**Instructor’s Manual**

to accompany

*The Mind’s Machine*, Fourth Edition

Watson • Breedlove

**Chapter 6: Hearing, Balance, Taste, and Smell**

**OVERVIEW OF THIS CHAPTER**

Each organism is equipped to sample only those fractions of physical reality that mattered to its evolutionary ancestors. Chapter 6 presents details of the general functioning of four senses that are ubiquitous, at least among the more complex vertebrates, while acknowledging that their exact form and function vary somewhat in different animals. For each sense, the mechanisms of transduction are explored, and the CNS targets of this information are discussed. In addition, classical psychophysics and recent experimental data are blended to highlight the performance characteristics of each system. Lastly, discussion turns to the theories of information processing that seek to explain the manner in which sensory information may be encoded both within and between individual afferent projections. By the conclusion of this chapter, the student is well prepared to tackle the remaining major topic in sensory processing—the visual system (Chapter 7).

**CHAPTER OUTLINE**

Introduction: Hold the Phone

**6.1 Hearing: Pressure Waves in the Air Are Perceived as Sound**

BOX 6.1: *The Basics of Sound*

The external ear captures, focuses, and filters sound

The middle ear concentrates sound energies

The cochlea converts vibrational energy into neural activity

RESEARCHERS AT WORK: *Georg von Békésy and the cochlear wave*

The hair cells transduce movements of the basilar membrane into electrical signals

Auditory signals run from cochlea to cortex

*How’s It Going?*

**6.2 Specialized Neural Systems Extract Information from Auditory Signals**

The pitch of sounds is encoded in two complementary ways

Brainstem systems compare the ears to localize sounds

The auditory cortex processes complex sound

**6.3 Hearing Loss Is a Widespread Problem**

SIGNS & SYMPTOMS: *Restoring Auditory Stimulation in Deafness*

*How’s It Going?*

**6.4 Balance: The Inner Ear Senses the Position and Movement of the Head**

Some forms of vestibular excitation produce motion sickness

*How’s It Going?*

**6.5 Taste: Chemicals in Foods Are Perceived as Tastes**

Tastes excite specialized receptor cells on the tongue

The five basic tastes are signaled by specific sensors on taste cells

The information is transmitted to several parts of the brain

*How’s It Going?*

**6.6 Smell: Chemicals in the Air Elicit Odor Sensations**

The sense of smell starts with receptor neurons in the nose

Olfactory information projects from the olfactory bulbs to several brain regions

Many vertebrates possess a vomeronasal system

*How’s It Going?*

**THE ROAD AHEAD (Learning Objectives)**

**6.1 Hearing: Pressure Waves in the Air Are Perceived as Sound**

**6.1.1** Explain how the external ear and middle ear capture and concentrate sound energy and convey it to the inner ear.

**6.1.2** Sketch the anatomy of the middle and inner ears, highlighting the location of sensorineural components.

**6.1.3** Explain how vibrations travel through the cochlea and how they are converted into neural activity.

**6.1.4** Describe the process by which the organ of Corti encodes the frequencies of sounds.

**6.1.5** Summarize the neural projections between the cochlea and brain.

**6.1.6** Identify the principal auditory pathways and structures of the brain, and describe the integration of signals from the left and right ears.

**6.1.7** Describe the orderly map of frequencies found at each level of the auditory system.

**6.2 Specialized Neural Systems Extract Information from Auditory Signals**

**6.2.1** Explain the relationship between frequency and pitch, and discuss the ranges of frequencies perceived by humans and other species.

**6.2.2** Describe the two major ways in which frequency information is encoded.

**6.2.3** Explain the principal features of sound that the nervous system uses for sound localization.

**6.2.4** Discuss the functions of auditory cortex, from an ecological perspective.

**6.2.5** Evaluate the importance of experience in the development and tuning of the auditory system, throughout the life span.

**6.2.6** Describe the relationship between musical experience and the development of auditory competencies in music and other domains.

**6.3 Hearing Loss Is a Widespread Problem**

**6.3.1** Define and distinguish between hearing loss and deafness.

**6.3.2** Describe and contrast the three major categories of hearing loss.

**6.3.3** Identify potential harmful noise intensities, and discuss the ways in which noise damages the auditory system.

**6.3.4** Summarize and evaluate methods for treating each form of hearing loss.

**6.4 Balance: The Inner Ear Senses the Position and Movement of the Head**

**6.4.1** Describe the anatomical features of the vestibular system.

**6.4.2** Explain how accelerations and changes in the position of the head are transduced into sequences of action potentials.

**6.4.3** Describe the vestibular projections to the brainstem, and summarize the functional importance of these projections.

**6.4.4** Discuss some of the consequences of vestibular dysfunction or abnormal vestibular stimulation.

**6.5 Taste: Chemicals in Foods Are Perceived as Tastes**

**6.5.1** Describe the structure, function, and distribution of the papillae on the tongue.

**6.5.2** Summarize the structure of taste buds, and discuss their relationship to papillae.

**6.5.3** Describe the basic tastes and the distribution of taste sensitivity across the surface of the tongue.

**6.6 Smell: Chemicals in the Air Elicit Odor Sensations**

**6.6.1** Describe the main structures of the olfactory system, with a focus on the cells and projections of the olfactory epithelium.

