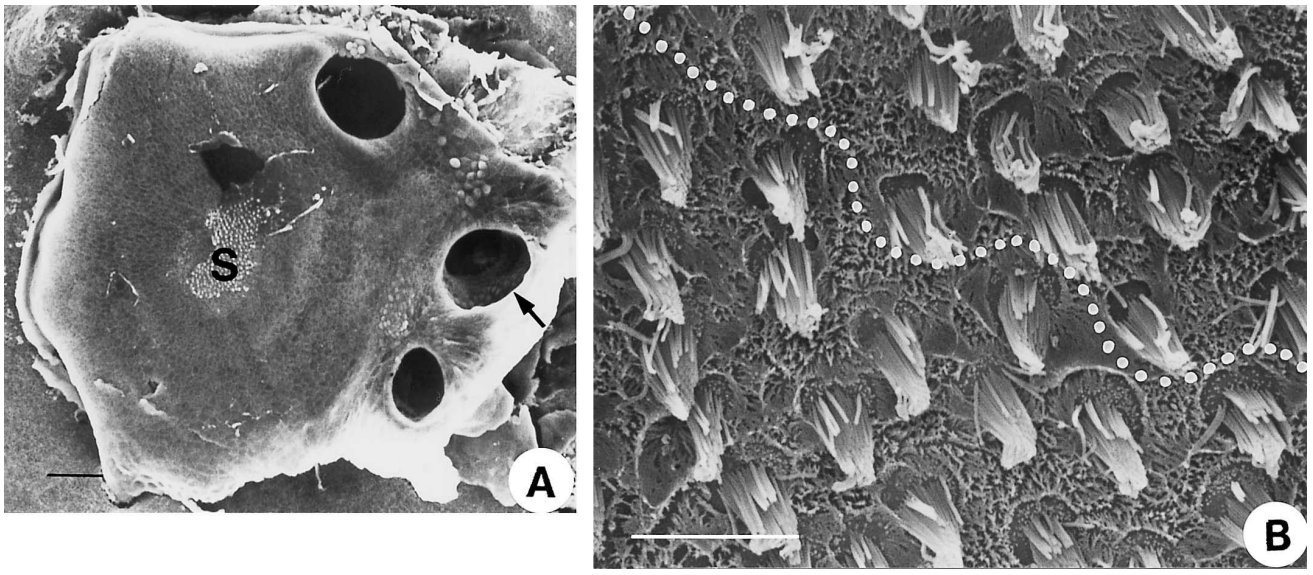

Fig. 7. Scanning electron microscopic views of the newt saccular region. A. A view of the saccule and the neighboring region. The saccular macula (S) is located in the center of the saccule. The arrow indicates the lagena. Bar, 100 μm. B. A higher magnification view of the striola region of the saccular macula. The dotted line indicates the striola. Bar, 10 μm.

