Chapter 8
Vestibular Nuclei and Their Cerebellar Connections

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Abstract The vestibular complex exists at a sensory-motor crossroad that is composed of five separate nuclei defined primarily by a common vestibular primary afferent projection. These five nuclei are located just beneath the dorsal surface of the medullary brainstem. They include: Descending, lateral, medial and superior nuclei (DVN, LVN, MVN and SVN) as well as the Parasolitary nucleus (Psol). Each vestibular nucleus can be recognized by a combination of boundaries that include fiber bundles and histological characteristics such as cell size. With the exception of Psol, a nucleus that is composed of small GABAergic cells (5–7 μm in diameter), the DVN, LVN, MVN and SVN contain a variety of cell types and cell sizes. Here we review the afferent and efferent connections of the vestibular nuclei and discuss how these characteristics might influence function.

Keywords Flocculus • Nodulus • Uvula • Vestibular complex • Purkinje cells

Five vestibular nuclei, defined by an ipsilateral projection of primary vestibular afferents, are located just below the dorsal surface of the medullary brainstem (Fig. 8.1). They include: Descending, lateral, medial and superior nuclei (DVN, LVN, MVN and SVN) as well as the Parasolitary nucleus (Psol). Each vestibular nucleus can be recognized by a combination of boundaries that include fiber bundles and histological characteristics such as cell size (Fig. 8.1c_{1-3}). With the exception of Psol, a nucleus that is composed homogeneously small GABAergic cells (5–7 μm in diameter), the DVN, LVN, MVN and SVN contain a variety of cell types. While the LVN includes the largest cells in the brain (>50 μm), it is also comprised of many smaller cell types (Brodal and Pompeiano 1957; Brodal 1974; Barmack et al. 1998). Here we review the afferent and efferent connections of the vestibular nuclei and discuss how these characteristics might influence function.

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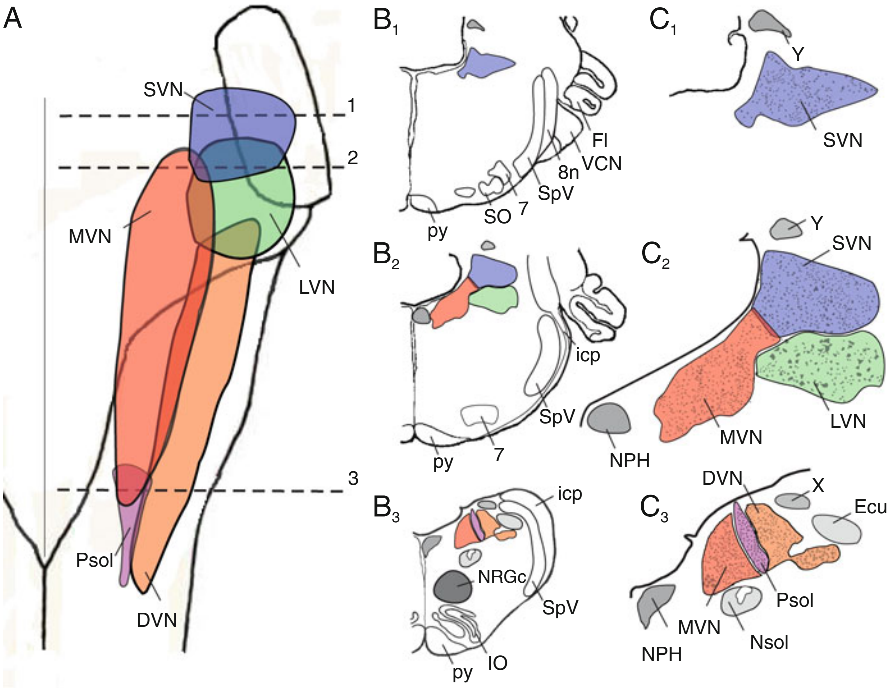

