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Foreword to the 3rd Edition

At the outbreak of World War II, Jerzy (George) Olszewski had just returned from the Salpêtrière Hospital, Paris, to his home town Vilnius, then part of Poland, to work in the University Neurology Clinic. As the tides of war changed, Olszewski was forced to work ‘underground’ in a civilian army hospital, where he was relatively safe from enemy search parties. Firm ties between the Polish neurological community at Vilnius and the Vogt Brain Research Institute of Buch-Berlin had been established before the war, through Prof. Maximilian Rose and Prof. Włodzimierz Godłowski, former chairman of the Stefan Batory University, Department for Neurology and Psychiatry. Drawn by these connections, Olszewski wrote to Vogt in 1943, and with incredible luck received an invitation from Vogt, and furthermore the official permission, to go and work as an assistant at Vogt’s Brain Research Institute, which by then had been forced out of Berlin and moved to Neustadt in the Black Forest [Olszewski, 1950; Baxter et al., 1987]. When Jerzy Olszewski arrived in Neustadt from Poland, Cécile and Oskar Vogt welcomed him warmly into their close scientific community [Klatzo, 2002]. As a research project they suggested to him the need for an investigation of the reticular formation of the brainstem, and the first plans for the present atlas Cytoarchitecture of the Human Brainstem were discussed. Due to the general economic difficulties after the war Olszewski emigrated to Canada, and with the help of Dr. Wilder Penfield took up a fellowship that included teaching in the Department of Neuroanatomy at the Montreal Neurological Institute [Klatzo, 2002]. In 1952 he resumed work on the cytoarchitectural subdivisions of the human brainstem, reinforced with the feeling that cytoarchitecture was an important tool for neuropathology. With the help of Donald Baxter and several others, the atlas was published in 1954.

Olszewski and Baxter’s Atlas Cytoarchitecture of the Human Brain Stem has proved to be a unique and useful atlas for over 50 years. One reason for this is that very few atlases consider cytoarchitecture of the brain in such detail. Furthermore, the subdivision of the brainstem reticular formation, and its associated cell groups, was based on very precise and astute observations after many years of experience in the field. These same cytoarchitectural features were found to be recognizable across the whole spectrum of mammalian species. But perhaps the most important reason for the lasting value of the atlas lies in the fact that ‘cytoarchitectural differences reflect functional differences’ – a premise not well established at the time when the atlas was compiled, but it was something that Olszewski firmly believed in, as a student of the ‘Vogt School’. He argues this point carefully in the ‘Introduction’, to convince the reader that the anatomical subdivisions will also provide a key to as yet unrecognized functional areas. That ‘cytoarchitectural differences reflect functional differences’ is a principle accepted now by every neuroanatomist: a cytoarchitectural difference in any nucleus is taken to reflect a functional difference, whether in the red nucleus, vestibular nucleus, or oculomotor nucleus. With a little practise at the microscope, and good histology, it is easy to recognize from which part of the brain a section is taken, just by the cytoarchitectural character of the individual neurons: abducens motoneurons, the mesencephalic trigeminal nucleus, the inferior olive, Purkinje cells, pyramidal cells of the cortex or the omnipause neurons in the pontine reticular formation, all have a very individual and characteristic appearance, and of course different functions.

Since the first edition of this atlas was compiled, neuroscience has progressed a long way, and revealed countless functional areas of the brainstem. In this edition we have combined the cytoarchitectural details of the brainstem nuclei described by Olszewski and Baxter with the current concepts of their function and connectivity. The atlas falls into 2 main parts: 42 plates of low-power views of the brainstem, followed by over a hundred descriptions or chapters of individual nuclei.

In this 3rd edition we have added new drawings and photographs to illustrate the rostral pole of the midbrain, and we have included several ‘new’ chapters to cover more recently recognized nuclei. Each chapter deals with a single nucleus, and starts with the original description of the ‘Location and cytoarchitecture’ from the previous edition. Any editing is indicated by square brackets, [...] indicates the omission of some phrases in the original edition, and [text] indicates the insertion of comments into the first edition manuscript. This is followed by a new section ‘Functional neuroanatomy’, which lays out current views on the function of the nucleus, and a short review of its connections. In addition, a selection of recent references is included to assist the reader in searching the literature for more details.