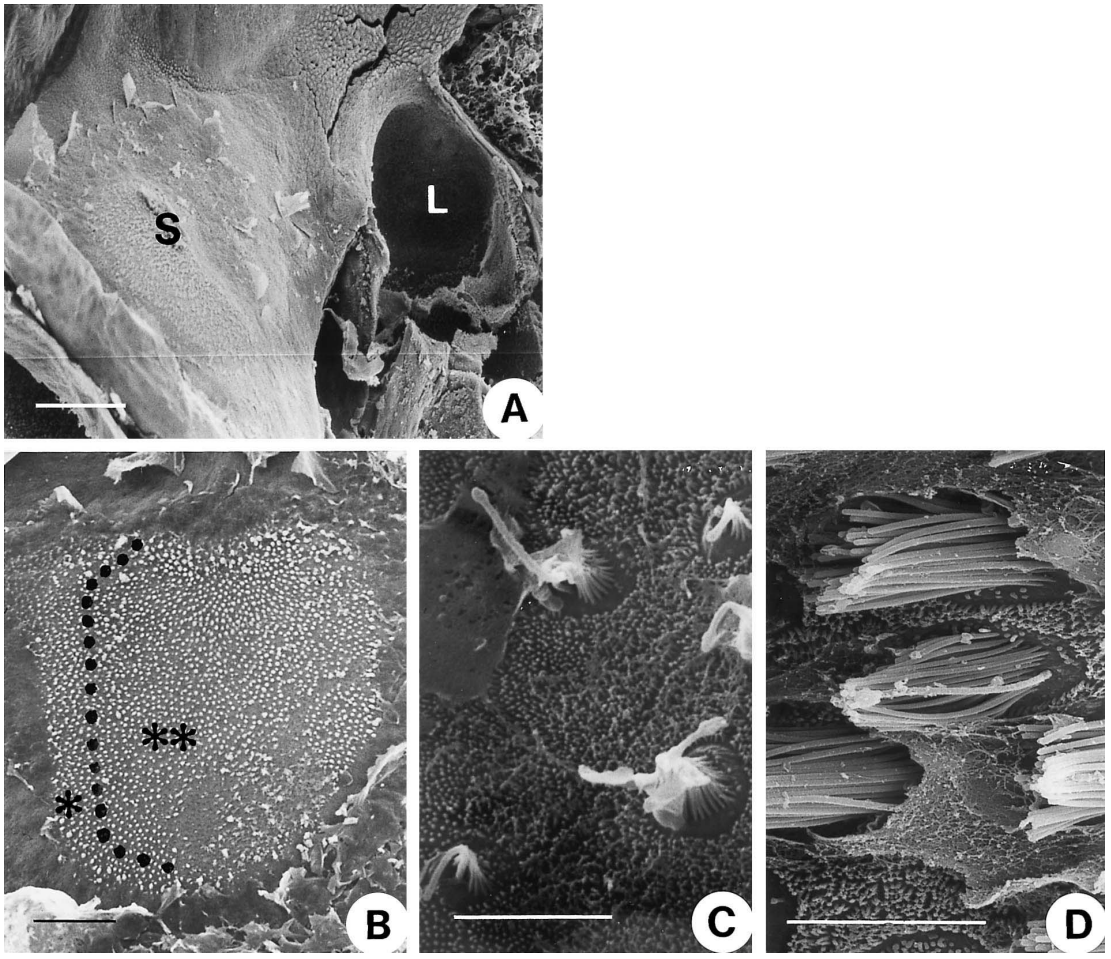

Fig. 8. Scanning electron microscopic views of the frog saccular region. A. A view of the saccule and neighboring region. The saccular macula (S) and lagena (L) are visible. Bar, 100 μm. B. A higher magnification view of the saccular macula. The dotted line indicates the striola. Bar, 100 μm. C. A higher magnification view of the region indicated by the asterisk in Fig. 8B. Bar, 5 μm. D. A higher magnification view of the region indicated by double asterisks in Fig. 8B. Bar, 5 μm.

Frogs (Fig. 6): The utricular macula of frogs was the same as that of newts in location and morphology (Fig. 6A). The ultrastructure of sensory hairs, however, differed from that of newts. A single bundle of stereocilia was about 2–3 μm in diameter and contained cilia that were 2.5–4 μm at the longest. Furthermore, the length of the kinocilia varied from 6–45 μm (Fig. 6B). The diameter of a single stereocilium was 0.1–0.15 μm, and that of a single kinocilium was 0.2 μm.

Saccular maculae

Newts (Fig. 7): The saccular macula was located in the vertical plane of the head (Fig. 7A). The saccular macula was reniform and convex in the front. The striola was located near the dorsal margin of the macula and divided the macula into dorsal and ventral parts. The kinocilia were oriented opposite each other, with the striola in between (Fig. 7B). The bundles of stereocilia were 4 μm in diameter and, at most, about 5 μm long. A single kinocilium was 6 μm long (Fig. 7B). The diameter of a single stereocilium was 0.1–0.15 μm and that of a single kinocilium was 0.2 μm.