Fig. 8.1 Vestibular nuclei. (**a**) Horizontal view of vestibular nuclei. The *horizontal dashed lines* indicate the anterior-posterior level of the three transverse sections illustrated in (**b**$_{1-3}$) and at higher magnification in (**c**$_{1-3}$). Abbreviations: *DVN*, *LVN*, *MVN* and *SVN* descending, lateral, medial and superior vestibular nucleus, *Ecu* external cuneate nucleus, *Fl* flocculus, *icp* inferior cerebellar peduncle, *IO* inferior olive, *NPH* nucleus prepositus hypoglossi, *NRGc* nucleus reticularis gigantocellularis, *Nsol* solitary nucleus, *Psol* parasolitary nucleus, *Py* pyramidal tract, *SO* superior olive; sol, *SpV* spinal trigeminal nucleus, *7* facial nucleus, *x* nucleus x, *Y* Y-group (Modified from Brodal and Pompeiano 1957)

8.1 Vestibular Primary Afferents

The peripheral vestibular apparatus consists of three semicircular canals and two otoliths. The semicircular canals are oriented orthogonally and sense angular acceleration about horizontal, vertical and oblique axes. Otoliths sense linear acceleration imposed by the gravitational vector during roll-tilt of the head about the longitudinal axis (utricule) and during pitch about the intra-aural axis (saccule). Each of the vestibular endorgans contributes primary vestibular afferents to the vestibular nerve that branches into two fiber bundles of unequal thickness as they enter the brain stem. The thicker branch enters the medulla between the ventral aspect of the inferior cerebellar peduncle and the dorsal aspect of the spinal tract of the trigeminal nucleus. It turns caudally and passes into the vestibular complex to terminate on secondary vestibular neurons. The thinner branch ascends to the cerebellum where it terminates on granule cells in the uvula-nodulus (Cajal 1911).

The primary vestibular afferent projection to the vestibular nuclei has regional specificity, but does not conform to the boundaries of individual vestibular nuclei. For example, neurons in the SVN respond to stimulation of the ipsilateral anterior semicircular canal and are found more laterally than are SVN neurons responsive to stimulation of the ipsilateral horizontal semicircular canal. Horizontal semicircular canal primary afferents project to the DVN, MVN and SVN, but not the LVN and Psol. Psol neurons are driven exclusively by stimulation of ipsilateral *vertical* semicircular canals and utricule. Secondary neurons within the LVN receive a primary vestibular projection from the ipsilateral saccule, but not from the utricule (Sato and Sasaki 1993).

8.2 Visual Projections to Vestibular Nuclei

Vestibular primary afferents comprise only one of the sensory inputs to the vestibular complex. Most secondary vestibular neurons are also driven by visual (optokinetic) stimulation (Henn et al. 1974). Although visual signals to the vestibular nuclei originate from a variety of brainstem and cortical sources, optokinetic signals reach the vestibular complex from the accessory optic system (AOS) (Simpson et al. 1988). Direction selective retinal ganglion cells project to the AOS. AOS neurons, in turn, project to vestibular nuclei, the cerebellum and the inferior olive. The AOS also receives a descending projection from the visual cortex. In primates this projection originates from the pre-striate cortex (areas OAa and PGa) (Ilg and Hoffmann 1996). Selective stimulation or inactivation of this region modifies the directional selectivity of neurons in the AOS.

8.3 Neck-Proprioceptive Inputs to Vestibular Nuclei

Signals from proprioceptors embedded in the intertransverse muscles at the base of the cervical vertebrae also activate secondary vestibular neurons (Hikosaka and Maeda 1973; McCouch et al. 1951). Injection of HRP into the caudal MVN and DVN retrogradely labels neurons in ipsilateral C_2-C_3 spinal ganglia, in the contralateral central cervical nucleus and bilaterally in C_1-C_6 dorsal horn cells (Bankoul and Neuhuber 1990; Sato et al. 1997). Neurons in the vestibular complex also receive secondary cervical afferents relayed through the external cuneate nucleus (Ecu) (Fig. 8.1b_3c_3) (Prihoda et al. 1991). Movement of the head with respect to the body stimulates neck proprioceptors and evokes reflexive eye movements as well as postural adjustments of the limbs (McCouch et al. 1951; Barmack et al. 1981; Hikosaka and Maeda 1973).

