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Commentary

Functional and Anatomical Organization of Floccular Zones: A Preserved Feature in Vertebrates

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Ever since Cajal's work, the cerebellum has been an attractive site for systems neuroscience investigation, in part because the circuitry appears to be simple. There are only two major inputs (mossy fibers and climbing fibers), a single output (the Purkinje cells), and few interneurons. Nevertheless, its function still remains elusive. Study of the cerebellar flocculus, in particular, has been important in addressing two major questions in modern neuroscience. The first involves neural transformations, because the flocculus is a site of multimodal sensory and sensory-motor integration important for retinal image stabilization. Visual and vestibular signals converge upon the flocculus, and its main output is to the extraocular muscles. Research by Simpson, Graf, and colleagues has shown that the visual inputs to the flocculus, the semicircular canals, and the extraocular muscles share a common three-dimensional frame of reference. That is, there is a very close correspondence between the axes of rotation of the three pairs of eye muscles, the axes of the three semicircular canal pairs, and the axis of rotation of the visual world that results in maximal modulation of the visual inputs to the flocculus (Simpson and Graf, 1981; see Fig. 3A,B). Second, the flocculus is an ideal site for studying the mechanisms underlying neural plasticity, because the flocculus is important for the adaptive modification of the vestibuloocular reflex (VOR).

The flocculus can be subdivided into compartments, each of which monitors rotation of the eye by two of the six extraocular muscles. The compartmentation of the mammalian flocculus has a long history, culminating in the paper by Sugihara et al. (2004) published in this issue of the *Journal*. This commentary was prompted by recent findings of a very similar arrangement in the avian flocculus, suggesting that this property of the cerebellum is a highly conserved feature (Winship and Wylie, 2003).

Many studies of the compartmentation of the flocculus are rooted in Ito's (1972) hypothesis on the role of the flocculus in long-term adaptation of the VOR. Simultaneous activation of parallel fibers, bearing a signal from the semicircular canals, and climbing fibers from the inferior olive bearing a signal of retinal slip caused by imperfect stabilization of the eyes, supposedly would cause a long-term reduction in the firing rate of the Purkinje cells, upon which the visual and vestibular signals converge. Subsequent disinhibition of vestibuloocular relay cells would compensate for the imperfect stabilization by the VOR. Ito established that stimulation of the flocculus of the rabbit affects six specific canal-ocular pathways. Two of these pathways link the horizontal canal with the medial and lateral recti. The pathway to the ipsilateral medial rectus and the contralateral lateral rectus is excitatory, and the pathway to the ipsilateral lateral rectus and the contralateral medial rectus muscle is inhibitory. Stimulation of the horizontal canal causes adduction of the ipsilateral eye and abduction of the contralateral eye (see Fig. 3A). Stimulation of the flocculus inhibits these pathways and the direction of the evoked eye movement is reversed (see Fig. 3C). The other four pathways arise from the anterior canal. They excite the ipsilateral superior rectus and the contralateral inferior oblique muscles and inhibit their antagonists, the ipsilateral inferior rectus and the contralateral superior oblique (Ito et al., 1973, 1977). These muscles rotate the eye about an axis located in the horizontal plane that is oriented at 135° ipsilateral azimuth/45° contralateral azimuth, i.e., an axis that is approximately orthogonal to plane of the ipsilateral anterior canal. The correspondence of the axis of the anterior canal and the rotation axis of the eyes on stimulation of this canal is illustrated in Figure 3B. The effects of stim-

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ulation of the flocculus, which inhibits the pathways in question and evokes the reverse eye movement, are illustrated in Figure 3E. Floccular stimulation did not affect the pathways originating from the posterior canal.

