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REVIEW

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Specializations in the lumbosacral vertebral canal and spinal cord of birds: evidence of a function as a sense organ which is involved in the control of walking

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Abstract Birds are bipedal animals with a center of gravity rostral to the insertion of the hindlimbs. This imposes special demands on keeping balance when moving on the ground. Recently, specializations in the lumbosacral region have been suggested to function as a sense organ of equilibrium which is involved in the control of walking. Morphological, electrophysiological, behavioral and embryological evidence for such a function is reviewed. Birds have two nearly independent kinds of locomotion and it is suggested that two different sense organs play an important role in their respective control: the vestibular organ during flight and the lumbosacral system during walking.

Keywords Accessory lobes · Vertebral canal · Hindlimb motor system · Embryonic development · Lesions

Introduction

Posture and locomotion in vertebrates are controlled by a variety of motor centers in the brain and spinal cord. To cope with environmental and internal demands these motor centers are supplied with information from all sensory systems (Orlovsky et al. 1999). This article deals with sensory input at the spinal level in birds. It will be shown that there is evidence that intraspinal sensory neurons are involved in the control of posture and locomotion on the ground. In the lamprey intraspinal sensory neurons (edge cells) have been shown to be part of the segmental neuronal network that coordinates propulsive locomotion (Grillner et al. 1984, 1995). It seems that there is another example of intraspinal sensory neurons which are involved in segmental control of locomotion of birds.

Birds use two different kinds of locomotion: flying in the air with their forelimbs modified into wings and walking on the ground with their hindlimbs. Because of a nearly horizontal orientation of the body and an insertion of the hindlimbs caudal to the center of gravity of the body, birds' bipedal walking on the ground needs special control of balance. The bipedal theropod dinosaurs had a long tail for balance which lacks in birds. In the upright walking bipedal humans the center of gravity is in line with the legs. It has been suggested long ago that there should be an extralabyrinthine sense of equilibrium in the abdomen of birds and there was also some experimental evidence of this (Singer 1884; Trendelenburg 1906; Mittelstaedt 1964; Biedermann-Thorson and Thorson 1973; Delius and Vollrath 1973). In a more recent investigation it was suggested that the peculiar glycogen body in the lumbosacral spinal cord might represent such a sense organ (Reese 1995; Grimm et al. 1997). The discovery of canals in the lumbosacral region which look similar to the semicircular canals in the inner ear led to the suggestion that some of the specializations in the lumbosacral region characteristic of birds may function as a sense organ of equilibrium which is involved in the control of hindlimbs (Necker 1999). The present review aims at summarizing experimental findings which speak in favor of such a sense organ.

The avian lumbosacral vertebral column and spinal cord show a number of specializations which are unique to birds. Lumbar and sacral vertebrae are melted with each other and with the bones of the pelvic girdle to form a synsacrum (Baumel and Witmer 1993). In the middle of this region the spinal cord is split dorsally to form a rhomboid sinus which houses a large glycogen body (Fig. 1a; De Gennaro 1982). At the level of the glycogen body there is a considerable widening of the vertebral canal. The glycogen body consists of large glycogen containing cells which have been shown to

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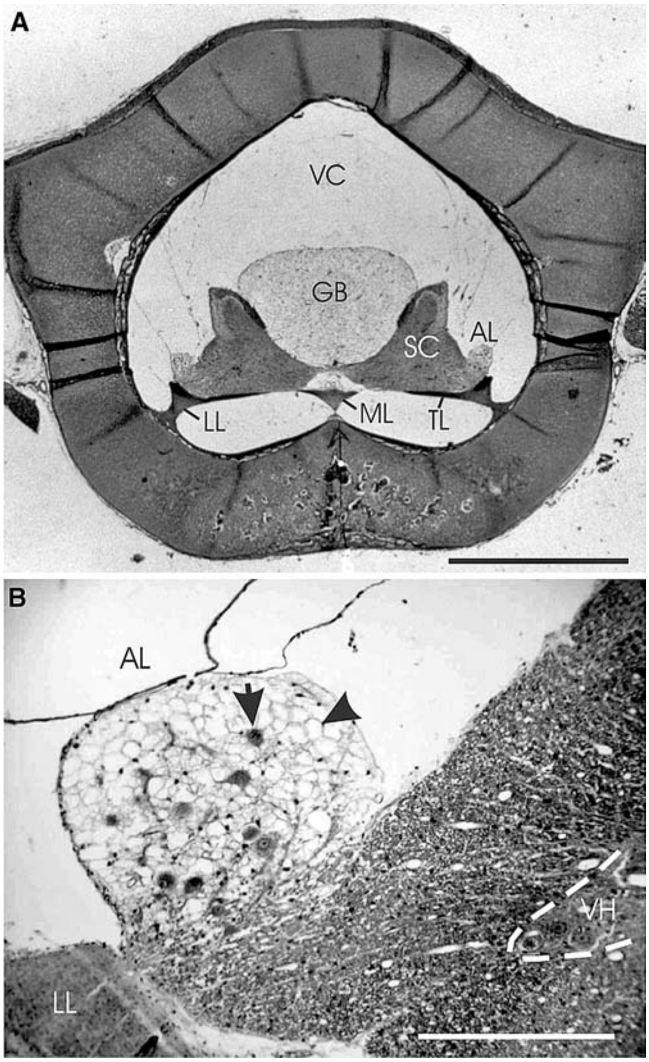