8.4 Cerebellar Projections to the Vestibular Complex

Cerebellar projections to the vestibular complex include, but are not restricted to efferents from the uvula-nodulus (folia 9-10) (Walberg and Dietrichs 1988). Purkinje cells located within sagittal zones in these folia as well as the flocculus project to different regions within the vestibular complex (De Zeeuw et al. 1994).

While Purkinje cells project onto the same vestibular nuclei from which cholinergic mossy fiber projections to the uvula-nodulus originate, the overlap is far from perfect. The dorso-caudal MVN and DVN receive dense projections from uvula-nodular Purkinje cells. Cells in this region of the MVN, DVN and LVN give rise to the medial vestibulo-spinal tract. The uvula-nodulus also projects to the SVN (Tabuchi et al. 1989; Shojaku et al. 1987; Bernard 1987; Walberg and Dietrichs 1988; Wylie et al. 1994).

Within the vestibular complex, LVN neurons receive the most dense cerebellar projection. This projection arises mostly from the "b zone" of the vermis (Andersson and Oscarsson 1978a, b). The "b-zone" receives climbing fiber projections conveying cutaneous information from the forelimbs and hind limbs. The non-uniform immunolabeling of Purkinje cell axon terminals within the MVN, NPH, SVN, DVN and Psol suggests that each vestibular nucleus contains a subset of neurons whose activity is modulated by cerebellar projections.

8.5 Projections Within Vestibular Nuclei

The pattern of interconnections within the vestibular complex has been mapped with microinjections of HRP into the vestibular complex of the rabbit. Interconnections between the SVN-DVN and SVN-MVN are mostly reciprocal (Epema et al. 1988). However, clusters of larger neurons in the rostro-ventral MVN, SVN and LVN receive inputs from smaller cell regions of MVN, SVN and DVN, but do not reciprocate (Ito et al. 1985). The MVN has a non-reciprocal projection to the DVN.

8.6 Commissural Projections Between Vestibular Nuclei

The vestibular nuclei, with the exceptions of the LVN and Psol, are interconnected through a commissural system. However, the connections are not restricted to homologous nuclei. Rather, cells within a nucleus on one side of the brainstem, say the left MVN, project to the contralateral SVN and DVN as well as the contralateral MVN (Epema et al. 1988; Newlands et al. 1989). Electrical stimulation of the utricular macula evokes excitation in ipsilateral secondary vestibular neurons and inhibition in more than 50 % of the contralateral secondary vestibular neurons excited by ipsilateral utricular stimulation. Only 10 % of secondary neurons responsive to ipsilateral stimulation of the saccule are inhibited by contralateral saccular stimulation.

8.7 Ascending Projections of Vestibular Nuclei

Targets of secondary vestibular afferents are diverse. The rostral halves of DVN, MVN and SVN provide an ascending input to cranial motor nuclei III, IV and VI, controlling the reciprocal contractions of extraocular muscles (Fig. 8.2a) (Büttner and Lang 1979; Deecke et al. 1977; Büttner-Ennever 1992; Graf et al. 1983).

Other brainstem nuclei that receive ascending projections from secondary vestibular neurons include: nucleus Darkschewitch, sensory trigeminal nucleus, interstitial nucleus of Cajal and the subparafascicular complex (Barmack et al. 1979). The subparafascicular complex projects reciprocally back to the ipsilateral MVN (Fig. 8.2c).