In rabbits and cats, the excitatory relay cells for the medial and lateral recti muscles, which are inhibited by the Purkinje cells of the flocculus, are located in the medial vestibular nucleus (VeM; see Fig. 3A; Precht and Baker, 1972; Highstein, 1973; Kawaguchi, 1985; Ohgaki et al., 1988). The excitatory pathways for the superior rectus and inferior oblique relay in the dorsal superior vestibular nucleus (VeS; see Fig. 3B) and the adjoining group Y (Highstein and Ito, 1971; Yamamoto et al., 1978, 1986; Hirai and Uchino, 1984; Sato and Kawasaki, 1991; Uchino et al., 1994). The inhibitory pathways to the inferior rectus and superior oblique are relayed by the central VeS (Highstein and Ito, 1971).

In rabbits, injections of retrograde tracers in the vestibular nuclei containing the relay cells of the horizontal and anterior canal-ocular pathways label Purkinje cells in the flocculus arranged in parallel zones, extending perpendicularly to the long axis of the folia. A central zone, labeled from the VeM, is flanked by two zones labeled from the VeS. The zones extend onto the first folium P of the ventral paraflocculus (Yamamoto and Shimoyama, 1977). A caudal floccular zone is labeled from the lateral cerebellar nucleus, and Purkinje cells in folium P are labeled from the nucleus prepositus hypoglossi (PH; Yamamoto, 1978). Local electrical stimulation of the flocculus causes horizontal or vertical eye movements and is effective in inhibiting the VORs of the ipsilateral medial rectus or the contralateral inferior oblique or ipsilateral superior rectus (Dufossé et al., 1977; Ito et al., 1982; Nagao et al., 1985), but it remains difficult to relate these effects to the zonal pattern.

In the flocculus, the complex spike activity of Purkinje cells, which reflects climbing fiber input, responds best to large-field visual stimulation resulting from rotation of the entire visual world. As first revealed by Simpson et al. (1981), there are two groups of neurons, those that respond best to rotation about a vertical axis (rVA neurons) and those that respond best to rotation about a an axis located close to the horizontal plane at 45° anterior azimuth (with respect to the midsagittal plane) for the contralateral eye and at 135° posterior azimuth for the ipsilateral eye (rH45 neurons; see also Graf et al., 1988). The climbing fiber projections to the flocculus originate from a cell column located alongside the caudal medial accessory olive, which is generally considered as a caudal extension of the principal olive. This column can be subdivided into a rostral segment, the ventrolateral outgrowth (VLO), and a caudal segment, the dorsal cap (DC). Recordings of single units in DC and VLO in the rabbit showed that neurons in the caudal DC contains rVA neurons, whereas the rostral DC and VLO contain rH45 neurons (Simpson et al., 1981; Leonard et al., 1988). The orientation of these axes is strikingly similar to that of the principal axis of the semicircular canals (Ezure and Graf, 1984). rVA neurons can be associated with the horizontal canal; the rH45 neurons in the flocculus can be associated with the ipsilateral anterior semicircular canal.

In 1995, Tan et al. described a system of five compartments, separated by clearly demarcated acetylcholinesterase-reactive borders in the white matter of the flocculus and the adjacent ventral paraflocculus of the rabbit (Fig. 1; Tan et al., 1995a). Each of these compartments contains the Purkinje cell axons of a cortical zone of the flocculus and their olivocerebellar climbing fiber afferents (Fig. 2A; De Zeeuw et al., 1994; Tan et al., 1995b,c). Compartments 4 and 2 contain Purkinje cell axons of the corresponding floccular zones 4 and 2, which project to VeM, and olivocerebellar fibers from the caudal DC. Compartments 3 and 1 contain efferents from the floccular zones 3 and 1, which innervate VeS and group Y and climbing fibers from the rostral DC and the VLO (Fig. 2A). The most lateral compartment contains Purkinje cell axons from the C_2 zone, which project to the posterior interposed nucleus and climbing fiber afferents from the rostral medial accessory olive. These observations confirmed and extended earlier observations of the target nuclei of the floccular zones (Yamamoto and Shimoyama, 1977; Yamamoto, 1978; Sato and Kawasaki, 1991) and their climbing fiber afferents (Yamamoto, 1979; Gerrits and Voogd, 1986; Sato and Kawasaki, 1991; Ruigrok et al., 1992).