The order of the chapters in the last part of the book is based on the following global concept of the brainstem. The brainstem and its nuclei have a similar organization throughout vertebrate species. In lower species they form almost the whole brain and can be considered as a complete nervous system, which accomplishes the main aim in life – survival. Higher centers, like the cerebral cortex, hippocampus and amygdala, are, from an evolutionary point of view, later additions that extend and modify the brainstem functions. In order to operate, the brainstem needs afferent inputs or sensory systems, to which the brain responds and then interacts with the environment.
through its motor systems; here, the somatic domain can be differentiated from the visceral domain. The input and output systems are interconnected in the brain by numerous control systems such as the reticular formation – a center for coordination –, or the cerebellum and precerebellar nuclei for motor coordination, or the neuromodulatory nuclei for modulating the intensity of signals, or level setting. Nuclei associated with emotionally relevant information are grouped under limbic relay nuclei, leaving a few brainstem nuclei with an unknown function. In this edition of the atlas, the brainstem nuclei have been grouped into these functional systems, sometimes with difficulty, due to lack of knowledge or because of multifunctional subdivisions (e.g. parvocellular and magnocellular parts of the red nucleus; or substantia nigra, pars compacta and reticulata).

Our special thanks are due to Thomas Karger who created the project, and whose friendly encouragement and patience enabled us to complete this edition. Second, we are extremely grateful to Rita Büttner, and are convinced that without her hard work and loyal persistence this book would not have been finished. Finally the support of our families, in particular Maximillian, Ludwig and Leopold Bochtler, has been greatly appreciated.

Jean A. Büttner-Ennever
Anja K.E. Horn
Munich 2013
Fig. 1. Organization of the brainstem. A schematic drawing of the dorsal aspect (cerebellum removed) to show the general organization of the brainstem cranial nuclei and the reticular formation (cross-hatching). It indicates the main subdivisions of the brainstem – the medulla oblongata, the pons and the mesencephalon – and shows their relationship to the cranial nerve nuclei in humans and the conventional nomenclature. The sensory cranial nerve nuclei are indicated on the left side and the motor nuclei on the right side; the reticular formation is shown on the left side only. The subsequent plates illustrating these nuclei are indicated by arrows. Abbreviations: III = oculomotor nucleus; IV = trochlear nucleus; MesV = mesencephalic trigeminal nucleus; MoV = motor trigeminal nucleus; NIV = trochlear nerve; PrV = principal sensory trigeminal nucleus; SpV = spinal trigeminal nucleus; VI = abducens nucleus; VII = facial nucleus; X = dorsal motor nucleus of the vagus nerve; XI = supraspinal nucleus and spinal accessory nucleus; XII = hypoglossal nucleus.
Plate 22. Semischematic representation of cross-section 1401.

Abbreviations:

- DLPN: Dorsolateral pontine nuclei
- γ: Pontine nuclei, possible subgroups
- GI: Gigantocellular nucleus
- LL: Lateral lemniscus
- LSO: Lateral superior olivary nucleus
- LVN: Lateral vestibular nucleus
- MCP: Medial cerebellar peduncle
- ML: Medial lemniscus
- MLF: Medial longitudinal fascicle
- MSO: Medial superior olivary nucleus
- NRPC: Nucleus reticularis pontis caudalis
- NVI: Abducens nerve
- LVII: Facial nerve
- PCR: Parvocellular reticular nucleus
- POC: Periolivary complex
- RIP: Nucleus raphe interpositus
- SEL: Subependymal layer
- SG: Supragenual nucleus
- SubCv: Nucleus subcoeruleus, ventral part
- SVN: Superior vestibular nucleus
- T5Pv: Spinal trigeminal tract
- VI: Abducens nucleus
- PT: Pyramidal tract
23 Periolivary Complex (POC)

**Original name:**
Nucleus trapezoidalis or nucleus of the trapezoid body

**Subdivisions:**
No subnuclei are evident in the periolivary complex of humans [Moore, 1987]; however, in lower animals over 10 subnuclei have been defined (see below)

**Location and Cytoarchitecture – Original Text**

In man, the periolivary nuclei or complex (POC) is less well developed than in other mammals. The area is composed of small, poorly defined cell groups which lie among the fibers of the trapezoid body, lateral, ventral and medial to the complex of the superior olive and dorsal to the pontine nuclei (PN). The periolivary nuclei are best developed about the caudal half of the superior olivary complex (SOC).