Frogs (Fig. 8): The saccular macula was located in the vertical plane of the head, as in newts (Fig. 8A). The ultrastructure of the macula differed dramatically from that of newts. The saccular macula was reniform and convex on the ventral side (Fig. 8B). The striola protruded forward, drawing a hemispherical locus, and divided the macula into anterior and posterior parts. The kinocilia were oriented opposite each other, with the striola in between. Furthermore, the ultrastructure of the sensory hairs appeared to differ between the anterior and posterior regions of the macula. The bundles of stereocilia in the anterior region were 3 μm in diameter, and were, at most, about 1.8 μm long (Fig. 8C). A single kinocilium was 7.5 μm long. In the posterior region, the bundle was 2.5 μm in diameter, and the longest cilium was 5.3 μm long. The kinocilia were about 5.5 μm long (Fig. 8D). The diameter of a single stereocilium was 0.1–0.15 μm, and that of a single kinocilium was 0.2 μm.

Lagenal macula

Newts (Fig. 9): The lagena was located in the posterior part of the saccule, and its macula was situated lower than the saccular macula, facing somewhat horizontally to its own plane (Fig. 7A). The lagenal macula was rectangular, and extended slightly anteroposteriorly (Fig. 9). The striola was located centrally on the anteroposterior axis of the macula and divided the macula into inner and outer parts. The kinocilia were oriented as in the saccular macula. The bundles of stereocilia were 2.7 μm in diameter and were, at most, about 3 μm long. The kinocilia were short, that is, about 3.8 μm long. The diameter of a single stereocilium was 0.1–0.15 μm, and that of a single kinocilium was 0.2 μm.

Frogs (Fig. 10): The lagena was located in the posterior part of the saccule, and its macula was at a level similar to the saccular macula, facing somewhat horizontally to its

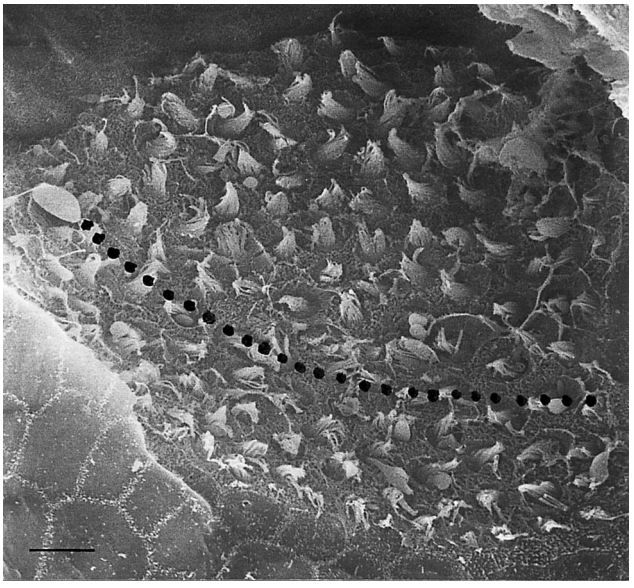

Fig. 9. Scanning electron microscopic view of the newt lagenal macula. The dotted line indicates the striola. Bar, 10 μm.