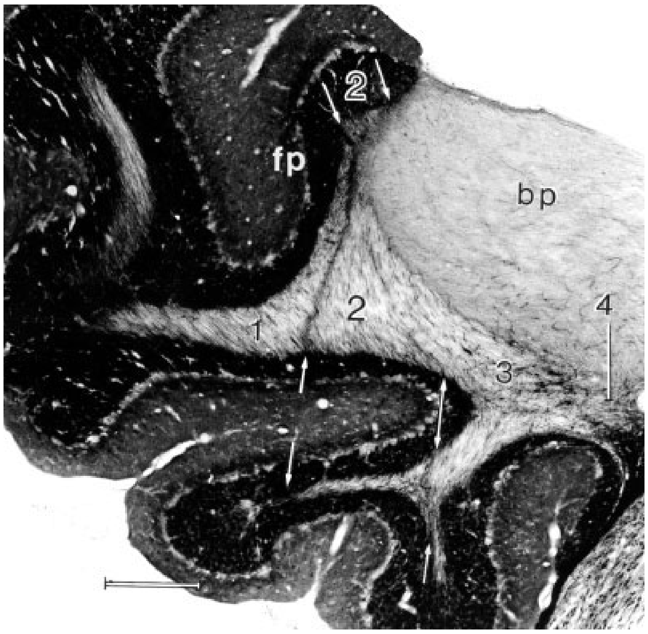
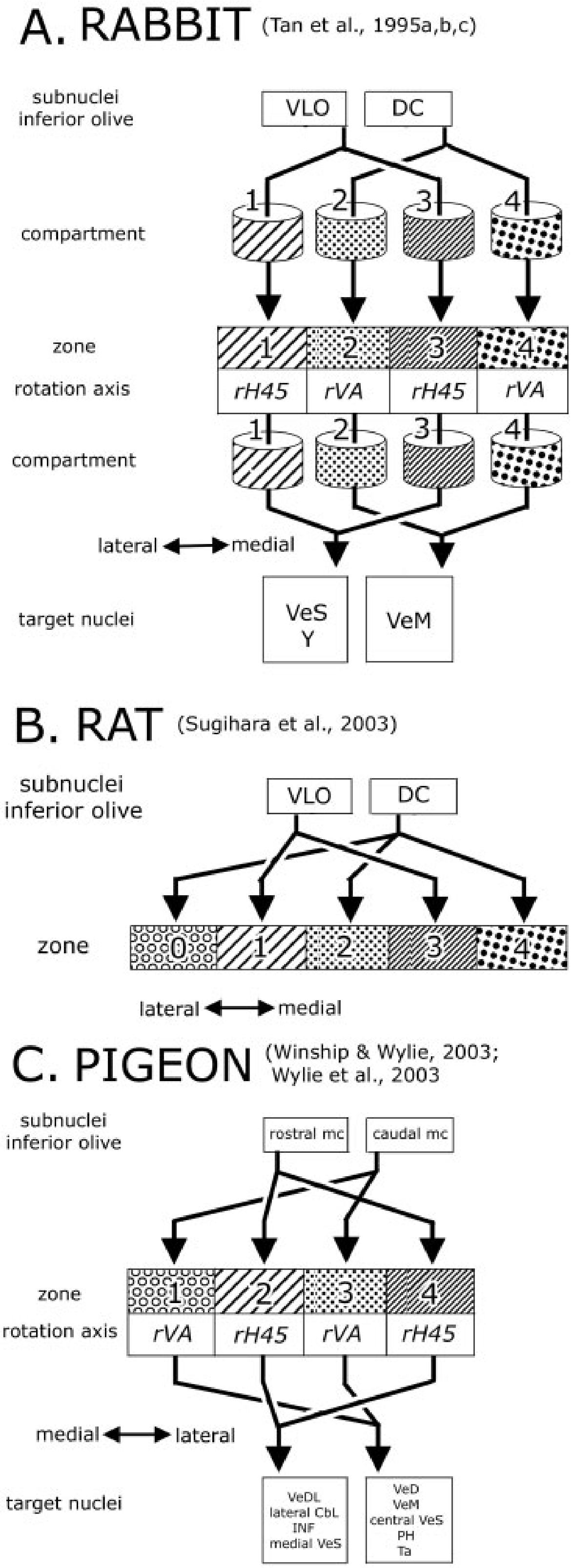


Fig. 1. Transverse section through the left rabbit flocculus reacted for acetylcholinesterase, showing the strongly reactive borders between white matter compartments 1–4 (arrows). 1–4, White matter compartments 1–4; bp, brachium pontis; fp, folium p. (Reproduced from Tan et al., 1995a). Scale bar = 500 μm.