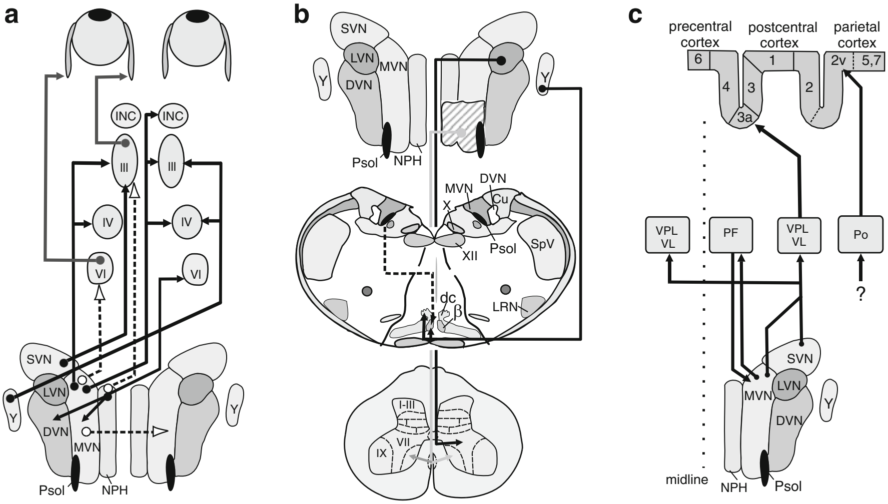

Fig. 8.2 Ascending and descending connections of the vestibular complex. (**a**) Projections of vestibular complex onto oculomotor apparatus. (**b**) Descending projections of vestibular complex to spinal cord and to inferior olive. **c** Ascending projections of vestibular complex to thalamus and cortex. *Dashed lines* indicate inhibitory projections. *Abbreviations*: *β* β-nucleus, *Cu* cuneate nucleus, *dc* dorsal cap of Kooy, *DVN*, *MVN*, *LVN*, *SVN* descending, medial, lateral and superior vestibular nuclei, *INC* interstitial nucleus of Cajal, *LRN* lateral reticular nucleus, *NPH* nucleus prepositus hypoglossi, *PF* parafascicular nucleus, *Psol* parasolitary nucleus, *SpV* spinal trigeminal nucleus, *PO* posterior thalamic nuclear group, *VL* ventrolateral nucleus, *VPL* ventral posterior lateral nucleus, *III*, *IV*, *VI* oculomotor cranial nuclei, *X* dorsal motor nucleus of vagus, *XII* hypoglossal nucleus, *Y* Y-group (Modified from Büttner and Lang (1979), Deecke et al. (1977), Büttner-Ennever (1992), and Graf et al. (1983))

Several ascending projections from the rostral part of the vestibular complex terminate on neurons in the ventro-basal thalamus (VPL, VPM, VPI and VPL) (Fig. 8.2c). Neurons in the ventro-basal complex are driven by stimulation of deep proprioceptors and joint receptors as well as vestibular inputs (Lang et al. 1979; Deecke et al. 1977; Bacskai et al. 2002; Shiroyama et al. 1999).

Thalamic neurons, in turn, terminate in Areas 3aV, T3 and parietal visual cortices (Fukushima 1997). These cortical areas receive optokinetic and somatosensory as well as vestibular inputs (Fig. 8.2c). The importance of this projection is illustrated by the observation that humans with damage to parietal cortex, and without visual cues, do not recognize true vertical (Leigh 1994). Vestibular cortices project reciprocally to vestibular nuclei, suggesting that these cortical regions may supersede reflexes evoked by primary vestibular afferents (Akbarian et al. 1993, 1994; Nishiike et al. 2000).

8.8 Cholinergic and GABAergic Vestibular Projections to the Cerebellum from the MVN, Nucleus Prepositus Hypoglossi and Y-Group

Although neurons in the nucleus prepositus hypoglossi (NPH) lack a vestibular primary afferent projection, they receive a secondary vestibular afferent projection as well as projections from cerebellum and cerebellar nuclei. NPH neurons project bilaterally to the vestibular nuclei as well as the inferior olive (McCrea and Baker 1985). The projection from NPH to the dorsal cap is both cholinergic and GABAergic (Barmack et al. 1993a; De Zeeuw et al. 1993).

Neurons in the caudal aspects of the NPH and MVN project to several folia within the cerebellum (uvula-nodulus, ventral paraflocculus, flocculus) (Epema et al. 1990; Barmack 2003). Immunohistochemical surveys show that most if not all of these ascending mossy fiber projections from the caudal MVN, NPH are cholinergic.

The NPH also projects to the reticular formation, medial rectus subdivision of the ipsilateral oculomotor nucleus (III), contralateral abducens nucleus (VI) and contralateral dorsal cap of the inferior olive (Fig. 8.2a).

The Y-group also receives bilateral projections from the SVN. The ventral division of the Y-group projects to the ipsilateral flocculus, nodulus and contralateral oculomotor complex. The dorsal division projects contralaterally to the dorsal cap and beta nucleus of the inferior olive (Fig. 8.2a, b). This projection is excitatory (Kumoi et al. 1987). Y-group and NPH neurons project directly to the cerebellum as mossy fibers. Y-group and NPH neurons also influence the activity of neurons in the inferior olive that make overlapping projections to the cerebellum as climbing fibers.

