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HISTORICAL NOTE

Perspective on the Vestibular Cortex Throughout History

JORGE EDUARDO DUQUE-PARRA

The human vestibular organ transmits sensory information to various components of the central nervous system related to head movement and, obviously, among these components, to its terminal region(s) in the vestibular parts of the cerebral cortex. Study of vestibular structures dates back to historical epochs when primitive considerations on cerebral global function were made without knowledge of a cerebral cortical region related to vestibular function. At the time of Menière in the 19th century, patients with vertigo were defined as having cerebral congestion. Cerebral mapping and computational anatomy in the 20th century significantly expanded our knowledge of cerebral structure and its function and the concept of cerebral processing of a variety of types of information, including that generated by the vestibular system. These modern techniques include nuclear magnetic resonance imaging, functional magnetic resonance imaging, and positron emission tomography. These techniques have allowed researchers to define the cortical representation of the vestibular system in human beings and in other species, a representation generally assumed to be located in various cerebral temporal and parietal regions. Although vestibular activation has been recorded in frontal lobe regions, the main vestibular cortical zone has been defined as being located in the parietal lobe; others have recognized a vestibular cortical function in the insula. ***Anat Rec (Part B: New Anat) 280B: 15–19, 2004.*** **© 2004 Wiley-Liss, Inc.**

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VESTIBULAR BRAIN THROUGH THE AGES

The human vestibular organ is a component of the inner ear, located at both sides of the head, in the temporal petrous bone. Its main function is to transmit sensory information related to head movement to various components of the central nervous system (Duque-Parra, 2003). Among the more important of these central targets within the neuroaxis are the vestibular nuclei, the thalamus, and the vestibular cerebral cortex. Early studies of the vestibular cortex date back to historical epochs when very primitive considerations about the global cerebral function were made. The study of this cortical structure appeared to be more direct than the study of its functions (Rains, 2004). Nevertheless, in ancient times the point of departure for the evaluation of the ideas about the cerebral areas that processed vestibular information was initially clinical assessments, without establishing a specific cerebral correlation. It is also important to consider the possible ancestral knowledge about the existence of vertiginous processes associated with the inner ear and the relationship of the inner ear with the loss of balance (Duque-Parra, 2003). Accordingly, there are references to vertigo episodes recorded in Roman times (Jay, 2000) and in the 19th century, before Menière. It was thought that vertigo was a cerebral symptom similar to epilepsy fits (Baloh, 2000). These records favor the conceptualization about some part of the brain being specifically related to vestibular dysfunction.

Dr. Duque-Parra is Professor of Neuroanatomy in the Program of Medicine, Department of Basic Sciences, University of Caldas, and Professor of Physiology in the Programs of Dentistry and Physical Therapy, Autonoma University of Manizales, Manizales, Colombia. He also has a position in the Division of Neuroscience, Pablo de Olavide University, Seville, Spain
*Correspondence to: Jorge Eduardo Duque-Parra, Cra 9C No 7A-48, Programa de Medicina, Departamento de Ciencias Básicas, Universidad de Caldas, Manizales, Colombia. E-mail: jorgedp@telesat.com.co

As neuroanatomic knowledge was very limited in the course of some epochs throughout history due to the prohibitions about human dissection existing in certain cultures at certain times, it was impossible to establish a direct and specific relationship about what part of the brain was associated with vestibular processing. With Erasistratus of Chios (304–250 B.C.), a first approach of vestibular processing from a global perspective was presented, as he made observations about the brain and supposed that the senses were located in the brain (Soubiran and De Kearney, 1997). Although they were not associated directly with balance, it is feasible to suppose that this sense was taken into account at that time, for the cardinal vestibular sense was more broadly studied (Baker, 1999), although superficially, by authors of the period.