Fig. 1 **a** Transverse section of the lumbosacral vertebral column of a one-week-old pigeon at the level of the glycogen body. **b** Accessory lobe with neurons (*arrow*) and glycogen cells (*arrowhead*). *AL* accessory lobe, *GB* glycogen body, *ML* medial ligament, *LL* lateral (dentate) ligament, *TL* transverse ligament, *VC* vertebral canal, *VH* ventral horn. *Scale bars* 2 mm in **a**, 200 μm in **b**

derive from astrocytes (Möller 1989). This gives the glycogen body a gelatinous appearance. The avian spinal cord has segmentally organized groups of neurons located in the ventrolateral white matter near the dentate ligament (Kölliker 1902; Huber 1936). These neurons form marginal nuclei (Huber 1936) or minor nuclei of Hofmann (Kölliker 1902), which become enlarged and protrude into the vertebral canal at lumbosacral segments. These protrusions have been named accessory lobes (Lachi 1889) or major nuclei of Hofmann (Kölliker 1902). Since the term accessory lobes describes the morphological appearance, it will be used here. The lobes consist of both neurons and glycogen cells (Fig. 1b). Neurons are of mean size (about 30 μm) and glycogen cells are similar to those in the glycogen body. These accessory lobes are located at the level of the processes of the dentate ligament which contact the wall of the vertebral canal and hence at the border of successive spinal segments. In the pigeon there are ten pairs of accessory lobes (Huber 1936; Fig. 2a) which distribute from the last thoracic/first lumbar segment (T6/L1) to the fifth/sixth sacral segment (S5/S6). The mass of the glycogen body is located in the middle of the segments with accessory lobes and extends only for about three segments, i.e., the extent of the glycogen body does not match the extent of the lobes. The dentate ligament shows considerable modifications in the lumbosacral region (Schroeder and Murray 1987). In addition to the typical lateral process there is a massive pillar-like ventral process contacting the wall of the vertebral canal (Fig. 1). Furthermore there are segmental transverse processes and a medial ligament which make up a ventral net-like structure of ligaments (Fig. 2b).

The recent suggestion that the lumbosacral specializations may be involved in sensorimotor functions which contribute to balanced walking on the ground (Necker 1999) provoked a new look at all these specializations and a number of studies have been carried out to see whether the supposed function may be valid. In addition to data published earlier (Necker 1997, 1999,

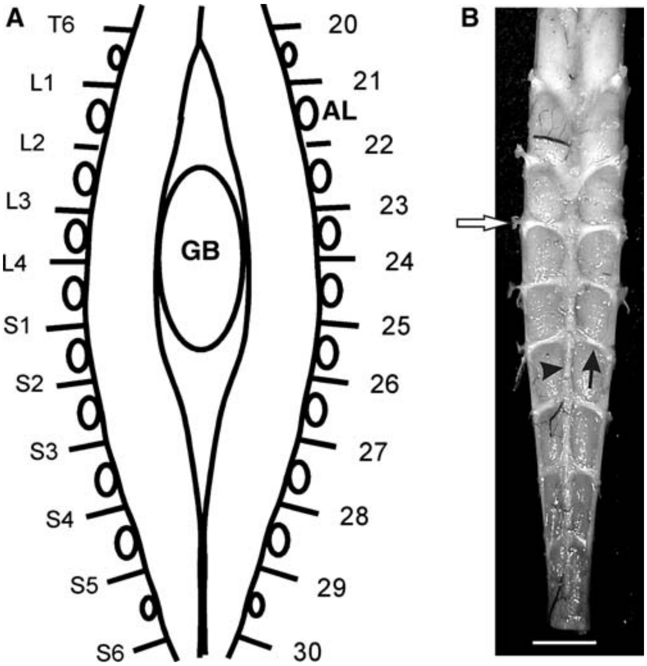


Fig. 2 **a** Sketch of the organization of the lumbosacral spinal cord as seen from dorsal. Rostrocaudal numbering of the spinal segments on the *right*, *T* thoracic, *L* lumbar and *S* sacral segments on the *left*. *Lines* indicate spinal nerves and ovals indicate accessory lobes (*AL*) which are located in between the nerves; *GB* glycogen body. **b** Photomicrograph of the ventral aspect of the spinal cord of a penguin (*Spheniscus humboldti*) showing the organization of the ligaments. *Arrowhead* medial ligament, *solid arrow* transverse ligament, *open arrow* process of lateral ligament. *Scale bar* in **b**, 5 mm

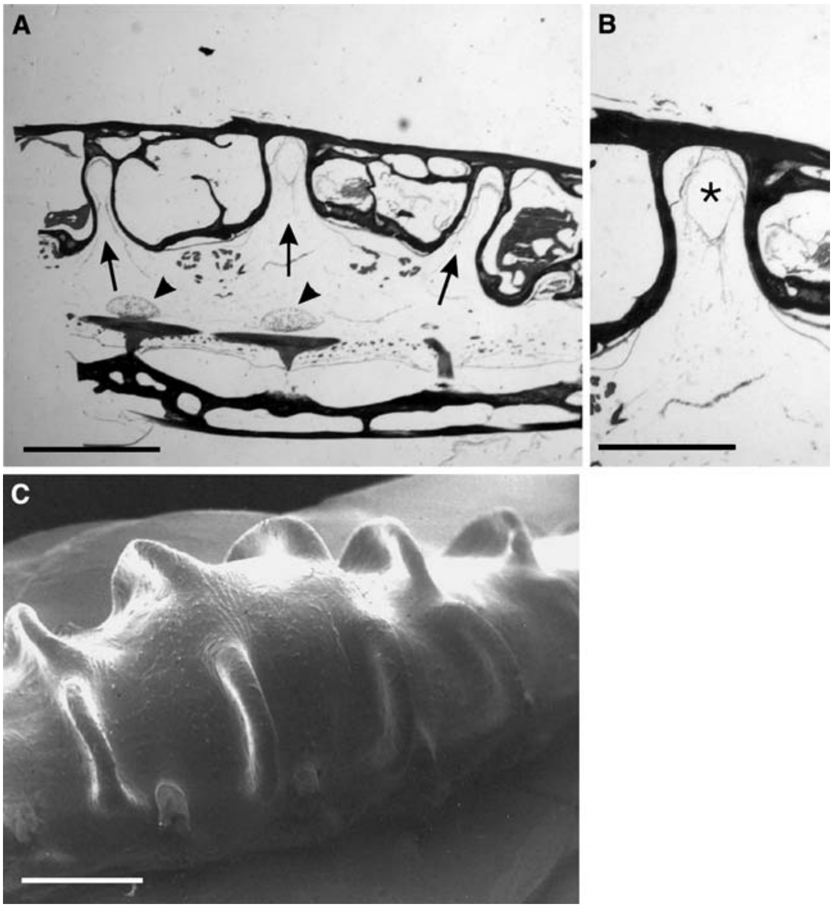


Fig. 3 Organization of the lumbosacral canals. **a** Parasagittal section at the level of the glycogen body showing three dorsal evaginations (*arrows*) which are transversely running canals. These canals open above accessory lobes (*arrowheads*). **b** *Enlarged view* of one canal; *asterisk* indicates the canal made up by the meninges. **c** Scanning electron micrograph of a cast of the vertebral canal showing the three-dimensional organization of the lumbosacral canals at the level of the glycogen body. *Scale bars*, 2 mm in **a**, 1 mm in **b**, **c**

2002, 2004, 2005a, b; Necker et al. 2000; Milinski and Necker 2001; Rosenberg and Necker 2002) some unpublished material will now be presented.

