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THE PHYSIOLOGY OF BALANCE

The vestibular system is the sensory apparatus of the inner ear that helps the body maintain its postural equilibrium. The information furnished by the vestibular system is also essential for coordinating the position of the head and the movement of the eyes. There are two sets of end organs in the inner ear, or labyrinth: the semi-circular canals, which respond to rotational movements (angular acceleration); and the utricle and saccule within the vestibule, which respond to changes in the position of the head with respect to gravity (linear acceleration). The information these organs deliver is proprioceptive in character, dealing with events within the body itself, rather than exteroceptive, dealing with events outside the body, as in the case of the responses of the cochlea to sound. Functionally these organs are closely related to the cerebellum and to the reflex centres of the spinal cord and brainstem that govern the movements of the eyes, neck, and limbs.

In vertebrates, the utricular maculae in the inner ear contain an otolithic membrane and otoconia (particles of calcium carbonate) that bend hair cells in the direction of gravity. This response to gravitational pull helps animals maintain their sense of balance. The cristae of the semi-circular ducts, which form one of the two sensory organs of balance (the second being the maculae of the utricle and saccule), respond to rotational movements and are involved in dynamic equilibrium. In vertebrates the utricular maculae in the inner ear contain an otolithic membrane and otoconia (particles of calcium carbonate) that bend hair cells in the direction of gravity. This response to gravitational pull helps animals maintain their sense of balance.

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Although the vestibular organs and the cochlea are derived embryologically from the same formation, the otic vesicle, their association in the inner ear seems to be a matter more of convenience than of necessity. From both the developmental and the structural point of view, the kinship of the vestibular organs with the lateral line system of the fish is readily apparent. The lateral line system is made up of a series of small sense organs located in the skin of the head and along the sides of the body of fishes. Each organ contains a crista, sensory hair cells, and a cupula, as found in the ampullae of the semi-circular ducts. The cristae respond to waterborne vibrations and to pressure changes.

There are assumptions that the entire inner ear, including the vestibular apparatus, is devoted to hearing. They were impressed by the orientation of the semi-circular canals, which lie in three planes more or less perpendicular to one another, and believed that the canals must be designed for localizing a source of sound in space. The first investigator to present evidence that the vestibular labyrinth is the organ of equilibrium was French experimental neurologist Marie-Jean-Pierre Flourens, who in 1824 reported a series of experiments in which he had observed abnormal head movements in pigeons after he had cut each of the semi-circular canals in turn. The plane of the movements was always the same as that of the injured canal. Hearing was not affected when he cut the nerve fibres to these organs, but it was abolished when he cut those to the basilar papilla (the bird’s uncoiled cochlea). The semi-circular canals were recognized as sense organs specifically concerned with the movements and position of the head.

Because the three semi-circular canals—superior, posterior, and horizontal—are positioned at right angles to one another, they are able to detect movements in three-dimensional space. When the head begins to rotate in any direction, the inertia of the endolymph causes it to lag behind, exerting pressure that deflects the cupula in the opposite direction. This deflection stimulates the hair cells by bending their stereocilia in the opposite direction. German physiologist Friedrich Goltz formulated the “hydrostatic concept” in 1870 to explain the working of the semi-circular canals. He postulated that the canals are stimulated by the weight of the fluid they contain, the pressure it exerts varying with the head position. In 1873 Austrian scientists Ernst Mach and Josef Breuer and Scottish chemist Crum Brown, working independently, proposed the “hydrodynamic concept,” which held that head movements cause a flow of endolymph in the canals and that the canals are then stimulated by the fluid movements or pressure changes. German physiologist J.R. Ewald showed that the compression of the horizontal canal in a pigeon by a small pneumatic hammer causes endolymph movement toward the crista and turning of the head and eyes toward the opposite side. Decompression reverses both the direction of endolymph movement and the turning of the head and eyes. The hydrodynamic concept was proved correct by later investigators who followed the path of a droplet of oil that was injected into the semi-circular canal of a live fish. At the start of rotation in the plane of the canal, the cupula was deflected in the direction opposite to that of the movement and then returned slowly to its resting position. At the end of rotation it was deflected again, this time in the same direction as the rotation, and then returned once more to its upright stationary position. These deflections resulted from the inertia of the endolymph, which lags behind at the start of rotation and continues its motion after the head has ceased to rotate. The slow return is a function of the elasticity of the cupula itself.

These opposing deflections of the cupula affect the vestibular nerve in different ways, which have been demonstrated in experiments involving the labyrinth removed from a cartilaginous fish. The labyrinth, which remained active for some time after its removal from the animal, was used to record vestibular nerve impulses arising from one of the ampullar cristae. When the labyrinth was at rest there was a slow, continuous, spontaneous discharge of nerve impulses, which was increased by rotation in one direction and decreased by rotation in the other. In other words, the level of excitation rose or fell depending on the direction of rotation.

The deflection of the cupula excites the hair cells by bending the cilia atop them: deflection in one direction depolarizes the cells; deflection in the other direction hyperpolarizes them. Electron-microscopic studies have shown how this polarization occurs. The hair bundles in the cristae are oriented along the axis of each canal. For example, each hair cell of the horizontal canals has its kinocilium facing toward the utricle, whereas each hair cell of the superior canals has its kinocilium facing away from the utricle. In the horizontal canals, deflection of the cupula toward the utricle—i.e., bending of the stereocilia toward the kinocilium—depolarizes the hair cells and increases the rate of discharge. Deflection away from the utricle causes hyperpolarization and decreases the rate of discharge. In superior canals these effects are reversed.

The gravity receptors that respond to linear acceleration of the head are the maculae of the utricle and saccule. The left and right utricular maculae are in the same, approximately horizontal, plane and, because of this position, are more useful in providing information about the position of the head and its side-to-side tilts when a person is in an upright position. The saccular maculae are in parallel vertical planes and probably respond more to forward and backward tilts of the head.

Both pairs of maculae are stimulated by shearing forces between the otolithic membrane and the cilia of the hair cells beneath it. The otolithic membrane is covered with a mass of minute crystals of calcite (otoconia), which add to the membrane’s weight and increase the shearing forces set up in response to a slight displacement when the head is tilted. The hair bundles of the macular hair cells are arranged in a particular pattern—facing toward (in the utricle) or away from (in the saccule) a curving midline—that allows detection of all possible head positions. These sensory organs, particularly the utricle, have an important role in the righting reflexes and in reflex control of the muscles of the legs, trunk, and neck that keep the body in an upright position. The role of the saccule is less completely understood. Some investigators have suggested that it is responsive to vibration as well as to linear acceleration of the head in the sagittal (fore and aft) plane. Of the two receptors, the utricle appears to be the dominant partner. There is evidence that the mammalian saccule may even retain traces of its sensitivity to sound inherited from the fishes, in which it is the organ of hearing.