The cells composing the POC are loosely arranged, small to medium sized, triangular or multipolar and possess long dendrites and large, darkly stained Nissl bodies (fig. 1–4). The distinction of these cells from those composing the lateral superior olive may be difficult. However, the cells of the latter are plumper, possess shorter dendrites and more discrete Nissl bodies. The cells of the adjacent PN are larger and more intensely stained than those of the POC. [...] 

**Functional Neuroanatomy**

**Function**
The POC in humans forms a ring of loosely arranged cell groups surrounding the SOC. It contributes ascending and descending pathways to the auditory system, and is the origin of the efferent olivocochlear bundles (OCB). The OCB modulate the discharge rate of cochlear afferent fibers and may, in part, play a role in the olivocochlear reflexes preventing overstimulation of the peripheral neurons. Many different cell types have been identified in the POC of the cat and rat, but a general function has not been recognized [for a review, see Moore, 1987; Heffert and Aschoff, 1997; Schofield, 2005].

**Connections**
The principal connections of the POC are (a) inputs from the posterior part of the ventral cochlear nucleus (VCN), more specifically from the ‘octopus cells’, and (b) efferent projections to the central nucleus of the inferior colliculus (IC), mainly ipsilaterally [Adams, 1983; Schofield and Cant, 1992; Thompson and Schofield, 2000]. The rostral POC is associated with motor neurons of the trigeminal nucleus and supports the middle ear reflex of the tensor tympani muscle, along with the cochlear nuclei; similarly the caudal POC interacts with the facial motor neurons innervating the stapedius muscle [Lee et al., 2006; Jones et al., 2008].

---

Fig. 1. Periolivary complex. Magnification ×150.

Fig. 2–4. Cells from the periolivary complex. Magnification ×1,000.
Periolivary Nuclear Homologues

The periolivary nuclei are named according to their location around the superior olive [Koutcherov et al., 2004]; however, homologues of the nuclei seen in lower mammals are not evident in humans [Moore, 1987, Schmidt et al., 2010]. A region that can be called the medioventral periolivary nucleus in humans may in part represent the homologue of the medial nucleus of the trapezoid body (MNTB) in lower mammals. The MNTB is usually included in the term ‘superior olivary complex’ but in humans its location is not clear, and it appears to be integrated into the POC [Richter et al., 1983]. The MNTB contains glycineric neurons enveloped by the calyces of Held (nucleus No. 24) [Kulesza, 2008]. These neurons are the ‘principal cells’ of the MNTB which send inhibitory signals to the lateral superior olivary nucleus (LSO), while the nonprincipal MNTB cells project to the IC [Schofield, 1994].

A medial region of the human POC is called the dorsomedial periolivary nucleus by Koutcherov et al. [2004]. It is equated with the superior paraolivary nucleus of the rat. The area receives a distinctly different projection from the cochlear nuclei to the medial superior olivary nucleus and LSO, namely inputs from ‘multipolar’ and ‘octopus cell’ groups of the contralateral VCN, and its GABAergic neurons provide a major projection to the ipsilateral IC [Schofield, 2005].

The POC is the source of the OCB, carrying efferents to the cochlea [Adams, 1983]. In general, the cochlea of adult mammals receives two types of efferent innervation: one division is called the medial OCB, which arises from large cells, usually lying in the medial POC, and projecting bilaterally to the type 2 outer hair cells; the second division is the lateral OCB, which arises from small cells and projects ipsilaterally to the type 1 inner hair cells. The OCB cells are strongly cholinergic and have been plotted in humans [Moore and Linthicum, 2004; Koutcherov et al., 2004]. The large ‘medial OCB cells’ lie scattered in several periolivary groups in humans, whereas the smaller ‘lateral OCB cells’ lie mainly dorsally. The efferent medial OCB may be the peripheral part of the descending auditory system, stretching from the cortex to the cochlea, which can enhance selective attention to auditory signals [for a review, see Moore and Linthicum, 2004; Cooper and Guinan, 2006]. The function of the lateral OCB is not known. Guinan [2006] reviews the efferent innervation of the cochlea and its association with otoacoustic emissions (low-level sounds produced in healthy cochlea, that can be measured noninvasively in humans with a sensitive microphone in the ear canal).

