Question 1: How is the conduction of sound to the cochlea facilitated by the ossicles of the middle ear?

Answer: Sound waves traveling through air move the tympanic membrane, which, in turn, moves the ossicles. These transfer the movement of the tympanic membrane to the oval window, and the movement at the oval window vibrates the fluid in the cochlea. However, the fluid in the inner ear resists movement more than air does, so greater pressure is needed to vibrate the fluid. The ossicles amplify the pressure. The surface area of the oval window is smaller than that of the tympanic membrane, and the force is greater at the oval window than at the tympanic membrane because the ossicles act as levers. Because of these two mechanisms, the pressure at the oval window is about 20 times greater than the pressure at the tympanic membrane. This increase in pressure is sufficient to move the fluid in the inner ear. The movement of fluid in the cochlea causes a response in sensory neurons.

Question 2: Why is the round window crucial for the function of the cochlea? What would happen to hearing if it suddenly didn't exist?

Answer: The round window is a membrane located at the base of the cochlea. When the ossicles move the membrane that covers the oval window, the inward movement at the oval window pushes the perilymph into the scala vestibuli. This increases the fluid pressure on the oval window, pushing the membrane at the round window outward. A complementary motion at the round window accompanies any motion at the oval window. This movement is crucial because the cochlea is filled with incompressible fluid held in a solid bony container. If it were absent, the fluid in the cochlea would not move in response to pressure at the oval window and the auditory receptors would not be stimulated.

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Question 3: Why is it impossible to predict the frequency of a sound wave simply by looking at which portion of the basilar membrane is the most deformed?

Answer: Frequency must be coded in some way other than the site of maximal activation in tonotopic maps for two reasons. First, tonotopic maps in the central auditory pathways do not contain neurons with low characteristic frequencies — below 200 Hz — so there must be some other way to distinguish them. Second, something other than tonotopy is needed because the region of the basilar membrane maximally displaced by sound depends on its intensity and frequency. At a fixed frequency, a more intense sound produces maximal deformation at a point further up the basilar membrane than a less intense sound does.

Question 4: Why would the transduction process in hair cells fail if the stereocilia as well as the hair cell bodies were surrounded by perilymph?

Answer: Endolymph, which is similar to intracellular fluid, surrounds stereocilia and hair cell bodies. It has a high K^+ concentration and a low Na^+ concentration. The high K^+ concentration is responsible for a K^+ equilibrium potential of 0 mV. As a result, when K^+ channels open, hair cells depolarize, moving toward the equilibrium potential of K^+, which is 0 mV. In contrast, neurons, which have a K^+ equilibrium potential of –80 mV, hyperpolarize when K^+ channels open. Perilymph has an ionic concentration similar to CSF, which is low K^+ and high Na^+. If perilymph surrounds the stereocilia and hair cell bodies, hair cells will not depolarize when K^+ channels open.

Question 5: If inner hair cells are primarily responsible for hearing, what is the function of outer hair cells?

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Answer: Outer hair cells amplify the movement of the basilar membrane during low-intensity sound stimuli. They are cochlear amplifiers. The key to this function is the action of motor proteins in the membranes of outer hair cells. The motor proteins change the lengths of the outer hair cells. This changes the physical relationship between cochlear membranes, which causes the stereocilia on the inner hair cells to bend more, increasing the transduction process and producing a greater response in the auditory nerve. This mechanism causes about a 100-fold increase in the peak movement of the basilar membrane.

Question 6: Why doesn't unilateral damage to the inferior colliculus or MGN lead to deafness in the ear?

Answer: Each auditory nerve projects to the dorsal and ventral cochlear nuclei on the ipsilateral side, so cochlear neurons listen to only one ear. On the other hand, cells in the ventral cochlear nucleus project to the superior olive on both sides of the brain stem. As a result, olivary neurons hear from both ears. The first binaural neurons in the auditory pathway are found at the level of the superior olive. This is in contrast to the visual system, where the first binocular neurons are found in the visual cortex of the occipital lobe. Binaural olivary neurons project to the inferior colliculus, which projects to the medial geniculate, so each structure hears from both ears. Because of the early convergence of input from both ears, only the destruction of cochlear nuclei can cause unilateral deafness.