Specializations in the vertebral canal

Due to the development of the glycogen body the vertebral canal is considerably enlarged in the middle of the lumbosacral region. However, there is not much change in the size of the nervous part of the spinal cord (the glycogen body is non-nervous tissue) despite the entrance of the sciatic plexus innervating the legs (Imhof 1905; Watterson 1949; Necker 2005b). The vertebrae are melted in the lumbosacral region but the borders between successive vertebrae are still visible as bilateral grooves in the dorsal wall of the vertebral canal (Imhof 1905; Jelgersma 1951). Recent investigations showed that these grooves form lumbosacral canals which look similar to the semicircular canals in the inner ear (Necker 1999, 2005b). These grooves are best seen in casts of the vertebral canals (Fig. 3c) and their organization becomes evident from parasagittal sections (Fig. 3a, b). An opening towards the lumen of the vertebral canal is covered by arachnoidal membranes which build a true canal (Fig. 3b) in the mediolateral aspect leaving openings in the midline and laterally (Necker et al. 2000; Necker 2005b). Laterally, the canals open above the accessory lobes (Fig. 3a) and all lumbosacral segments with accessory lobes have such canals. This suggests a functional interrelationship between the canals and the accessory lobes discussed later in this review.

Meninges and ligaments

Normally the meninges are tightly wrapped around the spinal cord leaving only a small subarachnoidal space. In the lumbosacral region there is a large subarachnoidal space near the accessory lobes which extends into the dorsal canals (Fig. 4a, b). This means that the accessory lobes reach into a large space of cerebrospinal fluid. The peculiar organization of the ligaments in the lumbosacral region (Fig. 1a) seems to provide strong support of the spinal cord. From a functional point of view it is important that the processes of the ligaments which contact the wall of the vertebral canal support the lobes only at a small fraction of their rostrocaudal extent, i.e., the lobes are exposed to cerebrospinal fluid at all its surface (Fig. 4b). There is a trabecle of the arachnoidea, which seems to support the lobes in their ventrolateral

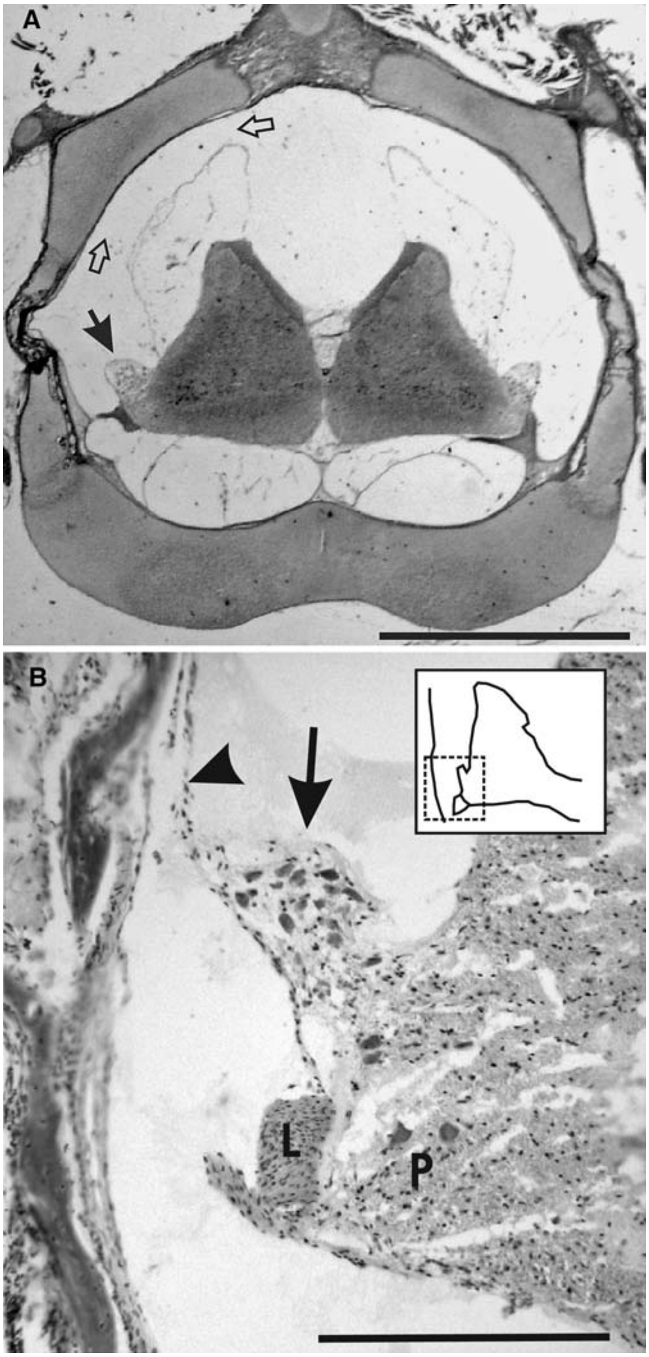


Fig. 4 **a** Transverse section of the vertebral column of a one-day-old chicken showing wide fluid spaces surrounding the accessory lobes (*solid arrow*); *open arrows* indicate the dorsolateral lumbosacral canals limited medially by meningeal membranes. **b** Transverse section of the vertebral canal of the common swift (*Apus apus*) showing an accessory lobe (*arrow*) with a laterally running arachnoidal trabecle (*arrowheads*) and the surrounding cerebrospinal fluid spaces. *Dashed box in inset* indicates section of the photomicrograph. *L* dentate ligament, *P* paragriseal cells. *Scale bars*, 1 mm in **a**, 500 μm in **b**

aspect (Rosenberg and Necker 2002; Fig. 4b), but because of the thinness of this membrane this support is probably not significant, i.e., movements of the subarachnoidal fluid may not be hindered by this trabecle. Altogether, there is a strong stabilization of the spinal cord within the vertebral canal but much less stabilization of the accessory lobes.