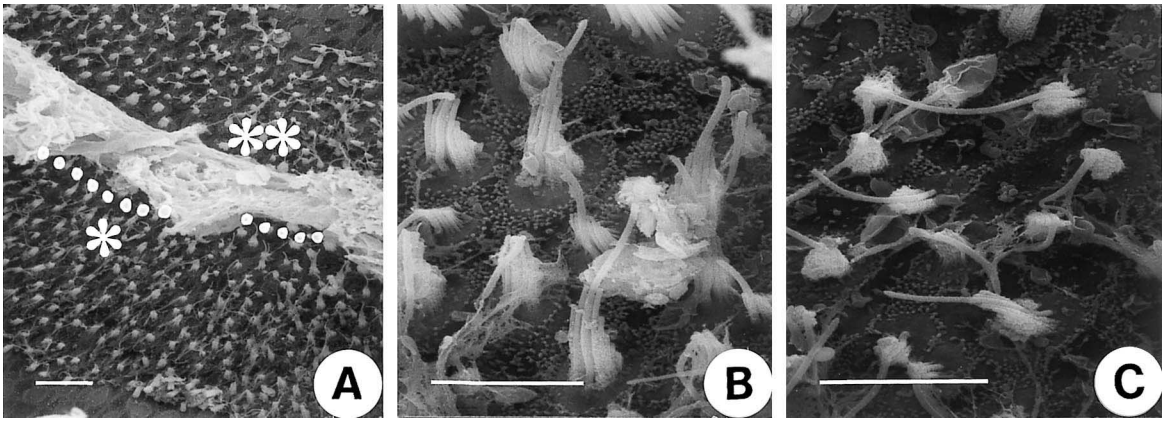

Fig. 10. Scanning electron microscopic views of the frog lagenal macula. A. A view of the whole lagenal macula. The white band over the macula is the residual otolithic membrane. The dotted line indicates the striola. Bar, 10 μm. B. A higher magnification view of the region indicated by the asterisk in Fig. 11A. Bar, 5 μm. C. A higher magnification view of the region indicated by double asterisks in Fig. 10A. Bar, 5 μm.

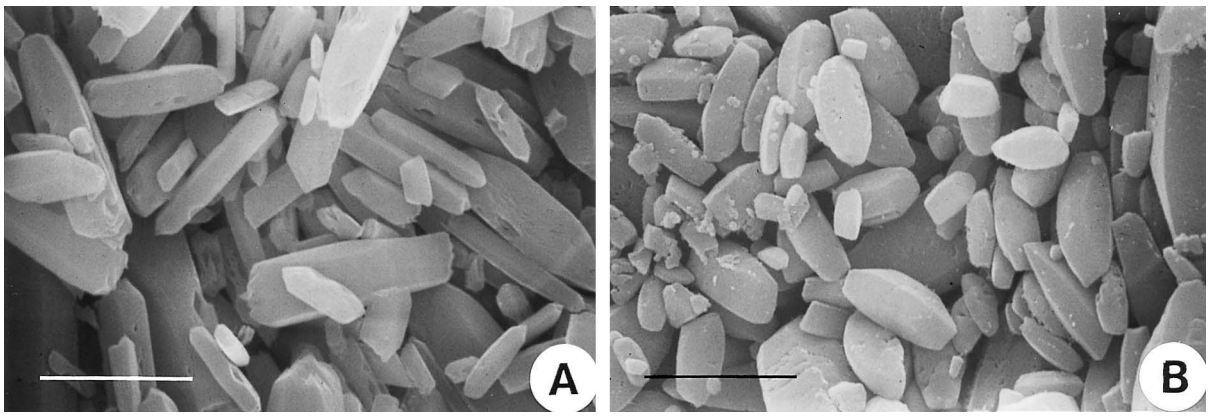

Fig. 11. Scanning electron microscopic views of the otoconia of newt (A) and frog (B). Bar, 10 μm.

own plane (Fig. 8A). The lagenal macula was reniform, like the saccular macula, and extended somewhat anteroposteriorly (Fig. 10A). The striola was located in the middle of the anteroposterior axis of the macula and divided the macula into inner and outer parts, in contrast to the saccule. The kinocilia were oriented opposite each other with the striola in between. The sensory hairs in the inner and outer parts of the macula differed ultrastructurally. The bundles of stereocilia in the inner region were 1.4 μm in diameter, and the longest stereocilia were about 2.4 μm. The kinocilia were about 4.6 μm long (Fig. 10B). In the outer region, the bundles were about 1.6 μm in diameter with stereocilia that were, at most, about 1.3 μm long. The kinocilia were 3.5–6.5 μm long (Fig. 10C). The diameter of a single stereocilium was 0.1–0.15 μm and that of a single kinocilium was 0.2 μm.

Otoconia

Otoconiae, crystals of calcium carbonate, were present in the utricle, saccule, and lagena in both newts and frogs. These crystals were all cylindrical with pyramidal ends (Figs. 11A and 11B). The difference in the otoconiae of two kinds of animals was that the central part of the otoconia of frogs tended to be more swollen than in newts.

DISCUSSION

This study compared the ultrastructures of the inner ears of Japanese red-bellied newts and black-spotted pond frogs relative to their different locomotory capabilities. The differences in the vestibular organs of two kinds of animals are schematically shown in Fig. 12.