The delineation of compartments in the rabbit flocculus not only proved to be useful for correlating the afferent and efferent connections of the corresponding floccular zones but also served as a frame of reference for studying the functional organization of eye movements in the flocculus (Van Der Steen et al., 1994). Electrical stimulation of compartment 2 caused abduction of the ipsilateral eye, with a varying amount of adduction of the contralateral eye (Fig. 3C); stimulation of compartments 1 and 3 caused a counterclockwise rotation about the ipsilateral 135° axis, accompanied by a smaller, clockwise rotation of the contralateral eye about its 45° axis (Fig. 3E). Ipsilateral abduction would result in a strong activation of the rVA climbing fibers from the caudal DC, terminating on Pur-



kinje cells of floccular zones 2 and 4, whereas the eye movements evoked from compartments 1 and 3 would result in activation of the rH45 climbing fibers from the rostral DC and the VLO, which terminate in the zones 1 and 3. The compartments of the flocculus, therefore, have a modular organization with respect to eye movement control, with zones 2 and 4 representing movements around the axis of the ipsilateral horizontal canal and zones 1 and 3 representing movements around the axis of the ipsilateral anterior canal. The function of the C_2 compartment is unclear, although it has been linked to head-movement control (De Zeeuw and Koekkoek, 1997).

Sugihara et al. (2004) reconstructed the course of individual olivocerebellar fibers, labeled with biotinylated dextran amine, to determine their course and their collateralization to the flocculus and the cerebellar nuclei. They confirmed and adopted the subdivision of the flocculus into two pairs of interdigitating zones and a C_2 zone. Zones 2 and 4 are innervated by the DC and zones 1 and 3 by the VLO (Fig. 2B). In addition, they identified a third, DC-innervated zone in the lateral flocculus (zone 0). For zones 1 and 3, Sugihara et al. found a subdivision into three subzones. They showed that some individual neurons of the DC and the VLO send collaterals to more than one of the zones innervated by a single subnucleus. Most neurons, however, innervate a single floccular zone. Axons from the DC and the VLO were found to collateralize to different regions in the ventral lateral cerebellar nucleus and the infracerebellar nucleus. Collateralization to the target vestibular nuclei of the flocculus was found to be absent, settling a long discussion on this subject.

Compartmentation of the Avian Flocculus

Winship and Wylie (2003), in a study of the climbing fiber projection to the flocculus in pigeons, noted a similar arrangement of floccular zones. The gross morphology of the flocculus in birds is quite different from that in mammals. The avian cerebellum consists of a vermis without hemispheres, and the flocculus corresponds to the lateral half of the two most ventral folia of the posterior vermis (folia IXcd and X), which extend rostrolaterally to form the auricle (Arends and Zeigler, 1991; Larsell, 1948). The pigeon's flocculus receives climbing fiber input from the medial column (mc) of the inferior olive (Arends and Voogd, 1989; Lau et al., 1998). As shown in Figures 2C and 5, Winship and Wylie (2003) found two floccular zones innervated by the caudal mc interdigitated with two zones innervated by the rostral mc. The caudal mc (and the zones that it innervates) contains rVA neurons, whereas