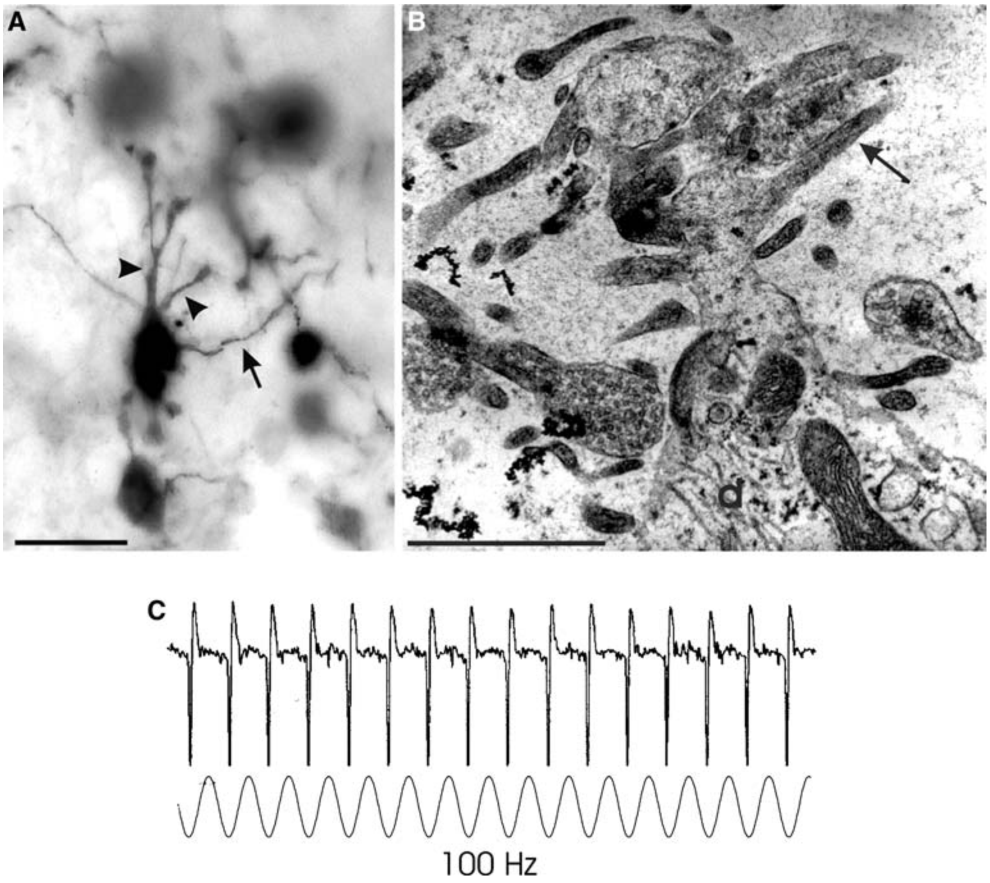
Paragriseal cells and accessory lobes

Neuronal somata are usually located within the gray substance of the spinal cord. There are, however, paragriseal neurons in the white matter of most vertebrates including humans (Kölliker 1902). In birds the number of paragriseal cells scattered in the white matter is exceptionally high in lumbosacral segments (Huber 1936; Fig. 4b) and a recent investigation showed that they are obviously displaced ventral spinocerebellar tract cells which are normally located in the intermediate gray or ventral horn (Necker 2005a). In addition to these scattered paragriseal cells there are segmentally organized groups of neurons near the dentate ligament, which form protrusions (accessory lobes) in the lumbosacral enlargement. Marginal nuclei outside the lumbosacral region and accessory lobes differ in that the latter ones contain numerous glycogen cells and few astrocytes whereas marginal nuclei contain no glycogen cells and many astrocytes (Necker 2004). The organization of the accessory lobes has been studied at the ultrastructural level (De Gennaro and Benzo 1978; Schroeder and Murray 1987), but only recently was it discovered that the neurons within the lobes show dendritic ramifications (Fig. 5a) with finger-like processes which reach into fluid-filled lacunae (Fig. 5b). These finger-like processes are similar to processes typical of cutaneous mechanoreceptors (Rosenberg and Necker 2002). Electrophysiological recordings of lobe neurons showed that they are indeed mechanosensitive (Necker 2002; Fig. 5c).

The possible function of lumbosacral canals and accessory lobes

Figure 6 shows a scheme to explain how the assumed sensory organ may work as compared to the semicircular canals. In the semicircular canals there is a sensory epithelium with a gelatinous cupula which reaches into an endolymphatic space. Movements of the head result in a bending of the cupula because of inertia of the fluid within the canals. This bending activates mechanosensitive channels of the hair cells of the sensory epithelium. In the lumbosacral region the accessory lobes may correspond to the cupula and the hair cells. Both, accessory lobe neurons and hair cells have processes which are exposed to mechanical stimuli. In the lumbosacral system the mechanical stimulus is assumed to result from inertia-generated fluid flow during roll movements of the body. Transverse fluid movements are only possible through the lumbosacral canals (Necker 2005b) and flow is directed to the accessory lobes where it may result in a mechanical stimulation of the lobes and hence of the

Fig. 5 **a** Photomicrograph of a fluorescent dye labelled accessory lobe neuron showing the axon (*arrow*) and dendrites (*arrowheads*). **b** Transmission electron micrograph showing a dendrite (*d*) of an accessory lobe neuron with finger-like processes (*arrow*) reaching into extracellular spaces (lacunae). **c** Action potentials (*upper trace*) recorded from an accessory lobe neuron driven by a 100 Hz vibratory stimulus (*lower trace*). *Scale bars*, 50 μm in **a**, 2 μm in **b**



finger-like processes (Rosenberg and Necker 2002). The large spaces near the accessory lobes are connected rostrocaudally. During pitch movements there may be a rostrocaudal inertia-based fluid flow which should again stimulate the accessory lobes. Roll movements generate asymmetric stimulation of the lobes on both sides and there is a need of asymmetric correction movements of the left and the right hindlimbs. Pitch movements induce symmetric stimulation and accordingly there is a need for symmetric correction movements of both hindlimbs. This may be the basis for a direction-selective function in the absence of direction-selective sensory patches or sensory cells typical for the inner ear. This is, however, speculative at the moment. Electrophysiological recordings from the intact system should help to clarify this issue.