References

Fig. 1. Posterior trigeminal nucleus. See plates 22 and 24. DLPN = Dorsolateral pontine nuclei; DRc = dorsal raphe nucleus, caudal part; ML = medial lemniscus; MLF = medial longitudinal fasciculus; NRPC = nucleus reticularis pontis caudalis; NRTP = nucleus reticularis tegmenti pontis; NVII = facial nerve; PCG = pontine central gray; PCR = parvocellular reticular nucleus; PoV = posterior trigeminal nucleus; SEL = subependymal layer; SubCv = nucleus subcoeruleus, ventral part; SVN = superior vestibular nucleus; $\alpha$ = pontine nuclei, possible subgroups. Magnification $\times$40.

Motor Systems – Somatomotor Nuclei

44 Abducens Nucleus (VI)

Original name:
Nucleus nervi abducentis

Alternative names:
Abducens nerve nucleus
Sixth cranial nerve nucleus

Location and Cytoarchitecture – Original Text
The abducens nucleus (VI) is located beneath the facial colliculus in the floor of the midpontine portion of the fourth ventricle. It appears at the level of the oral pole of the facial nucleus (VII), extends orally for approximately 3 mm, and terminates at, or just oral to, the level in which the most caudal cells of the motor trigeminal nucleus appear.
On cross-section, the nucleus forms an ovoid cell group in the dorso-medial portion of the midpontine tegmentum. It is related medially to the medial longitudinal fasciculus (MLF), ventrally to the nucleus reticularis pontis caudalis, and laterally to the parvocellular reticular nucleus. Dorsomedially the nucleus is related to the fibers of the facial genu, and the oral portion of the nucleus is separated from the floor of the fourth ventricle by horizontally coursing facial fibers. A few abducens cells lie among these latter fibers and between them and the ependyma of the ventricular floor. The caudal portion of the nucleus is related dorsally to the suprapontual nucleus.

The cells of the VI, trochlear and principal oculomotor nuclei (III), although similar to those of other somatic motor nuclei, are, in general, more plump, smaller and more lightly stained. Further, their Nissl granules are smaller and less regular (fig. 1–5).

**Functional Neuroanatomy**

**Function**
The VI contains the motoneurons of the ipsilateral lateral rectus muscle (LR), which control the horizontal abduction of the eye. However, the nucleus is not a homogeneous cell population. First, there are at least 2 types of motoneurons, those controlling the twitch muscle fibers and those controlling the nontwitch muscle fibers. The neural activity of nontwitch motoneurons is probably highly tonic [Dieringer and Precht, 1986], but their function is still unclear [Büttner-Ennever, 2006]. One hypothesis suggests that they control the tonic properties of the muscles (e.g. length or stiffness), whereas the twitch fibers drive the eye movements (see below).

Apart from motoneurons, there are 2 other major neuronal populations within the VI; the abducens internuclear neurons (INT), and paramedian tract neurons (PMT cell groups). The INT project to the contralateral medial rectus (MR) subgroup in the III. Their function is to coordinate the activity of the contralateral MR and LR for all horizontal conjugate eye movements (including the vestibulo-ocular reflex, saccades and smooth pursuit). Lesions to the internuclear neurons or their axons in the MLF cause paralysis of the contralateral MR for all horizontal conjugate eye movements, but vergence movements of the MR remain possible.

Finally the cytological boundaries of the rostral VI enclose cell groups which project to the cerebellar flocculus bilaterally. They are part of a continuum of cells called the PMT cell groups (nucleus No. 96), and may be important in the cerebellar control of gaze-holding in the horizontal or vertical plane [Dean and Porrill, 2008]. Experimentally, lesions to the different PMT cell groups close to the VI result in the lack of gaze-holding to the ipsilateral side, or to downbeat nystagmus [Cheron et al., 1992; Nakamagoe et al., 2000; Leigh and Zee, 2006].