Fig. 2. Diagram showing the possible homology of the zones in the flocculus in rabbit (**A**), rat (**B**), and pigeon (**C**) and their afferent olivocerebellar and efferent connections. Note that an equivalent of zone 0 of the rat is absent in the rabbit and that the rat's zone 4 is not represented in pigeons. The labels *medial* and *lateral* refer to the true position of the flocculus. Because the flocculus in mammals is bent upon itself (Fig. 4), the order of the zones is reversed in rabbit and rat. 0–4, Zones (compartments) 0–4; CbL, lateral cerebellar nucleus; DC, dorsal cap; INF, inferior cerebellar nucleus; mc, medial cell column; PH, nucleus prepositus hypoglossi; rH45, horizontal 45° rotation axis; rVA, vertical rotation axis; Ta, tangential nucleus; VeD, descending vestibular nucleus; VeDl, dorsolateral vestibular nucleus; VeM, medial vestibular nucleus; VeS, superior vestibular nucleus; VLO, ventrolateral outgrowth; Y, group Y.

the rostral mc contains rH45 neurons (Winship and Wylie, 2001; Wylie et al., 2003). In this respect, the caudal and rostral mc correspond to the mammalian caudal DC and VLO with rostral DC, respectively.

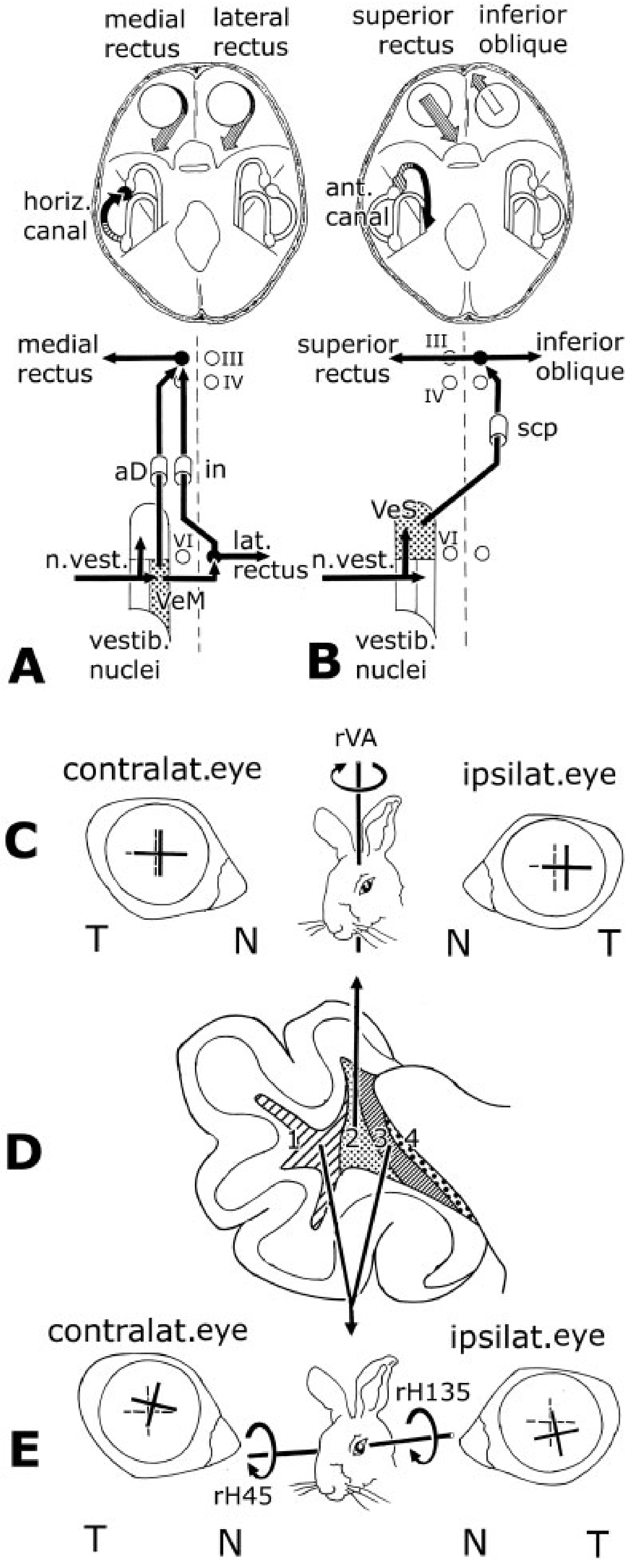


Fig. 3. Diagram of the vestibuloocular connection of the horizontal (**A**) and anterior (**B**) semicircular canal showing alignment of semicircular canals and extrinsic eye muscles in dorsal view and of the classes of short-latency eye movements evoked by electrical stimulation of white matter compartments 1, 2, and 3 of the rabbit flocculus (**C,D**). A: Excitation of the horizontal semicircular canal causes ipsilateral adduction by the medial rectus and contralateral abduction by the lateral rectus muscle. The excitatory vestibuloocular pathways are illustrated in the lower panel. B: Excitation of the anterior semicircular canal causes an inward rotation of the ipsilateral eye by the superior rectus and an outward rotation of the contralateral eye by the inferior oblique muscle, around an axis approximately colinear with the axis of this canal. The excitatory pathways are illustrated in the lower panel. C: Stimulation of white matter compartment 2 of the rabbit flocculus evoked abduction of the ipsilateral eye, with a varying amount of adduction of the contralateral eye. That is, the eye rotated about the vertical axis (rVA), corresponding to the axis of the horizontal semicircular canal. The rotation is reversed with respect to A, because the action of the flocculus is an inhibitory one. The 0 position is indicated with dashed lines, the position during stimulation with solid lines. D: Localization of the stimulation sites