In the second century, Claudius Galen stated that cerebral convolutions did not play an important role in any kind of cerebral activity (Smith, 1986), but Erasistratus had already highlighted the influence they had on intellectual development. It is also important to note that the convolutions were described as being more numerous in humans than in the rest of the animal kingdom (Soubiran and De Kearney, 1997)—an aspect not considered by Galen—as the result from multiple dissections carried out in various animal species (Falconí Villagómez, 1961; Seara Valero, 1995), such as dogs, pigs, goats, and monkeys, especially on Macaque monkeys (Seara Valero, 1995). Some centuries later, the Amsterdam anatomy professor Frederik Ruysch (1628–1731) pointed out that the cerebral cortical substance was not glandular as some anatomists had stated, for the convolutions were considered as mechanisms with the aim to protect the delicate cortex blood vessels. Thomas Willis described them as "spirals of the thin intestine," as suggested initially by Erasistratus (Gross, 1999). Thomas Willis (1621–1675) focused his attention on the cortex gray matter. For him, the functions of the cerebral convolutions were to store sensory impressions and to allow these impressions to be recalled on certain occasions (Finger, 1994; Marshall and Magoun, 1998). No corticovestibular approximations were done at this time as the cerebral study focused on other aspects.

The way functional neuroanatomical problems had been approached at this time ranged progressively from a somewhat philosophical speculation to reality. The differences between the vestibular and the cochlear nerves were established in the 18th century, as they were considered only one nerve prior to that time. It was necessary to wait one more century for a full understanding of the role that convolutions played in balance and not in hearing (Duque-Parra, 2004). It is therefore understandable why the early literature did not report specific brain areas as being responsible for vestibular functions. However, the concept that the patterns and organization of convolutions may relate more directly to particular functions was strengthened by 19th-century scholars such as Vicq d'Azyr in France and Felix Fontana in Italy (Marshall and Magoun, 1998). The interest focusing on cerebral convolutions at that time evolved and reached its highest point with the phrenologists (Canguilhmen, 1997; Duque-Parra and Angulo García, 2001). Their exaggerated points of view, especially those of Franz Joseph Gall and the German neuroanatomist Spurzheim in the 19th century (Canguilhmen, 1997), suggested that some cortical areas were responsible for some mental attributes (Smith, 1986; Springer and Deutch, 1998; Duque-Parra and Angulo García, 2001). Historically, the oldest data suggesting localization of human cerebral function comes from subjects with injuries caused by disease or trauma (Savoy, 2001). Gall basically initiated the concept of cerebral localization (Wong-Riley, 2000) when he proposed, for the first time, that the brain was not a uniform mass (Kandel et al., 1997) and that various mental faculties may be localized in different parts of the brain (Kandel et al., 1997; Wong-Riley, 2000). As time progressed, and this general concept matured, a specific cortical relationship with the vestibular organ would evolve.

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The basic idea of different functions controlled by different regions in the brain attracted the attention of Jean Baptiste Bouillaud, a French professor of medicine who stated that Gall was correct when he localized articulated language in the frontal lobe. This fact was corroborated in a meeting of the Anthropological Society of Paris in 1861, when Ernest Auburtin confirmed Bouillaud's postulate that the center that controlled articulated language was located in the frontal lobes. His observations had an impact on the young surgeon Pierre Paul Broca (1824–1880), who documented eight cases in which an injury in the left frontal lobe had affected the production of language and proposed that the expression of language was controlled mainly by the cortex of the inferior frontal gyrus located on the left side (Wong-Riley, 2000). At the end of the 1820s, before Broca, the French physiologist Pierre Jean Marie Flourens concluded that specific behaviors did not depend exclusively on specific regions of the encephalon when he extirpated, in animals, some encephalon functional centers that had been identified by Gall (Kandel et al., 1997). Flourens also stated that he had discovered the brain regions that controlled, among others, the voluntary movements and the visual and auditory reflexes associated with vestibulo-ocular reflexes (Carlson, 1996). This brilliant and excellent physician identified parts of the brain endowed with specific functions, although he affirmed that sensations were equally represented throughout the whole cortex (Marshall and Magoun, 1998).

Although the knowledge of a corticovestibular relationship did not basically exist, it was possible to infer it from clinical observations due to the fact that symptoms of vertigo had been recognized for thousands of years and had been documented by the pioneering clinical descriptions of Prosper Menière in the middle of the 19th century. In more recent times, Hallpike and Cairns made the initial clinicopathological correlation with hydrops of the labyrinth in 1938 (Baloh, 1999). It was considered then, since Menière's time, that vertigo could result from a damage to the inner ear, although before that time, patients with vertigo defined themselves as having cerebral congestion (Baloh, 2000), a state in which some cortical region was implicated. In this same century, Luigi Rolando provided a description of the general patterns of the cerebral convolutions, although his description was not as precise as that available for other organs. This may have been due to the relatively inaccessible location of the brain in the skull, difficulties of fixation/preservation, and distortion of the brain during dissection (Rains, 2004). Although in the Middle Ages specimens were fixed with aromatic substances, spices, resins, etc., this had no practi-