8.9 Descending Projections of Vestibular Nuclei

Descending lateral and medial vestibulospinal tracts originate from the LVN and MVN and DVN (Brodal 1981). The lateral vestibulospinal tract is organized within the LVN topographically. Fibers to the lumbosacral spinal cord originate from the dorso-caudal LVN. Fibers to the cervical cord originate from the rostro-ventral LVN (Fig. 8.2b). Axons in the lateral vestibulospinal tract terminate in the ipsilateral lumbosacral region where they make monosynaptic and polysynaptic connections with motoneurons (Rose et al. 1992). Axons in the medial vestibulospinal tract terminate bilaterally in the medial part of the cervical ventral horn. The bilateral representation of vestibulospinal axons is most dense in the cervical enlargements from which motoneurons supplying the suboccipital muscles originate. These motoneurons participate in vestibulocollic reflexes.

The output of Psol is GABAergic. It descends to the ipsilateral inferior olive where it modulates the activity of cells in the β-nucleus (β) and dorsomedial cell column (dmcc) (Fig. 8.1b) (Barmack et al. 1993b, 1998). These olivary neurons terminate as climbing fibers in the contralateral uvula-nodulus (Fig. 8.2b). In route to the inferior olive, Psol neurons also distribute collateral axon terminals to nuclei in the reticular formation, particularly the nucleus reticularis gigantocellularis (Fig. 8.1a) (Fagerson and Barmack 1995).

8.10 Autonomic Influences of the Vestibular Nuclei

The vestibular nuclei not only participate in reflexes mediated by skeletal muscles, but also are part of the circuitry through which autonomic reflexes (blood flow, respiration rate and heart rate) are regulated (Kaufmann et al. 2002; Rossiter et al. 1996; Kerman et al. 2000). Specifically this circuitry includes projections from the caudal vestibular nuclei (DVN, MVN and Psol) to the solitary nucleus (Nsol). The Nsol receives autonomic afferents, from the heart, esophagus and stomach, carried chiefly by branches of the IX and X cranial nerves.

8.11 Functions of Vestibular Nuclei

The vestibular nuclei are at a sensory-motor crossroad. The discharge of secondary vestibular neurons is influenced by visual and neck proprioceptive signals as well as signals generated by cerebellar and cerebral cortices. Consequently the discharge of secondary vestibular neurons comprises an adaptive hierarchy of sensory-motor responses. This hierarchy renders the famed “three neuronal arc” under central control (Lorente de Nó 1933).

References

Akbarian S, Grusser OJ, Guldin WO (1993) Corticofugal projections to the vestibular nuclei in squirrel-monkeys – further evidence of multiple cortical vestibular fields. J Comp Neurol 332:89–104

Akbarian S, Grüsser O-J, Guldin WO (1994) Corticofugal connections between the cerebral cortex and brainstem vestibular nuclei in the macaque monkey. J Comp Neurol 339:421–437

Andersson G, Oscarsson O (1978a) Climbing fiber microzones in cerebellar vermis and their projection to different groups of cells in the lateral vestibular nucleus. Exp Brain Res 32:565–579

Andersson G, Oscarsson O (1978b) Projections to lateral vestibular nucleus from cerebellar climbing fiber zones. Exp Brain Res 32:549–564

Bacskai T, Szekely G, Matesz C (2002) Ascending and descending projections of the lateral vestibular nucleus in the rat. Acta Biol Hung 53:7–21

Bankoul S, Neuhuber WL (1990) A cervical primary afferent input to vestibular nuclei as demonstrated by retrograde transport of wheat germ agglutinin-horseradish peroxidase in the rat. Exp Brain Res 79:405–411

Barmack NH (2003) Central vestibular system: vestibular nuclei and posterior cerebellum. Brain Res Bull 60:511–541

Barmack NH, Henkel CK, Pettorossi VE (1979) A subparafascicular projection to the medial vestibular nucleus of the rabbit. Brain Res 172:339–343

