BRAIN RESEARCH REVIEWS 67 (2011) 119–146

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BRAIN RESEARCH REVIEWS

Review

The thalamocortical vestibular system in animals and humans

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A R T I C L E I N F O

Article history:
Accepted 30 December 2010
Available online 9 January 2011

Keywords:
Vestibular cortex
Multisensory integration
Neuroimagery
Electrophysiology
Neurology
Caloric and galvanic vestibular stimulation

A B S T R A C T

The vestibular system provides the brain with sensory signals about three-dimensional head rotations and translations. These signals are important for postural and oculomotor control, as well as for spatial and bodily perception and cognition, and they are subtended by pathways running from the vestibular nuclei to the thalamus, cerebellum and the "vestibular cortex." The present review summarizes current knowledge on the anatomy of the thalamocortical vestibular system and discusses data from electrophysiology and neuroanatomy in animals by comparing them with data from neuroimagery and neurology in humans. Multiple thalamic nuclei are involved in vestibular processing, including the ventroposterior complex, the ventroanterior–ventrolateral complex, the intralaminar nuclei and the posterior nuclear group (medial and lateral geniculate nuclei, pulvinar). These nuclei contain multisensory neurons that process and relay vestibular, proprioceptive and visual signals to the vestibular cortex. In non-human primates, the parieto-insular vestibular cortex (PIVC) has been proposed as the core vestibular region. Yet, vestibular responses have also been recorded in the somatosensory cortex (area 2v, 3av), intraparietal sulcus, posterior parietal cortex (area 7), area MST, frontal cortex, cingulum and hippocampus. We analyze the location of the corresponding regions in humans, and especially the human PIVC, by reviewing neuroimaging and clinical work. The widespread vestibular projections to the multimodal human PIVC, somatosensory cortex, area MST, intraparietal sulcus and hippocampus explain the large influence of vestibular signals on self-motion perception, spatial navigation, internal models of gravity, one's body perception and bodily self-consciousness.

Abbreviations: 3aHv, 3a-hand-vestibular area; 3aNv, 3a-neck-vestibular area; ASS, anterior suprasylvian cortex; DVN, descending vestibular nucleus; FEF, frontal eye fields; Ig, insula granularis; IL, intralaminar nuclei; LD, lateral dorsal nucleus; LGN, lateral geniculate nucleus; LP, lateral posterior nucleus; LVN, lateral vestibular nucleus; MGmc, medial geniculate nucleus, *pars magnocellularis*; MGN, medial geniculate nucleus; MIP, medial intraparietal area; MST, medial superior temporal area; MT, middle temporal area; MVN, medial vestibular nucleus; PIVC, parieto-insular vestibular cortex; PO, posterior group of the thalamus; Reipt, area retroinsularis pars parietalis; Ri, area retroinsularis; SGN, suprageniculate nucleus; SVN, superior vestibular nucleus; TPJ, temporo-parietal junction; VA, ventroanterior thalamic nucleus; Vim, *nucleus ventralis intermedius*; VIP, ventral intraparietal area; VL, ventrolateral thalamic nucleus; VP, ventro-posterior thalamus; VPI, ventral posterior inferior nucleus; VPL, ventral posterior lateral nucleus; VPM, ventral posterior medial nucleus; VPP, ventral posterior nucleus, *pars posterior*; VPS, visual posterior sylvian area

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0165-0173/$ – see front matter
doi:10.1016/j.brainresrev.2010.12.002

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1. Introduction

The vestibular system has a unique role in the sensorimotor control and perception. By sensing the angular and linear accelerations, the vestibular system codes three dimensional head movements in space. By sensing gravitational acceleration, the vestibular receptors are also an essential basis for a spatial frame of reference allowing the brain to organize the erected human posture with respect to the ground (Berthoz, 2000). In turn, activation of the vestibular receptors is responsible for many reflexes acting on extraocular muscles devoted to gaze stabilization, as well as reflexes acting on postural muscles devoted to body orientation and stabilization in space (Wilson and Melvill Jones, 1979).

There is increasing evidence that the vestibular system is not only involved in perception, oculomotor and postural control, but also takes part in spatial cognition. In particular, how animals and human navigate in space – i.e. integrate and memorize the paths taken, elaborate and use cognitive maps of the spatial displacements – has been associated with vestibular processing (Berthoz et al., 1995; Mittelstaedt, 1999; Smith et al., 2010). In addition, vestibular signals, and the neural structures involved in vestibular processing, are crucial for distinguishing self-motion and object-motion (Straube and Brandt, 1987), perceiving the world as upright (Brandt and Dieterich, 1994; Lopez et al., 2007; Mittelstaedt, 1999), elaborating an internal model of gravity and of one's body motion (Angelaki et al., 2004; Merfeld et al., 1999), as well as for visual perception related to gravity (Indovina et al., 2005; Lopez et al., 2009). More recent studies conducted in neurological patients even suggested that vestibular signals are crucial for various aspects of one's body perception and awareness (Bottini et al., 1995; Vallar et al., 1993), and more generally for human bodily self-consciousness (Blanke et al., 2002; Lopez et al., 2008).