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Review Article

Brief review of vestibular system anatomy and its higher order projections

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ABSTRACT

The vestibular system is one of the most complex systems of the human brain. A very small peripheral organ in the inner ear, the labyrinth, forms the peripheral receptor. This receptor forms connections with centers at all levels within the central nervous system. These centers in turn, will project back to vestibular structures in the brain stem who will control the geography of the body providing balance and an accuracy in visual movements as well as posture and gait. This review aims to give the readers a brief overview as to what the vestibular system is; its related structures and defined anatomical pathways. ***Neuroanatomy; 2005; 4: 24–27.***

Key words [vestibular system] [anatomy] [review] [connections]

Introduction

The vestibular system provides orientation in three dimensional space, modification of muscle tone and balance [1]. It is essential for the coordination of motor responses, eye movement and posture. However, compared to other sensory modalities, the sense of balance appears to be rather poorly represented in centers of consciousness.

To maintain balance and body posture, there has to be a continuous flow of information about position and movement from every part of the body, including head and eyes. The vestibular system detects motion of the head and maintains stability of images on the fovea of the retina as well as postural control during movements of the head. Signals representing angular and translational motion of the head as well as the tilt of the head relative to gravity are translated by the peripheral vestibular organs in the inner ear. This sensory information is used in turn to control reflexes used for maintaining the stability of the images on the retina during movements of the head. Feedback information from the head and eyes must be independent from each other since the eyes can be fixed on a target when the head is moving [2]. Vestibular information is also important for posture and gait. When vestibular function is normal these reflexes operate with exquisite accuracy and, in the case of eye movements, at very short latencies [3].

The peripheral part of the vestibular system is located in the labyrinth, the inner ear. The vestibule and semicircular canals which are dilations and carvings within the petrous temporal, form a large part of the bony labyrinth. They contain the membranous labyrinth which is similar in shape, but much smaller. Between the bony and membranous labyrinth circulates a fluid called perilymph which in composition is similar to the cerebrospinal fluid. The membranous labyrinth on the other hand is filled with a fluid called endolymph with a high concentration of K^+ and a low concentration of Na^+. The stria vascularis in the cochlear duct and secretory cells in the transitional epithelium surrounding sensory epithelia are probably responsible for the production of endolymph.

The part of the membranous labyrinth related to vestibular function consists of three semicircular ducts (superior, lateral or horizontal, posterior) and the utricle and saccule. Within these structures are areas containing neuroepithelial cells which form the peripheral receptors of the vestibular system.

The Semicircular Ducts

The semicircular ducts open into the utricle. The posterior limbs of the superior and posterior ducts unite before opening into the utricle, thus forming a common limb. One end of each duct is dilated and is called the *ampulla* and epithelial cells here thicken to form the *ampullary crest*. This zone contains neuroepithelial hair cells covered by a gelatinous substance, the *cupula*, which extends to the roof of the ampulla. These receptor cells are innervated by afferent peripheral processes from the vestibular ganglion. Hair cells contain a kinocilium arising from the cytoplasmic surface of the cell and stereocilia, their numbers varying between 40-70. The longest stereocilium is the one nearest to the kinocilium gradually decreasing in length with accordance to their distance to the kinocilium [2]. The semicircular ducts respond to angular acceleration (rotation of the head). When the head is rotated, movement of the endolymph causes displacement of the cupula resulting in deflection of the hair cells. Movement towards the kinocilium depolarizes the hair cells causing stimulation, whereas movement away from the kinocilium hiperpolarizes the hair cell decreasing firing of the afferent fibers [2]. The superior duct of one side lies approximately in the same plane as the posterior of the opposite side forming a functional pair. Similarly, the horizontal ducts of the two sides lie in the same plane again forming a functional pair. Movement of the endolymph on one side will cause excitation of hair cells on same side while inhibiting hair cells of its partner on the opposite side.

The Utricle And Saccule

The utricle and saccule on the other hand are related to static equilibrium (position of the head in space which is very important for the control of posture) and to changes in gravitational forces. Hence they are also sensitive to linear acceleration. Saccular neurons appear to detect vertical acceleration while utricular neurons are sensitive to dorsoventral acceleration and sideways movement. The utricle and saccule also contain an area of neuroepithelial cells, in this instance called the *macula*. Here, hair cells come into contact with a gelatinous substance containing particles of calcium carbonate. This structure is called the *otolithic membrane*. All hair cells have their kinocilium at one end but they are not oriented in the same direction. Hair cells that come from all directions are oriented towards a curved border on the surface of the macula called the *striola*. When the head is bent in any direction a group of cells is stimulated while another group is inhibited, having no effect on yet a different group. This complicated pattern sends accurate messages to the brain related to the position of the head at any given time [2].