Projections of the accessory lobe neurons

Accessory lobe neurons are commissural interneurons which project segmentally to the contralateral ventromedial spinal gray (Eide 1996; Necker 1997; Fig. 7) and to the lateral white matter where they contact spinocerebellar paragriseal cells (Necker 1997). The target neurons in the ventromedial gray substance (lamina VIII) are again commissural neurons which project to the contralateral ventral horn including lamina VIII as shown in tracer experiments (Fig. 8). Figure 9 summarizes the projection patterns at the segmental level.

One important issue is the classification of the neurons within the accessory lobes and their target neurons in the ventromedial gray substance with regard to the sensorimotor network of the lumbosacral spinal cord. In mammals, commissural lamina VIII neurons are thought to be an essential part of crossed reflexes to coordinate movements of left and right limbs (e.g., Jankowska 1992). There are only preliminary data with birds, therefore the situation in mammals may help to identify the possible network in avian species. Mammalian commissural lamina VIII neurons receive a peripheral input from group Ia, Ib as well as group II proprioreceptive afferents and flexor reflex afferents (FRA). In addition, there is an input from vestibulospinal and reticulospinal pathways which run in the ventral funiculus both in mammals (Hammar et al. 2004) and in birds (Cabot et al. 1982). Mammalian commissural lamina VIII neurons have been shown to contact motoneurons (Harrison et al. 1986; Birinyi et al. 2003) and the same seems to be true for birds (Fig. 8). Nothing is known about functional aspects of lamina VIII neurons in birds but it seems that the innervation and projection pattern is similar to the one found in mammals. Therefore it seems reasonable to assume that avian lamina VIII neurons are also involved in the left–right coordination of limb movements. The activity of acces-

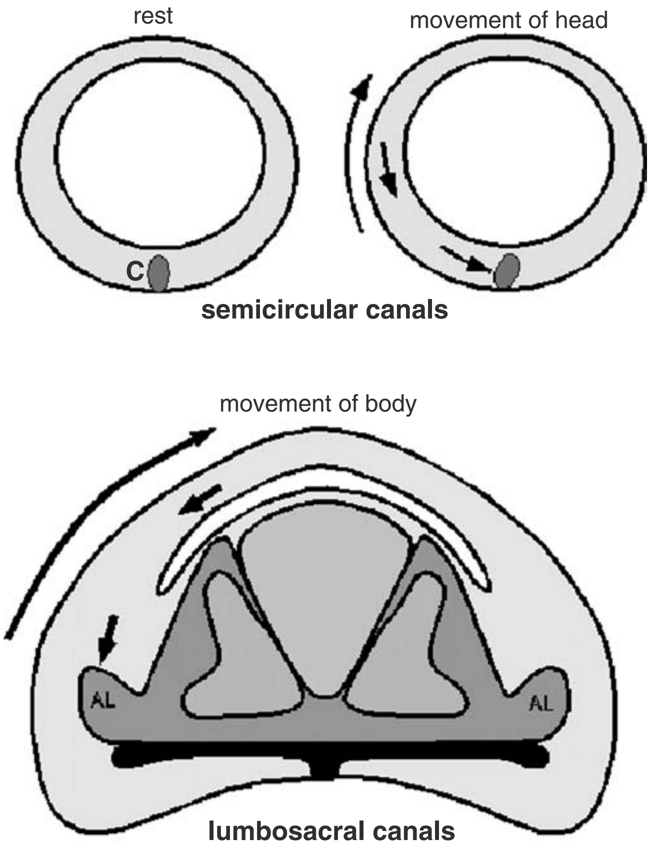


Fig. 6 Scheme of the possible function of the lumbosacral canals (*bottom*) as compared to the function of the semicircular canals (*top*). Movements of the head result in an inertia-driven bending of the cupula (*C*) which excites the sensory hair cells whose stereocilia reach into the cupula. Similarly, during rotations of the body inertia of the fluid in the lumbosacral canals and near the accessory lobes (*AL*) is thought to mechanically distort the lobes, which then results in a mechanical stimulation and excitation of the finger-like processes of the lobe neurons

sory lobe neurons should effect motoneurons at least via lamina VIII neurons. A direct innervation of motoneurons by accessory lobe neurons cannot be excluded but has not yet been demonstrated unambiguously, i.e., at the ultrastructural level.

Accessory lobe neurons as well as neurons of the marginal nuclei are commissural neurons (Eide 1996; Necker 1997). Their projection to contralateral lamina VIII suggests that they are displaced lamina VIII cells. A reciprocal innervation of lamina VIII neurons has been documented well recently (Birinyi et al. 2003). As with mammalian lamina VIII neurons, cervical marginal nuclei of the pigeon receive an input from proprioreceptors but such an input seems to be absent with accessory lobes (Terni 1926; Necker 2001). Furthermore, there seems to be no input from descending brainstem-spinal systems (unpublished own tracer experiments) whose pathways in the ventral funiculus are at a location which is not suited to supply the lobes with such an input. It has been suggested that accessory lobe neurons generate a sensory signal of balance of their own which is then