**Histochemistry**
The nontwitch motoneurons innervating the orbital muscle layer lie mostly around the boundaries of the VI, medially and dorsally [Büttner-Ennever et al., 2001; Ugolini et al., 2001]. The two motoneuron populations, twitch and nontwitch, can be differentiated using histochemical techniques: both types are cholinergic but only the twitch motoneurons have perineuronal nets [Eberhorn et al., 2005]. The INT are morphologically similar to motoneurons [McCrea et al., 1986], possess perineuronal nets, but they use glutamate and aspartate as transmitter [Nguyen et al., 1999; Nguyen and Spencer, 1999].

**Development**
The site of generation of the VI is in the ventral pons (rhombomere 5), whereas the origin of the VII lies rostrally and dorsally in rhombomere 4. At an early embryological stage the VI migrates dorsally to its adult position in the floor of the fourth ventricle, while the VII migrates medially to the VI, and caudolaterally to rhombomere 6 [Jacobs, 1970; Nieuwenhuys et al., 2008]. It has been suggested that the complex route of the facial nerve and the facial genu result from these migrations. In some animals the migration does not take place and the VI remains in the ventral pons (e.g. goldfish).
Connections

Efferents. The VI is the largest of the extracocular motor nuclei, with two major efferent systems: one through the abducens nerve (NVI) to the lateral rectus muscle, and the second projecting into the contralateral MLF, crossing the midline at the level of the VI and ascending in the MLF to the contralateral III. The VI carries efferents to the ipsilateral LR for abduction of the eye [Sylvestre and Cullen, 2002]; the fibers arise from the twitch motoneurons within the VI, and from the nonwirch motoneurons, whose distribution in the VI is still unclear. Recently the exciting possibility has been raised that the putative sensory receptors of eye muscles, called palisade endings, send their axons centrally in the VI, and their sensory ganglion cells lie close to the nonwirch motoneurons of the VI, and similar results were obtained for the III and oculomotor nerve (NIII) [Lienbacher et al., 2011a, b; Zimmermann et al., 2011]. These results imply that the NVI (and NIII) also carry a sensory component.

The second major efferent pathway from the VI originates from abducens INT which compose about 25–30% of the VI population [Steiger and Büttner-Ennever, 1978]. In monkeys, the neurons lie rostrally, but in humans their location is not clear. The INT efferents cross the midline at the level of the VI and ascend in the MLF to the contralateral III, terminating on the MR subgroups, thereby forming the anatomical basis for conjugate eye movements.

Afferents. The motoneurons and internuclear neurons receive afferents from secondary vestibulo-ocular neurons in the magnocellular region of the medial vestibular nucleus; these are essential for the vestibulo-ocular reflex. For a review on this and subsequent connections see Büttner-Ennever [2006] and Horn and Adamczyk [2012]. Nonsecondary vestibular neurons in the marginal zone and the adjacent parvocellular medial vestibular nucleus also project to the VI: a rostral group targeting the ipsilateral VI and a caudal glycinergic group targeting the contralateral VI [Langer et al., 1986; McFarland et al., 1992]. Less is known about these nonsecondary vestibular inputs. In contrast, the monosynaptic inputs from the pontine reticulotegmental nucleus (nucleus No. 56) and dorsal paragigantocellular nucleus (nucleus No. 55) where the excitatory and inhibitory burst neurons for saccades lie, respectively, have been closely studied [Horn et al., 1995, 1996; Zhou and King, 1998]. Afferents to the VI arise from the prepositus nucleus, from internuclear neurons of the III and the central mesencephalic reticular formation [Langer et al., 1986; Spencer et al., 1989; Lahouji et al., 1995; Büttner-Ennever, 2006; Ugolini et al., 2006]. Finally the superior colliculus has also been shown to project directly to the VI [Izawa et al., 1999].

The twitch and nonwirch motoneurons receive different afferent inputs indicating that they have different functions [Wasaki et al., 2004]. The nonwirch motoneurons of the VI receive monosynaptic inputs from the prepositus nucleus, parvocellular medial vestibular nucleus and the supraoculomotor area along with its adjacent mesencephalic reticular formation.