Diseases of the labyrinth produce severe symptoms such as vertigo, nausea, vomiting, nystagmus. Following lesions, the static deficits usually disappear in a few days, whereas recuperation of the dynamic, vestibular-related synergies is much slower and merely partial [4].

Vestibular Ganglion [Scarpa's Ganglion]

The vestibular ganglia, one on each side, lie in the lateral part of the internal auditory meatus, near the fundus. The vestibular ganglia contain the cell bodies of afferents innervating the peripheral vestibular apparatus. Each ganglion contains about 20,000 cells [2]. The vestibular ganglion appears to be divided into a superior and inferior part united by an isthmus. Peripheral processes from the superior ganglion innervate the ampullary crests of the superior and lateral semicircular ducts and macula of utricle, while peripheral fibers from the inferior ganglion innervate the macula of the saccule. Some peripheral fibers from the inferior ganglion pass through the singular foramen at the bottom of the internal auditory meatus and innervate the ampullary crest of the posterior semicircular duct [1]. Central processes from the vestibular ganglion form the vestibular nerve. Together with the cochlear nerve, the vestibular nerve courses in the internal auditory meatus as the vestibulocochlear nerve in close relation with the facial nerve and passes through the cerebellopontine angle and enter the pons to terminate in the vestibular nuclear complex. Few fibers however pass directly to the flocculo-nodular lobe of the cerebellum. These fibers coming from the vestibular apparatus to be relayed to the vestibular nuclei or directly to the cerebellum are called *primary vestibular fibers*. The vestibular complex and uvula-nodulus are responsible for the initial processing of vestibular information by the central nervous system [5].

Vestibular Nuclear Complex

The vestibular nuclei lie in the lateral recess of the rhomboid fossa extending from a level rostral to the hypoglossal nucleus to a level slightly above the abducens nucleus. There are four vestibular nuclei: superior, lateral, medial and inferior (descending) vestibular nuclei. The lateral nucleus contains the largest cells and the inferior nucleus has the smallest cells [6]. The vestibular nuclei form two distinct cell columns. The medial vestibular nucleus which is the largest forms the medial cell column while the superior, lateral and inferior vestibular nuclei form the lateral cell column [1]. There is evidence that most of the vestibular nuclei are topographically interconnected through a commissural system. However, commissural connections are not restricted to homologous nuclei [5]. 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 ipsilaterally saccular-sensitive secondary vestibular neurons are inhibited by contralateral saccular stimulation [7]. Interconnections within the vestibular complex have also been shown.

Besides the main vestibular nuclear complex other nuclei related to the vestibular system are present. One is the nucleus prepositus hypoglossi which recieves scarce primary vestibular afferents but has its main input from secondary vestibular projections as well as projections from the flocculo-nodular lobe. Another is the parasolitary nucleus located between the medial vestibular and inferior vestibular nuclei. Two smaller nuclei adjacent to the vestibular complex are thought to have vestibular connections: Nucleus x, lateral to the caudal part of the inferior vestibular nucleus and nucleus z, located rostral to the anterior pole of the nucleus gracilis [5].

Secondary Vestibular Fibers

Secondary vestibular fibers are fibers that arise mainly:

1) from the medial and inferior vestibular nuclei destined for the flocculo-nodular lobe and uvula,

2) from all vestibular nuclei travelling within the medial longitudinal fasciculus to reach cranial nerve motor nuclei innervating extraocular muscles and axial musculature of the neck,

3) from the lateral vestibular nucleus to all spinal levels forming the lateral vestibulospinal tract to regulate extensor muscle tone.

4) Outputs of vestibular nuclei not only evoke reflexes mediated by skeletal muscles, they evoke autonomic reflexes as well. Vestibulo-sympathetic reflexes modulate local changes in blood flow, respiration and heart rate. These reflexes are abolished in lesions of certain parts of the vestibular nuclei in cats. The circuit which induces these vestibulo-autonomic effects, includes projections from the inferior, medial vestibular nuclei and parasolitary nucleus to the solitary nucleus. The solitary nucleus recieves afferents from the heart, oesophagus and stomach, mediated mainly by branches of the glossopharyngeal and vagus nerves. Additionally, stimulation of certain nuclei in the cerebellum causes changes in blood pressure, heart rate and respiration [5].