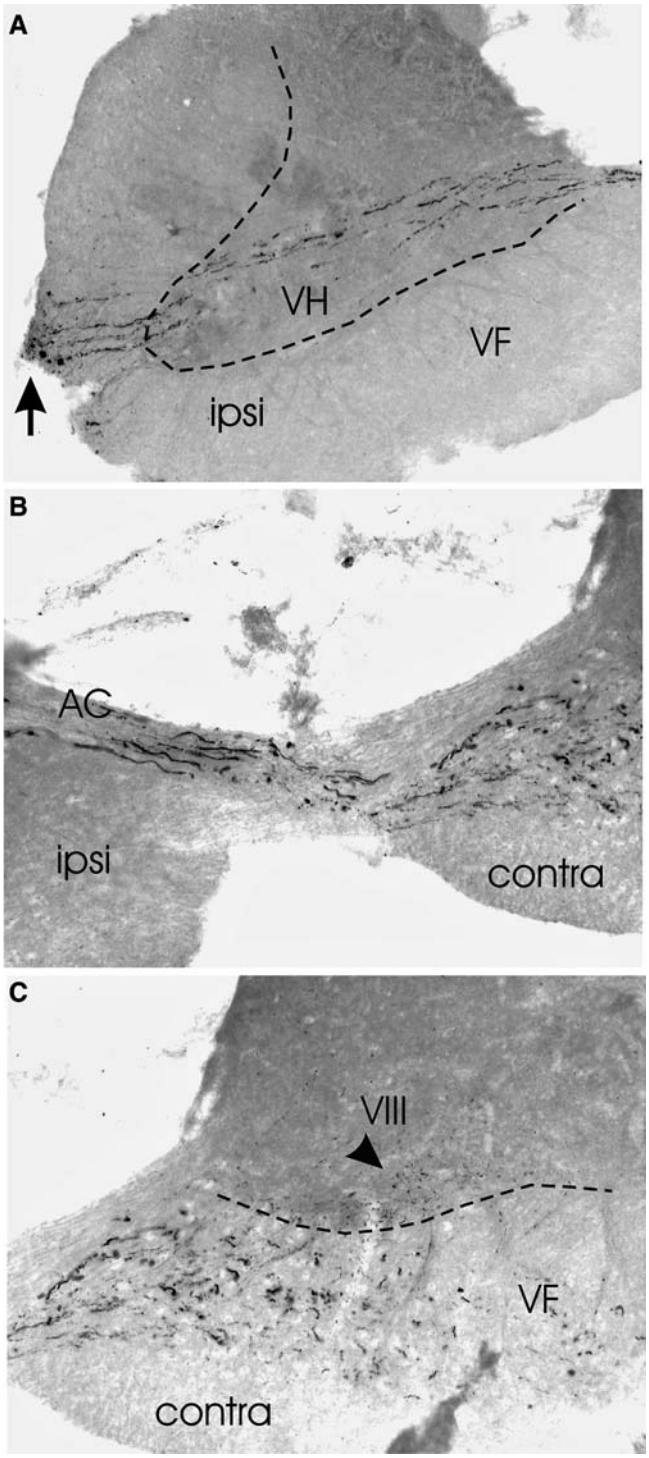


Fig. 7 Projection of the axons of the accessory lobe neurons as revealed by tracer injection (rhoamine dextrane amine, *RDA*) into one lobe (see Fig. 9 for a schematic representation). **a** Transverse section of the spinal cord near the injection site (*arrow*) which shows labelled fibres running transversely through the ipsilateral ventral horn towards the anterior commissure. **b** Labelled fibres running in the anterior commissure towards contralateral ventral funiculus. **c** Labelled fibres in the contralateral ventral funiculus and terminals in lamina VIII (*arrowhead*). *AC* anterior commissure, *VF* ventral funiculus, *VH* ventral horn, *ipsi* ipsilateral to the injection site, *contra* contralateral to the injection site

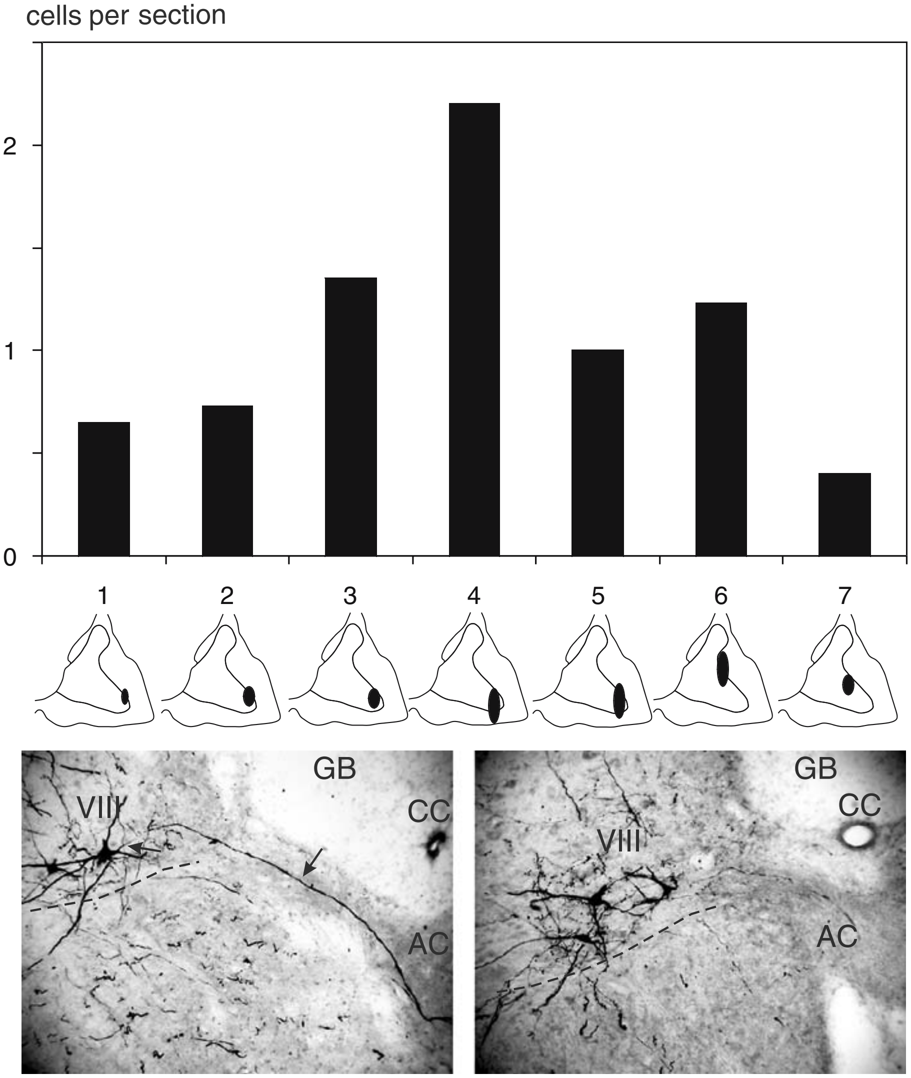


Fig. 8 Projection of commissural lamina VIII neurons as revealed by tracer injection into the ventral horn of pigeons (unpublished own experiments). Graph at the *top* shows the mean number of contralateral lamina VIII neurons per section evaluated throughout the lumbosacral enlargement (there is both a rostral and a caudal projection of lamina VIII neurons). Site and extent of the injection is shown as a *sketch below each column*. Photomicrographs at the *bottom* show examples of labelled contralateral lamina VIII neurons; *arrows* on the left photomicrograph indicate origin and course of an axon. *AC* anterior commissure, *CC* central canal, *GB* glycogen body

distributed to the local motor system (Necker 1997). Taking into account all lines of evidence it seems reasonable to assume that accessory lobe neurons are displaced commissural interneurons which have no peripheral input but generate their own equilibrium related signal to contribute to the coordination of balanced walking with the hindlimbs. These local connections allow a rapid compensation of disturbances during walking.