The semicircular canal of vertebrates consists of anterior, horizontal, and posterior parts. Each of these parts has an ampulla, containing crista with sensory cells. The anterior and posterior ampullae detect vertical rotatory acceleration, while the horizontal ampulla detects horizontal rotatory acceleration. In this study, we found morphological differences between newts and frogs in the shape of the anterior and posterior ampullae. Frogs had an eminentia cruciata in

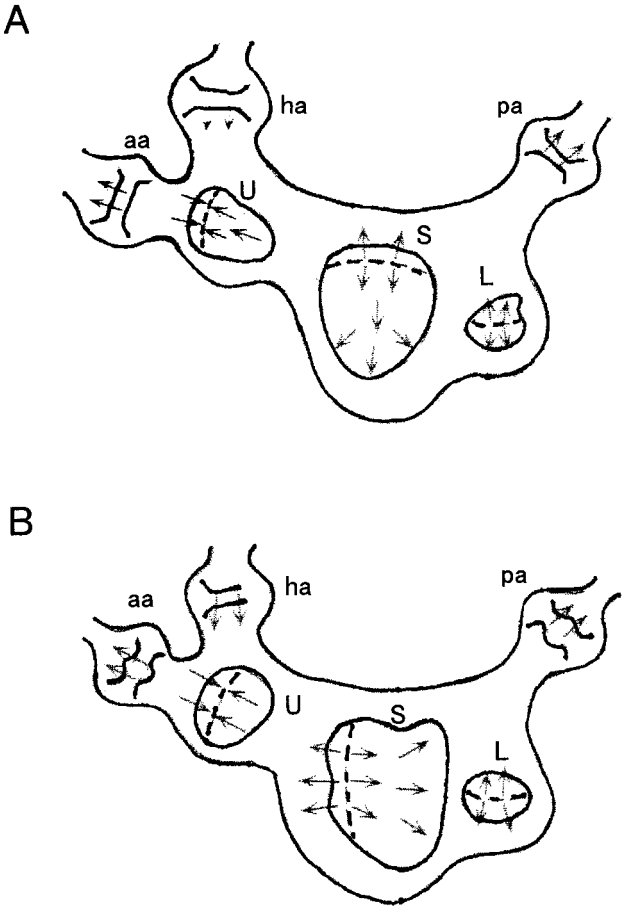

Fig. 12. Schematic representations of the polarity of the vestibular sensory organs of newt (A) and frog (B). Arrows and dotted lines indicate the direction of kinocilia and striolae, respectively. aa: anterior canal ampulla, ha: horizontal canal ampulla, pa:posterior canal ampulla, U: utricular macula, S: saccular macula, L: lagenal macula.

the central part of the cristae of both ampullae, but newts had no such structure. The eminentia cruciata is well developed in birds (Igarashi and Yoshinobu, 1966; Harada, 1972b, 1988). Harada (1972b) suggested that eminentia cruciata of birds might related to their complicated flying

motions. This suggests that the difference in the presence of eminentia cruciata between the two kinds of animals might be related to differences in their locomotory capabilities. Frogs jump and briefly stay in the air when they escape from enemies and catch insects for food. Existence of the eminentia cruciata in frogs implies that the motions of jumping and flying requires an exact sense of vertical rotatory acceleration.

In the ultrastructural analysis of the vestibular organs, there were no differences between the newts and the frogs other than the location of the striola in the saccular macula. In the saccular macula, the striola of newts divided the macula into dorsal and ventral parts, but that of frogs divided the macula into anterior and posterior parts. The saccular and utricular maculae were perpendicular to each other in both animals. The former is involved in the sense of vertical balance, and the latter in the sense of horizontal balance (Werner, 1960). The significance of the difference in the location of the striola is unclear. In the saccular macula of fishes, the striola exists on the posterior half of the macula and divides it into dorsal and ventral parts (Popper, 1977). By contrast, in mammals, the striola of the saccular macula divides it into anterior and posterior parts (Harada, 1988). From these mentions, the location of the striola of frogs is the same as in mammals. On the other hand, that of newts is the same as in fishes. This suggests that frogs have more evolved than newts in respect of the sense of horizontal balance.