With all these main projections the vestibular system controls eye movements, reflex postural head and neck movements and balance during stance and gait as well as modulation and modification of autonomic function to maintain homeostasis during changes in body posture. Radtke et al., in their study of vestibulo-autonomic control in man in normal control and labyrithine-defective subjects exposed to abrupt head acceleration, concluded that a delayed increase of heart rate in response to postural challenge occurred in patients with vestibular loss. These authors postulated that this condition could be the reason of the autonomic distress experienced by these patients [8].

It is a fact that the vestibular system is a complex system involving not only the posterior labyrinth and cerebellum but also central structures such as striatum, thalamus, frontal and prefrontal cortex to assure balance, movements and gait. Information reaching the vestibular system are not purely vestibular but also from visual and somatosensory origins. Equilibrium is equally a complex physiological function needing harmony of vestibular, visual and somatosensory information together with an integrity of the central nervous system [9].

Vestibular projections to higher order neurons appear to be very complex and not very clearly defined. However some connections of the vestibular system with these higher centers have been established.

Vestibular Projections To Thalamus

Vestibular projections to the thalamus originate from the rostral part of the vestibular nuclear complex and are destined to the VPL (ventral posterolateral), VPM (ventral posteromedial) and VPI (ventral posteroinferior) nuclei (ventrobasal thalamus). Neurons in the ventrobasal nuclei respond to stimulation of deep proprioceptors and joint receptors as well as vestibular inputs [1, 5].

Vestibular-hippocampal Interactions

The hippocampus is thought to be important for spatial representation processes that depend on the integration of both self-movement and allocentric cues. The vestibular system is an important source of self-movement information that may contribute to this spatial representation [10]. This system contributes to spatial information processing and the development of spatial memory in the hippocampus. Anatomical studies have suggested that various parts of the thalamus are likely to transmit vestibular information to the hippocampus perhaps via the parietal cortex; however, it is possible that more direct pathways exist. In recent years, electrophysiological studies have shown that vestibular stimulation affects cells in the anterior thalamic nuclei and the hippocampus. These studies demonstrate the importance of vestibular-hippocampal interaction for hippocampal function but also suggests that the hippocampus may be an important site for compensation of vestibular function following peripheral or central vestibular lesions [11].

Does A Vestibular Cortex Exist?

Different areas of the primate cortex have been named ‘vestibular’. Guldin and Gurusser [12] have defined in three different primate series the existence of a vestibular cortical system. Based on the verification of their study in three different species of primates, they postulate that a similar pattern exists in the human.

There is considerable evidence from studies on cats and monkeys that several cortical areas such as area 2v at the tip of the intraparietal sulcus, area 3av in the central sulcus, the parietoinsular vestibular cortex next to the posterior insula (PIVC) and area 7 in the inferior parietal lobule are involved in the processing of vestibular information.

Recordings from these areas have shown that:

1) these cortical neurons are connected to the vestibular labyrinth,

2) they receive converging vestibular, visual and somatosensory inputs.

In humans, positron emission tomography (PET) scans and functional magnetic resonance imaging (fMRI) have shown these data to be correct [13].

It is stated by some authors that vestibular thalamo-cortical projections end in areas 3av and T3, parietal visual cortex and parietoisular cortex. These areas in humans are involved mainly in percieving both verticality and self-motion [14]. Humans with damage to parietal cortex do not recognize true vertical. Deprived of surrounding visual cues, they cannot align a disk with a line on it so that the line has a true vertical orientation [5]. Corticofugal connections in the macaque monkey where cortical vestibular areas project back to vestibular nuclei have been shown [15].

Vestibular System And Aging

Falling and loss of balance among the geriatric population is a frequent and serious problem. The reason has been attributed to the progressive deterioration of the anatomical components of the vestibular system. In a study investigating quantitative differences in the number, density or types of hair cells or the length of the crista ampullaris in young and aged gerbils, no difference was found, suggesting that the cause of vestibular dysfunction during aging should be looked for elsewhere [16]. On the other hand, a study regarding age-related change in the number of neurons in the human vestibular ganglion, proved that age-related decline in primary neurons existed, providing an anatomical basis for the increased incidence of imbalance seen with age [17].

Another interesting finding is that although the auditory and vestibular apparatus are closely related anatomically, age-related changes are not correlated. In the same individual, the two systems may age at different rates [18].

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