Behavioral studies

The lumbosacral specializations described above are thought to work as a sense organ of equilibrium. Movements of the body, e.g., during walking, may generate a mechanical stimulus to the accessory lobe neurons via inertia of the cerebrospinal fluid surrounding the accessory lobes as described above. Provided that this idea is correct, one would expect that lesions of the system should be followed by disturbances when walking on the ground. One way to disturb the system is

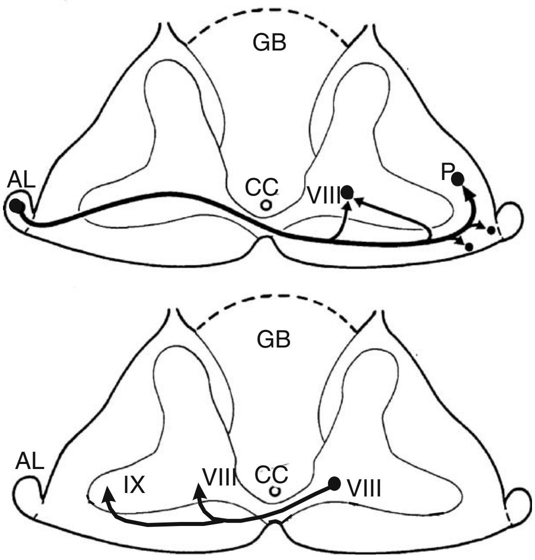


Fig. 9 Sketches of the projection of accessory lobe neurons (*top*) and of lamina VIII neurons (*bottom*). *AL* accessory lobe, *CC* central canal, *GB* glycogen body, *P* paragriseal cells, *roman numerals* indicate laminae of the *grey* substance

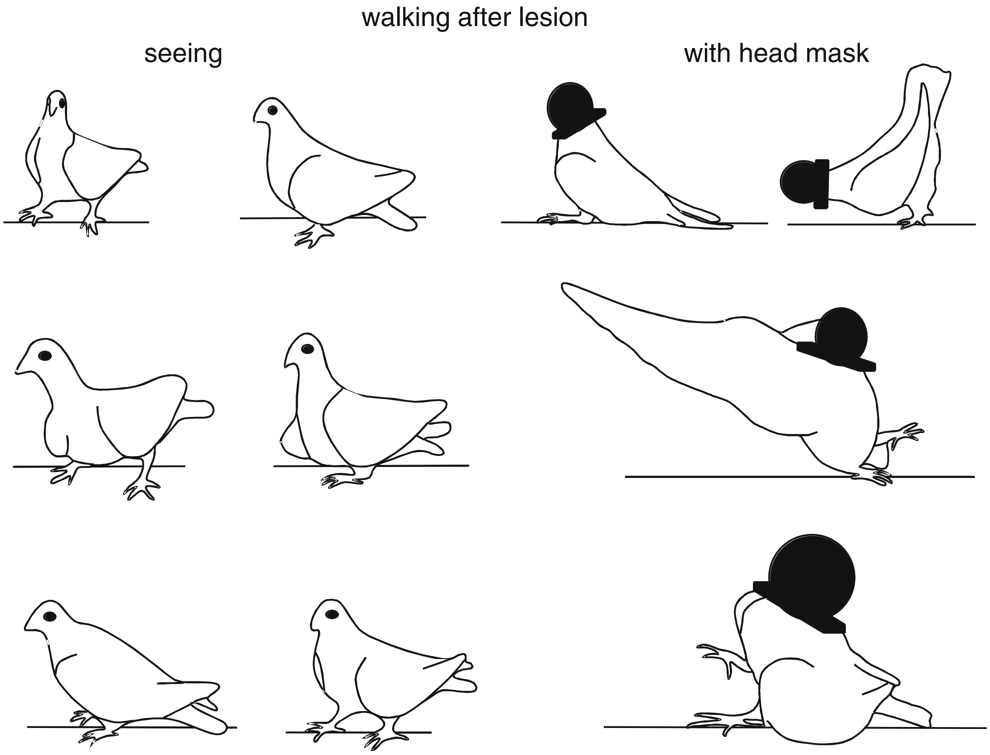


Fig. 10 Examples of the effect of lesions of the lumbosacral canals on walking in the pigeon. When seeing, walking is impaired only slightly (examples on the *left*). When blinded by a head mask, posture and walking are disturbed heavily (examples on the *right*)

to remove the dorsal canals. This opens the fluid space surrounding the lobes but leaves spinal cord and accessory lobes intact. Animals treated in this way had severe problems keeping their balance when walking on the ground but flight was normal (Necker et al. 2000; Fig. 10). This effect was especially severe and long-lasting when sight was impaired by a head mask; it is well known that seeing contributes considerably to keeping balance and to locomotion (e.g., Bosco and Poppele 2001). When staggering around, the lesioned animals showed wing and tail reflexes which were, however, unable to stabilize balance. This is probably due to the fact that such reflexes would help to keep the body in position under aerodynamic conditions, i.e., when flying in the air but are not very effective when moving on the ground. As shown already by Mittelstaedt (1964) hand-held pigeons extend their left wing when being rolled to the left side whereas humans stretch the right arm to keep balance. In a control experiment a similar lesion was applied to the semicircular canals (unpublished data). Opening of the semicircular canals on both sides did not affect keeping balance on the ground but the animal refused to fly. Similar results have been reported by Ewald (1892) after the removal of the sensory epithelia of the labyrinth. The destruction of the labyrinth resulted in a strong reduction of the muscle tone (Ewald