Barmack NH, Nastos MA, Pettorossi VE (1981) The horizontal and vertical cervico-ocular reflexes of the rabbit. Brain Res 224:261–278

Barmack NH, Fagerson M, Errico P (1993a) Cholinergic projection to the dorsal cap of the inferior olive of the rat, rabbit and monkey. J Comp Neurol 328:263–281

Barmack NH, Fagerson M, Fredette BJ, Mugnaini E, Shojaku H (1993b) Activity of neurons in the beta nucleus of the inferior olive of the rabbit evoked by natural vestibular stimulation. Exp Brain Res 94:203–215

Barmack NH, Fredette BJ, Mugnaini E (1998) Parasolitary nucleus: a source of GABAergic vestibular information to the inferior olive of rat and rabbit. J Comp Neurol 392:352–372

Bernard J-F (1987) Topographical organization of olivocerebellar and corticonuclear connections in the rat – an WGA-HRP study: I. Lobules IX, X, and the flocculus. J Comp Neurol 263:241–258

Brodal A (1974) Anatomy of the vestibular nuclei and their connections. In: Kornhuber HH (ed) Handbook of sensory physiology, vestibular system, morphology, vol 6. Springer, Berlin

Brodal A (1981) Neurological anatomy, 3rd edn. Oxford University Press, New York

Brodal A, Pompeiano O (1957) The vestibular nuclei in the cat. J Anat 91:438–454

Büttner U, Lang W (1979) The vestibulocortical pathway: neurophysiological and anatomical studies in the monkey. In: Granit R, Pompeiano O (eds) Reflex control of posture and movement. Elsevier/North-Holland Biomedical Press, Amsterdam, pp 581–588

Büttner-Ennever J (1992) Patterns of connectivity in the vestibular nuclei. In: Cohen B, Tomko DL, Guedry F (eds) Sensing and controlling motion. Annals of the New York Academy of Sciences, New York, pp 363–378

Cajal SR (1911) Histologie du système nerveux de l'homme et des vertebrés. Maloine, Paris

De Zeeuw CI, Wentzel P, Mugnaini E (1993) Fine structure of the dorsal cap of the inferior olive and its GABAergic and non-GABAergic input from the nucleus prepositus hypoglossi in rat and rabbit. J Comp Neurol 327:63–82

De Zeeuw CI, Wylie DR, DiGiorgi PL, Simpson JI (1994) Projections of individual Purkinje cells of identified zones in the flocculus to the vestibular and cerebellar nuclei in the rabbit. J Comp Neurol 349:428–447

Deecke L, Schwarz DWF, Fredrickson JM (1977) Vestibular responses in the rhesus monkey ventroposterior thalamus. II. Vestibulo-proprioceptive convergence at thalamic neurons. Exp Brain Res 30:219–232

Epema AH, Gerrits NM, Voogd J (1988) Commissural and intrinsic connections of the vestibular nuclei in the rabbit: a retrograde labeling study. Exp Brain Res 71:129–146

Epema AH, Gerrits NM, Voogd J (1990) Secondary vestibulocerebellar projections to the flocculus and uvulo-nodular lobule of the rabbit: a study using HRP and double fluorescent tracer techniques. Exp Brain Res 80:72–82

Fagerson MH, Barmack NH (1995) Responses to vertical vestibular stimulation of neurons in the nucleus reticularis gigantocellularis in rabbits. J Neurophysiol 73:2378–2391

Fukushima K (1997) Corticovestibular interactions: anatomy, electrophysiology, and functional considerations. Exp Brain Res 117:1–16

Graf W, McCrea RA, Baker R (1983) Morphology of posterior canal related secondary vestibular neurons in rabbit and cat. Exp Brain Res 52:125–138

Henn V, Young L, Finley C (1974) Vestibular nucleus units in alert monkeys are also influenced by moving visual fields. Brain Res 71:144–149

Hikosaka O, Maeda K (1973) Cervical effects on abducens motoneurons and their interaction with vestibulo-ocular reflex. Exp Brain Res 18:512–530

Ilg UJ, Hoffmann KP (1996) Responses of neurons of the nucleus of the optic tract and the dorsal terminal nucleus of the accessory optic tract in the awake monkey. Eur J Neurosci 8:92–105