Question 7: What mechanisms function to localize sound in the horizontal and vertical planes?

Answer: Horizontal sound localization results from two mechanisms: interaural time delay and interaural intensity difference. For example, if the sound source is on the right, sound reaches the right ear sooner than it reaches the left ear. Specialized neurons in the brain stem detect

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this interaural delay. Comparing continuous tones localizes them when the same phase of the sound wave reaches each ear. The second mechanism, interaural intensity difference, localizes high, continuous frequencies of 2,000-20,000 Hz. The head casts a sound shadow that alters the intensity of sound in each ear, depending on its origin. The resulting difference in sound intensity localizes sound. Neurons in the superior olive are sensitive to interaural delays. Vertical localization depends on the sweeping curves of the outer ear, which are essential for assessing the elevation of a source of sound. Bumps and ridges produce reflections of entering sound, and the delays between the direct path and the reflected path change as a sound source moves vertically. The combination of direct and reflected sound is different for different elevations. High-frequency sounds also enter the auditory canal more effectively when they come from an elevated source.

Question 8: What symptoms would you expect to see in a person who had recently had a stroke affecting A1 unilaterally? How does the severity of these symptoms compare with the effects of a unilateral stroke involving V1?

Answer: Lesions of the auditory cortex are less severe than lesions of the visual cortex. The main symptom of a stroke affecting the A1 unilaterally is the inability to localize the source of a sound. It is possible to detect the side from which the sound is coming but not its precise location. In contrast, a unilateral lesion of the visual cortex produces complete blindness in the part of the visual field corresponding to the site of the lesion.

Question 9: What is the difference between nerve deafness and conduction deafness?

Answer: Nerve deafness is caused by the loss of neurons in the auditory nerve or the loss of hair cells in the cochlea. Tumors affecting the inner ear and specific drugs, such as quinine and

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some antibiotics, may cause nerve deafness. Explosions and loud music can also cause nerve deafness. A disturbance of sound from the outer ear to the cochlea causes conduction deafness. This deficit may be due to simple problems, such as excessive wax in the ear, or serious problems, such as rupture of the tympanic membrane or pathology of the ossicles.

Question 10: Each macula contains hair cells with kinocilia arranged in all directions. What is the advantage of this as compared to an arrangement with all cells in the same direction?

Answer: Each macula contains enough hair cells to cover a full range of directions. The direction preferences of hair cells vary in a systematic way. When the head moves, the mirror image orientation of the saccule and utricle on either side of the head excites some hair cells, inhibits others, and has no effect on the rest. The central nervous system can clearly interpret all possible linear movement. If the arrangement of hair cells is in the same direction, a slight movement of the head may excite all hair cells.

Question 11: Imagine a semicircular canal rotating in two different ways, around its axis — like a rolling coin, or end-over-end — like a flipped coin. How well would its hair cells respond in each case, and why?

Answer: When the semicircular canal rotates around its axis, the wall of the semicircular canal and the cupula begins to spin but the endolymph remains behind because of inertia. The endolymph exerts force on the cupula. The cupula bows, which bends the cilia. This bending either excites or inhibits the release of neurotransmitters from the hair cells on to the vestibular nerve axons, depending on the direction of rotation. When the semicircular canal is flipped end-over-end, the hair cells do not bend right or left and do not respond as a result.

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However, this type of motion corresponds to rotation around the axis of another semicircular canal, which would register the movement for the vestibular system.

Question 12: How would you expect the functions of otolith organs and semicircular canals to change in the weightless environment of space?

Answer: Otolith organs detect the force of gravity and the tilt of the head. Semicircular canals are sensitive to the rotation of the head. In the weightless environment of space, the lack of gravity might hinder the functioning of the otolith organs that help detect the force of gravity.

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