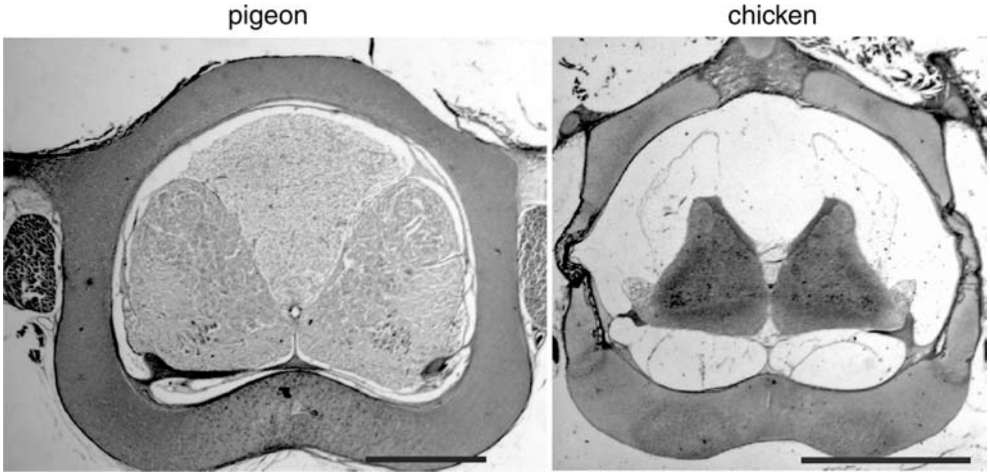


Fig. 11 Comparison of the vertebral canal of a pigeon and of a chicken at the time of hatching. Note large fluid spaces in the chicken. *Scale bars*, pigeon 1 mm, chicken 2 mm

1892). Bilo and Bilo (1978) showed that the vestibular system is strongly activated during flight, i.e., when mechanoreceptors connected with the feathers are stimulated by the air stream. It has been suggested that the vestibular system mainly controls flight whereas walking is assumed to be controlled by an abdominal sensory system (Bilo and Bilo 1978). The reduced function of the vestibular system on the ground and the activation of reflexes useful during flight in the air could explain the ineffective reflexes in the lumbosacral lesion experiments.

Embryonic development

The embryonic development of the lumbosacral specializations (mainly accessory lobes and glycogen body) has been studied earlier in the chicken (Imhof 1905; Watterson 1949) and recently in the pigeon (Necker 2005b). The accessory lobes appear very early during development and the glycogen body somewhat later, and both are well developed at the time of hatching. A comparative study between a semiprecocial nidiculous bird (pigeon) and a precocial nidifugous bird (chicken) revealed that the dorsal canals and the large subarachnoidal spaces surrounding the accessory lobes are not yet fully developed in the hatching pigeon but already adult-like in the chicken hatchling (Necker 2005b; Fig. 11). Newly hatched chickens walk around immediately after hatching and the lumbosacral specializations are in a state to be able to work as the assumed sensory organ.

Comparative aspects

Earlier studies reported that glycogen body and accessory lobes are typical of a large number of avian species (Kölliker 1902; Imhof 1905) and the same was reported for the dorsal grooves (Jelgersma 1951) now identified as lumbosacral canals (Necker 1999). A re-evaluation especially of the dorsal canals showed that there is little variation among birds. As extreme kinds of locomotion the flightless ostrich (*Struthio camelus*) and the common swift (*Apus apus*), which spends most time of its life in the air, may be compared. Both avian species have well-developed accessory lobes (ostrich: Streeter 1904; swift: Fig. 4b) but differ in the shape of the dorsal canals. There are very deep evaginations in the ostrich but rather shallow grooves in the swift (Fig. 12). Pigeons, chickens, quails, geese, swans, songbirds (blackbird, tits, goldcrest) showed normal canals (unpublished own data). Shallow grooves were found in the cormorant and the penguin, both of which spend much time in water. Altogether it seems that the specializations are characteristic of all birds. This seems to make sense since all birds spend some time on the ground. Even swifts have to move on the ground during reproduction.

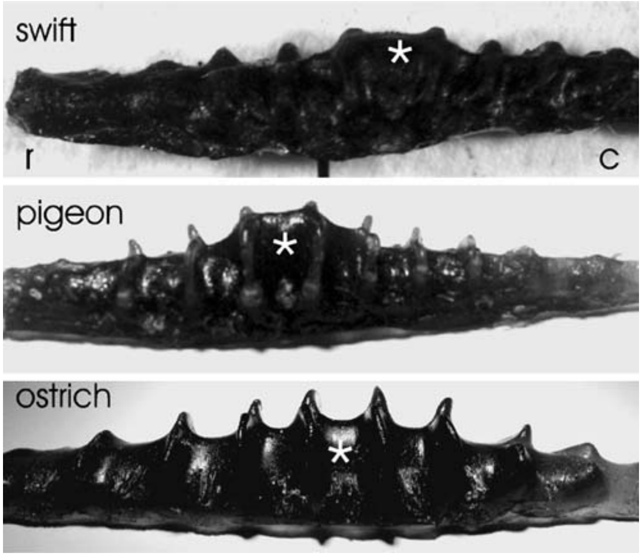


Fig. 12 Casts of the vertebral canal of three different avian species. Note differences in the heights of the lumbosacral canals. *Asterisks* indicate location of the glycogen body. *r* rostral, *c* caudal

Conclusions

The experimental evidence presented in this review supports the assumption that the lumbosacral specializations act as a sense organ involved in the control of posture and locomotion when staying or moving on the ground. The organization of the canals and the accessory lobes and its surroundings suggest a function similar to that of the semicircular canals in the inner ear, i.e., there may be a fluid inertia-driven mechanical stimulation of the accessory lobes. The local organization of the neuronal network favors rapid and hence effective control. Furthermore, the activity of lobe neurons is transmitted to the cerebellum via paragriseal cells which are at the origin of a ventral spinocerebellar pathway (Necker 1992, 2005a). This allows additional control of the coordination of hindlimb locomotion. As stated at the beginning, birds use two kinds of locomotion: flying in the air and walking on the ground. Both kinds of locomotion are used nearly independently. It seems that two different sense organs are involved in their respective control: the vestibular organ during flight and the lumbosacral system during walking.

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