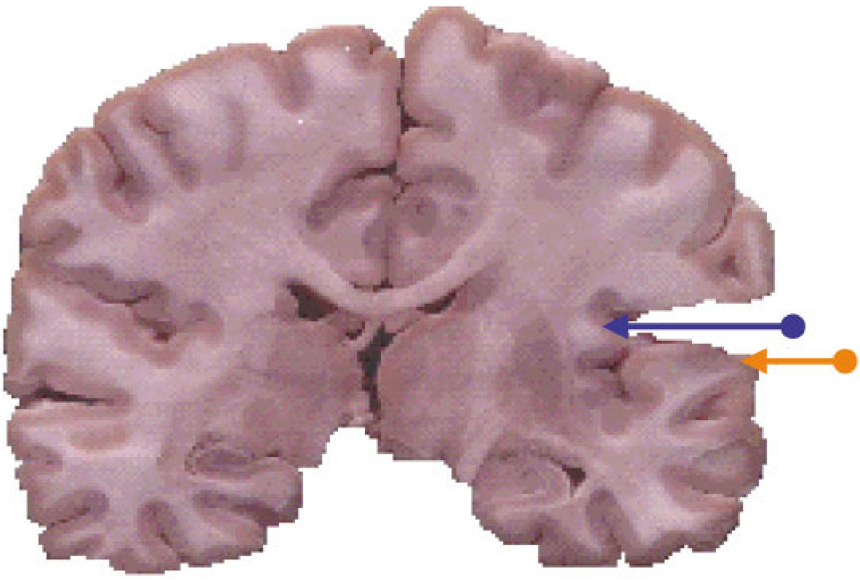

Figure 1. Coronal section of human brain when the cortical area near lateral sulcus has been removed to see the insula (dark arrow) and temporal lobe (light arrow) related to vestibular function. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

cal value in the fixation and conservation of tissues. Later, mercury bichloride or sublimate and then alcohols were used with comparatively good success. After the discovery of formic aldehyde by the German chemist August Wilhelm von Hoffmann in 1868, it was possible to prepare formalin, a watery solution, generally processed at 10%, which was used in preparations for anatomic conservation to prevent excessive hardening of tissues and for yielding little tissue distortion (Kleiss and Simonsberger, 1964; García Del Moral, 1993), but the use of this aldehyde started only in 1893 (Sholl, 1962).

MORPHOLOGICAL AND FUNCTIONAL TECHNIQUES

The morphological fixation techniques produced excellent anatomical preservation and provided outstanding morphological information, but did not provide information concerning function. It was necessary to wait until the 20th century to count on Allan MacLead Cormack and Sir Godfrey N. Hounsfield's studies, winners of the physiology and medicine Nobel prizes in 1979 (Hernández, 2003), to explore in vivo cerebral structures departing from the limitations of traditional radiological explorations. The studies initiated by Cormack and Hounsfield gave rise to subsequent research and the rise of the modern method of brain imaging known as CT. It thus created the first prototype for cerebral exploration that permitted us to analyze layers of several millimeters of thickness, which represented very fine and defined neuroanatomic sections, thus resulting in the development of computerized axial tomography. This development broadened cerebral mapping and computational anatomy in the 20th century and has significantly strengthened the ability to analyze cerebral structure and function (Toga and Thompson, 2001), including those cerebral centers associated with balance and equilibrium. Other types of imagery advances followed, such as nuclear magnetic resonance imaging (MRI), developed by Paul C. Lauterbur and Peter Mansfield, the 2003 Nobel prize winners. The rapid advance of this technique (Toga and Thompson, 2001), an indispensable tool in clinical diagnosis, has become available for experimental research, thus providing information about tissue physiological parameters (Beckmann et al., 2001). After MRI, there followed functional magnetic resonance (fMRI) and positron emission tomography (PET), both being techniques based on neuronal activity. When many neurons in a region of the brain increase their firing, the local flow of blood to that cerebral region is then increased (Zeineh et al., 2001).