The PMT cell groups receive collaterals, from all known premotor inputs supplying the abducens motoneurons [Büttner-Ennever et al., 1989; Dean and Porrill, 2008]. However, some PMT groups encode horizontal eye signals and others vertical ones, and the inputs from premotor structures reflect this segregation. Thus, it is rather surprising but understandable, in the nonhuman primate, to find afferent projections from the interstitial nucleus of Cajal and the rostral interstitial nucleus of the MLF terminating in the rostral VI on a vertical PMT cell group [Büttner-Ennever and Horn, 1996].

References

The trochlear nucleus (IV) is located in the tegmentum of the midbrain at the level of the inferior colliculus and consists of 1 large oral cell group and 1 or 2 smaller, more caudally situated groups which lie partially embedded in the dorsal part of the medial longitudinal fasciculus (MLF). Orally, the large cell group is separated from the caudal pole of the oculomotor nucleus (III) by a very narrow cell-free band. All of these features can be clearly demonstrated on sagittal sections (fig. 1).

On cross-section the nucleus is round in outline at all levels and is usually composed of 3–40 cells, depending upon whether components of the MLF, oculomotor, or trochlear cells are included. Dorsally and dorsolaterally the IV and the MLF are related to the dorsal raphe nucleus. The distinction between the oral pole of the IV and the caudal pole of the III may at times be difficult, particularly on cross-sections. [...] The differentiation can usually be made on the basis of the following observations: (a) the IV lies in the MLF; the caudal pole of the III lies on the MLF; (b) trochlear cells do not infiltrate the surrounding MLF; oculomotor cells may be found scattered among and ventral to the fibers of the MLF.

The IV is composed of irregularly arranged plump, multipolar motoneurons similar to those of the III and abducens nucleus (fig. 1–4). Pearson [1943] has observed cells of the type found in the mesencephalic trigeminal nucleus (sensory ganglion-like neurons) along the course of trochlear nerve (NIV) fibers and within the IV.

**Functional Neuroanatomy**

**Function**

The IV gives rise to somatic efferent fibers which provide the motor innervation for the contralateral superior oblique (SO) muscle. The pulling direction of the SO, from the resting position, is downward with an outward rotational component. Lesions of either the IV, or NIV, cause a trochlear palsy, which is quite common. They result in a hypertropia of the affected eye, producing a diplopia which is largest when there is attempted gaze in the ‘down and medial’ quadrant of vision [for a comprehensive review, see Leigh and Zee, 2006]. The contribution of the SO motor units to convergence and counter-rolling during static tilt is not well understood [Mays et al., 1991; Sasaki et al., 1991].

Trochlear motoneurons, like all extraocular motoneuron groups, can be divided into two categories, those that innervate twitch motoneurons and those that innervate nontwitch motoneurons. The function of the nontwitch motoneurons in the dorsal cap of the IV is not clear, but they may participate more in the tonic properties of the SO, in contrast to the twitch motoneurons which are essential for movement of the eye [Büttner-Ennever, 2006].

**Connections**

**Afferents.** The IV motoneurons receive a strong input from the magnocellular regions of the vestibular nuclei via the MLF, which mediate the vertical component of vestibulo-ocular eye movements [Büttner-Ennever, 2006]. The excitatory pathway arises from the magnocellular part of the contralateral medial vestibular nucleus, the inhibitory pathway from the magnocellular part of the superior vestibular nucleus [Goldberg et al., 2012].

The premotor inputs to the IV for vertical and torsional saccadic eye movements arise from the rostral interstitial nucleus of the medial longitudinal fascicle (RIMLF) and the interstitial nucleus of Cajal (INC), whereby the latter is more involved in vertical gaze-holding [Fukushima et al., 1992]. The afferents from the RIMLF are excitatory and predominantly ipsilateral, those from the INC project bilaterally to the IV with the fibers crossing within the posterior commissure. The afferents from the ipsilateral INC are excitatory, and at least a portion of the contralateral afferents are GABAergic [Horn et al., 2003]. Interestingly, the motoneurons of all vertical-pulling eye muscles in the III and IV receive a strong GABAergic input from secondary