Depolarization of sensory cells is induced by sliding of the cupula in the semicircular canal and by tilting of the otolithic membrane in the vestibular organ. In sensory hairs, Barber and Emerson (1980) suggested that the length of a kinocilium was related to the function of sensory cells. Sensory cells with longer kinocilium than the long stereocilia play a role in controlling the postures because the kinocilium inserts into otolitic membrane. On the other hand, sensory cells with kinocilium equally long with the longest stereocilia play a role in hearing. According to the classification of Barber and Emerson (1980), the semicircular canals and utricles play a role in controlling the postures of both newts and frogs. The saccules of newts play a role in hearing (i.e.,receiving vibration from the ground), while those of frogs are involved in both posture and hearing. Furthermore, the lagenal maculae of newts are involved in hearing and those of frogs are involved in posture (Tables 1 and 2). The observed morphological differences in the saccules and lagena of newts and frogs might be related to the presence of a tympanum. Since newts have no tympanum, their saccules and lagenae fulfill a hearing function.

Platt (1977) reported that the diameter of the bundles of stereocilia is related to the capacity to receive stimuli, and that sensory cells with thick bundles of stereocilia respond more precisely to environmental stimuli than do sensory cells with thin bundles. In this study, the diameter of the bundles of stereocilia of frogs was thicker than that of newts in the semicircular canal. On the other hand, in saccule and lagena, the diameter of frogs was thinner than that of newts (Table 1). From these results, it was suggested that the semicircular canal might be more sensitive in frogs than in newts, while the saccule and lagena might be more sensitive in newts than in frogs. This is interpreted to mean that differences in the semicircular canals might relate to locomotive capability, and those in vestibular organs might be due to the existence of a tympanum. It is thought that the inner ear of amphibians is the organ responsible for maintaining balance rather than an organ for hearing, because it has no cochlear duct. At the same time, it is suggested that the saccules and lagenae of both newts and frogs function in hearing rather than in maintaining balance.

Table 1. The diameter of the sensory hair bundle and the length (in μm) of the kinocilium of newt and frog sensory cells.

	SCDB		SCLL		KCL	
	Newt	Frog	Newt	Frog	Newt	Frog
CA	2	3–4	8–10	3–6	16–40	10–35
CH	2	3–4	8–10	3–6	16–40	10–35
CP	2	3–4	8–10	3–6	16–40	10–35
UA	1	2–3	1.5	2.5–4	6	6–45
UP	2	2–3	2	2.5–4	6	6–45
SD	4	–	5	–	6	–
SV	4	–	5	–	6	–
SA	–	3	–	1.8	–	7.5
SP	–	2.5	–	5.3	–	5.5
LGI	2.7	1.4	3	2.4	3.8	4.6
LGO	2.7	1.6	3	1.3	3.8	3.5–6.5

SCDB: Stereocilia diameter of bundle, SCLL:Stereocilia Length of the longest, KCL:Kinocilium length, CA: Crista anterior, CH: Crista horizontal, CP: Crista posterior region, UA: Utlicle anterior region, UP: Utlicle posterior region, SD: Saccule dorsal region, SP: Saccule ventral region, SA: Saccule anterior region, SP: Saccule posterior region, LGI: Lagena interior region, LGO: Lagena outer region

Table 2. Length Kinocilium (LK) in relation to that of the longest stereocilium (LLS) and the predicted functions of the inner ears of newts and frogs.

	SCC	U	SA	SP	LG
Newt	LK>LLS	LK>LLS	LK=LLS	LK=LLS	LK=LLS
	Posture	Posture	Hearing	Hearing	Hearing
Frog	LK>LLS	LK>LLS	LK>LLS	LK=LLS	LK>LLS
	Posture	Posture	Posture	Hearing	Posture

Scc: Semicircular canal, U: Utricle, SA: Saccule anterior region, SP: Saccule posterior region, LG: Lagena

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