Ito JI, Matsuoka I, Sasa M, Takaori S (1985) Commissural and ipsilateral internuclear connection of vestibular nuclear complex of the cat. Brain Res 341:73–81

Kaufmann H, Biaggioni I, Voustianiouk A, Diedrich A, Costa F, Clarke R, Gizzi M, Raphan T, Cohen B (2002) Vestibular control of sympathetic activity – an otolith-sympathetic reflex in humans. Exp Brain Res 143:463–469

Kerman IA, McAllen RM, Yates BJ (2000) Patterning of sympathetic nerve activity in response to vestibular stimulation. Brain Res Bull 53:11–16

Kumoi K, Saito N, Tanaka C (1987) Immunohistochemical localization of g-aminobutyric acid- and aspartate-containing neurons in the guinea pig vestibular nuclei. Brain Res 416:22–23

Lang W, Büttner-Ennever JA, Büttner U (1979) Vestibular projections to the monkey thalamus: an autoradiographic study. Brain Res 177:3–17

Leigh RJ (1994) Human vestibular cortex. Anal Neurol 35:383–384

Lorente de Nó R (1933) Vestibulo-ocular reflex arc. Arch Neurol Psychiatr (Chic) 30:245–291

McCouch GP, Deering ID, Ling TH (1951) Location of receptors for tonic neck reflexes. J Neurophysiol 14:191–196

McCrea RA, Baker R (1985) Anatomical connections of the nucleus prepositus of the cat. J Comp Neurol 237:377–407

Newlands SD, Kevetter GA, Perachio AA (1989) A quantitative study of the vestibular commissures in the gerbil. Brain Res 487:152–157

Nishiike S, Guldin WO, Bäurle J (2000) Corticofugal connections between the cerebral cortex and the vestibular nuclei in the rat. J Comp Neurol 420:363–372

Prihoda M, Hiller MS, Mayr R (1991) Central projections of cervical primary afferent-fibers in the guinea-pig – an Hrp and Wga/Hrp tracer study. J Comp Neurol 308:418–431

Rose PK, Wainwright K, Neuber-Hess M (1992) Connections from the lateral vestibular nucleus to the upper cervical spinal cord of the cat: a study with the anterograde tracer PHA-L. J Comp Neurol 321:312–324

Rossiter CD, Hayden NL, Stocker SD, Yates BJ (1996) Changes in outflow to respiratory pump muscles produced by natural vestibular stimulation. J Neurophysiol 76:3274–3284

Sato F, Sasaki H (1993) Morphological correlations between spontaneously discharging primary vestibular afferents and vestibular nucleus neurons in the cat. J Comp Neurol 333:554–556

Sato H, Ohkawa T, Uchino Y, Wilson VJ (1997) Excitatory connections between neurons of the central cervical nucleus and vestibular neurons in the cat. Exp Brain Res 115:381–386

Shiroyama T, Kayahara T, Yasui Y, Nomura J, Nakano K (1999) Projections of the vestibular nuclei to the thalamus in the rat: a *Phaseolus vulgaris* leucoagglutinin study. J Comp Neurol 407:318–332

Shojaku H, Sato Y, Ikarashi K, Kawasaki T (1987) Topographical distribution of Purkinje cells in the uvula and the nodulus projecting to the vestibular nuclei in cats. Brain Res 416:100–112

Simpson JI, Leonard CS, Soodak RE (1988) The accessory optic-system – analyzer of self-motion. Ann NY Acad Sci 545:170–179

Tabuchi T, Umetani T, Yamadori T (1989) Corticonuclear and corticovestibular projections from the uvula in the albino rat: differential projections from sublobuli of the uvula. Brain Res 492:176–186

Walberg F, Dietrichs E (1988) The interconnection between the vestibular nuclei and the nodulus: a study of reciprocity. Brain Res 449:47–53

Wylie DR, DeZeeuw CI, DiGiorgi PL, Simpson JI (1994) Projections of individual Purkinje-cells of identified zones in the ventral nodulus to the vestibular and cerebellar nuclei in the rabbit. J Comp Neurol 349:448–463