indicated in a transverse section through the left flocculus. **E:** Stimulation of compartments 1 and 3 produced ipsilateral eye movements about a horizontal 135° axis (rH135) of the ipsilateral eye or about a 45° of the contralateral eye (rH45). That is, the eyes rotated around an axis corresponding to the axis of the ipsilateral anterior canal. aD, ascending tract of Deiters; IV–VI, oculomotor nuclei IV–VI; in, internuclear pathway; N, nasal ; n.vest., vestibular nerve; rH135, horizontal 135° rotation axis; rH45, horizontal 45° rotation axis; rVA, vertical axis of rotation; scp, superior cerebellar peduncle; T, temporal; VeM, medial vestibular nucleus; VeS, superior vestibular nucleus. (A and B reproduced from Nieuwenhuys et al., 1998; C and D reproduced from Van Der Steen et al., 1994).

There is some confusion regarding an appropriate comparison regarding the order of the zones in pigeons vs. rabbits (Winship and Wylie, 2003). At first glance, it appears that the order of the zones in pigeons is the same as that in mammals, insofar as the most medial zone in pigeons and mammals is a VA zone. However, the area of the mammalian VbC that contains the flocculus, the terminal hook (Bolk, 1906), folds back upon itself such that the order of zones viewed in transverse sections becomes reversed (see Fig. 4). In light of this, the zonal order of the pigeon appears reversed relative to that of rabbits. However, given the data of Sugihara et al. (2004), perhaps it is most appropriate to consider that the order of the floccular zones in the pigeon corresponds to that of the medial four zones in the rat. Among the rVA zones, zone 0 is represented in the pigeon but absent in the rabbit, and zone 4 is present in the rabbit but seems to be lacking in the pigeon flocculus (Fig. 2). As yet there is no evidence of a C_2 zone equivalent in the pigeon, which should lie medial to the medial most rVA zone. The absence of a particular zone in the flocculus of a species is not unusual: Primates seem to lack an equivalent of the rat and rabbit's zone 4 (Voogd et al., 1987).

The projections of the floccular zones in mammals and birds appear quite similar, though not identical. As in mammals, the rVA zones project heavily to VeM and also to PH, central VeS, and the descending vestibular nucleus (VeD). The rH45 zones project heavily to the infracerebellar nucleus (INF; homologue of dorsal group Y; Arends et al., 1991) and the medial VeS and also to the lateral edge of the lateral cerebellar nucleus (CbL) and the dorsolateral vestibular nucleus (VeDL; putative homologue of ventral group Y; Arends et al., 1991). CbL corresponds to the