In human beings, the cortical representation of the vestibular system is commonly assumed to be located in distinct parietal and temporal regions of the brain (Figure 1), although the vestibular activation has been recorded in regions of the frontal lobe. In fact, PET has provided results indicating a frontal area involvement in vestibular function. Vertigo induction through direct stimulation, or epileptic activity, permits one to draw a functional conclusion—anatomic correlation—as it was reported in the case of a boy who experienced epileptic vertigo, generated near an astrocytoma located in the left middle frontal gyrus. This tumor constituted a locus for the generation of vertigo and is one bit of evidence for vestibular processing in the human frontal lobe (Kluge et al., 2000). It is also important to take into account Gregory's classical example: if one removes a resistor from a radio and it squawks, this does not mean that the resistor is a squawk suppressor (Kosslyn et al., 1999), although nowadays the cerebral functioning is compared with a social organization and not with a complex machine (Rains, 2004).

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VESTIBULAR CORTICAL ZONES

The zone located in the parietal lobe, between the junction of intraparietal and ascending parietal sulci, has also been considered a main vestibular cortical receptive area. This has a functional implication, for that region of the somatosensory cortex participates in the conscious appreciation of the position of the body (Williams et al., 1998). With respect to this region, it has been demonstrated in monkeys that the neurons in the lateral intraparietal area encode the localization of visual stimuli and the direction of saccades (Toth and Assad, 2002) as directly related to the vestibular system. It is also known that the cortical areas related to the vestibular apparatus vary in their anatomical localization according to the phylogenetic scale. In the most primitive mammals, the cortical area that receives these signals is located in the sensory motor region corresponding to the representation of the limbs. In the higher mammals (Escudero Gonzáles and Delgado García, 1999), including humans, the cortical area is located in the temporal lobes that deal with balance (Bucy, 1967), specifically within the superior temporal convolution. Studies on evolution suggest that the vestibulocortical area tends to migrate from somatosensory areas to the associative parietal cortex and is less associated with auditory signals but more with proprioreceptive input. This is confirmed with the record of intraparietal vestibular neurons that were activated by head movements, which suggests their role as vestibulocortical neurons that function as an interface between the sensory and motor cortex and that associate with the formation of motor planning as well as with representations of the vestibular space (Klam and Graf, 2003).

Studies with monkeys have demonstrated that posterior temporal and frontal regions receive vestibular afferents (Cascino et al., 1997). In addition to general concepts concerning these vestibulocortical regions, it is also known that the insula plays an important role in the vestibular function (Naidich et al., 2004) and it has also been established that the parieto-insular cortex is also associated with vestibular function (Figure 1). In some animals, this seems to be a main relay center for the processing of vestibular information. Similar to the vestibular nuclei, this vestibulocortical area is multisensory: two-thirds of the neurons in this area respond to vestibular stimulation and the remaining one-third responds principally to somatosensory stimulation from the neck and shoulders. Almost all of the neurons that respond to vestibular stimulation also become activated by movements from the visual environment and from somatosensory stimulation. Vestibular receptors are not only movement sensors, they are also immobility sensors and have a basic discharge whose need of variation is interpreted as immobility by the brain. The properties of the vestibular system, i.e., the rotation detection by the semicircular canals and the translation detection by otoliths, are dissociated sensations at the receptor level that are reconstructed in the brain with complex codes necessary for perception and action (Berthoz, 2000).

Indirect evidence of a vestibular cortical area appeared early in history, but it remained for the technological developments of the 20th century to make possible important discoveries confirming this function of the cerebral cortex.

CONCLUSION

As can be seen in the above abbreviated consideration, indirect evidence of a vestibular cortical area appeared early in history, but it remained for the technological developments of the 20th century to make possible important discoveries confirming this function of the cerebral cortex. Although various regions of the cerebral cortex have been implicated in this function, the frontotemporoparietoinsular region best fits the definition of a cortical area with vestibular functions. Maybe Pierre Jean Marie Flourens's perspective, although lacking a detailed experimental basis, would have led him to consider cerebral vestibular function as a global function due to the involvement of at least four of the five main lobes of the brain. Detailed experimentation in the years to come may lead us to recognize this cerebral specific zone as a multisensory substrate for vestibular corticalization.

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