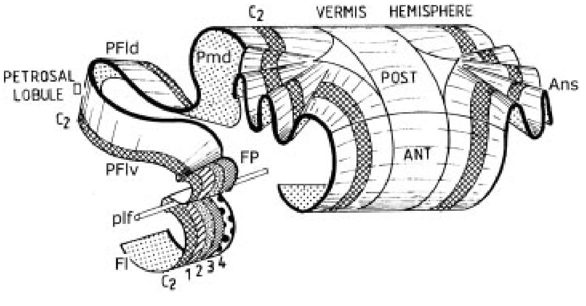


Fig. 4. Diagram of the three-dimensional configuration of the zones of the paraflocculus (PFld/v) and the flocculus (Fl) of the rabbit. The folial chain of the flocculus and the paraflocculus is bent upon itself. Consequently, the lateral border of the cerebellar hemisphere (indicated by a heavy line) is continuous with the medial border of the flocculus. plf, posterolateral fissure; Pmd, paramedian lobule.

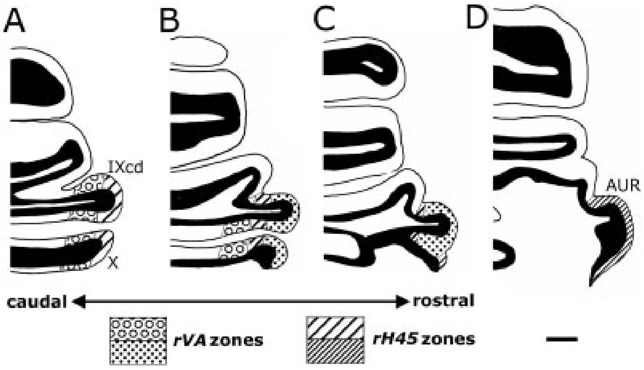


Fig. 5. Zonal organization of the pigeon flocculus. This series of coronal sections, caudal to rostral (**A–D**), through the cerebellum shows the rVA and rH45 zones in folia IXcd and X. AUR, auricle. Scale bar = 1 mm. (Adapted from Winship and Wylie, 2003).

mammalian interposed nucleus. In mammals, the posterior interposed nucleus does receive input from the flocculus, but from the nonvisual C_2 zone.

Although the zonal organization and projections of the flocculus are quite similar in aves and mammals, there is a striking difference between mammals and aves with respect to the ventral uvula and nodulus. The olivary input to the uvula/nodulus in mammals is largely from the same subnuclei that innervate the flocculus, DC, and VLO, but also from the beta subnucleus and the dorsomedial cell column (see, e.g., Voogd et al., 1996). As in the flocculus, there are visually responsive zones containing rVA and rH45 cells (Kano et al., 1990) and also neurons responsive to vestibular stimulation originating in the otolith organs (Barmack and Shojaku, 1992). In contrast, in the ventral uvula and nodulus, the zones receive climbing fiber input from areas lateral to those subnuclei projecting to the flocculus (Lau et al., 1998; Crowder et al., 2000), and neurons respond to patterns of optic flow resulting from self-translation along a particular axis, rather than self-rotation (Wylie et al., 1993, 1998; Wylie and Frost, 1999). Climbing fiber-collateral projections to the target nuclei of the floccular zones thus far have not been studied in aves.

CONCLUSIONS

The position of the semicircular canals and the innervation of the six eye muscles by the oculomotor, trochlear, and abducens nerves has remained very similar throughout vertebrate evolution (Simpson and Graf, 1981; Heaton and Wayne, 1983; Ezure and Graf, 1984; Nieuwenhuys et al., 1998). Apparently, the zonal organization of the olivofloccular and flocculovestibular projections according to the axes of the horizontal and anterior semicircular canals is also a highly preserved feature. Unfortunately, little is known about this organization in reptiles, the common ancestors of aves and mammals. Furthermore, an explanation of how the presence of paired or triple floccular zones with very similar afferent and efferent connections offers an advantage in VOR adaptation still eludes us. Future studies of this system in reptiles, amphibians, and fish may solve this problem and shed light on the compartmentation of the cerebellum in general.

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