**6.6.2** Explain the process of olfactory transduction, and discuss the function and variety of olfactory receptors that have been discovered.

**6.6.3** Trace the projection route of olfactory information, and main olfactory structures, from the olfactory epithelium to the cortex.

**6.6.4** Compare and contrast human olfactory capabilities with those of other species.

**6.6.5** Describe the structure and function of the vomeronasal system, and weigh the evidence for and against the idea that humans detect pheromones.

**KEY CONCEPTS**

1. The auditory system is adapted to capture vibratory energy traveling in air (or other appropriate medium) at varying frequencies and amplitudes. The sensitivity of a species’ auditory system has been shaped by natural selection to emphasize the frequency range that is important to the ecology of that species.

2. The external ears (pinnae) capture and process sound energy and guide it into the auditory canal. The placement and (in some species) the motility of the pinnae aid in sound localization.

3. Vibratory energy is captured and amplified by the tympanic membrane and ossicles, which then focus the energy on the oval window of the fluid-filled cochlea. This system is modulated by tiny muscles of the middle ear, under the control of the brain.

4. Movement of the oval window establishes traveling waves that cause the basilar membrane to ripple, with the location of the greatest basilar membrane response corresponding to the frequency of the traveling wave.

5. In the organ of Corti, atop the basilar membrane, hair cells release neurotransmitter when movement of the basilar membrane causes their stereocilia to sway. Fibers leading away from inner hair cells (IHCs) transmit neural impulses that give rise to sound perception and make up most of the auditory part of the eighth cranial nerve. Fibers from outer hair cells (OHCs) convey information about movement of the basilar membrane and do not give rise to conscious percepts. Efferent fibers leading to IHCs modulate sound transmission; OHC efferents alter the length of OHCs, allowing the brain to actively sharpen the basilar membrane’s mechanical properties.

6. When the stereocilia sway, cation channels open, and the resultant depolarization of the hair cell causes calcium channels in the base of the hair cell to open, leading to transmitter release.

7. Tuning of auditory inputs is sharpened through the convergence of auditory inputs on neurons at higher levels of the nervous system.

8. Auditory projections course from the cochlea to the cochlear and superior olivary nuclei of the brainstem, at which level the first binaural processing is evident. From there, projections converge on the inferior colliculi, then the medial geniculate nuclei of the thalamus, and finally to the auditory cortex. A tonotopic organization of the projections is maintained throughout. Most mammals seem to have several cortical auditory fields, and humans exhibit auditory mechanisms unique to speech processing.

9. Pitch may be encoded either by the location of the basilar membrane that is maximally displaced (place coding) or by the frequency of neural impulses generated in response to a stimulus (temporal coding). In practice, the auditory system relies on both coding processes to encode pitch.

10. Experiences with sound stimuli in early life can alter the response properties of the auditory system in later life. This is exemplified by studies with language distinction in newborns and early musical exposure. Plasticity in the adult auditory system is also evident.

11. Disorders of any level of the auditory system may cause hearing impairments. In conduction deafness, mechanical defects of the middle ear prevent the transmission of kinetic energy to the cochlea. In sensorineural deafness, cochlear damage such as the loss of hair cells may impede the transduction of kinetic energy into neural impulses. In central deafness, damage to auditory pathways or auditory cortex may produce any of a wide variety of hearing disorders, such as word deafness.

12. Brainstem systems compare the intensity and latency differences between ears to localize sounds

13. Treatments for hearing loss continue to be developed. Cochlear implants directly stimulate the auditory nerve and are especially useful in verbal language acquisition. Research shows that hair cell regeneration can be stimulated in vertebrates, including rats; such research provides hope for future treatments for deafness.

14. The vestibular apparatus is made up of the semicircular canals, which detect angular acceleration in a particular direction, and the saccule and utricle, which detect the static position and linear accelerations of the head.

15. Vestibular stimuli are transduced by hair cells (distinct from cochlear hair cells); in the case of the semicircular canal, the hair cells are contained within ampullae at the bases of the semicircular canals.

16. Vestibular system afferents form the vestibular part of the eighth cranial nerve. These projections synapse in the vestibular nuclei of the brainstem, from which projections travel to numerous targets concerned with the control of movements (cerebellum, thalamus, and cerebral cortex).

17. Abnormal activation of the vestibular system produces motion sickness. Sensory conflict theory suggests that the mismatch between visual and vestibular signals under some circumstances provokes motion sickness, but recent research suggests that that motion sickness results from postural instability rather than sensory conflict.

18. Taste buds are collections of taste cells studded with receptor proteins located in the sides of papillae of the tongue.

19. We are sensitive to five tastes. Salty tastes are produced by the entry of Na+ ions into taste cells, and sour tastes arise from H+ ions. Sweet and bitter tastes are more complex and are mediated by metabotropic receptors on taste cells. Bitter tastes are biologically important because they often signal toxins. The fifth taste, umami (meaty/savory tastes), is detected by two kinds of receptors. The first probably involves a variant of the glutamate receptor and the second a combination of T1R1 and T1R3 receptor proteins.

20. Each taste axon carries information about more than one taste; consequently, taste discrimination involves higher-level processing across numerous inputs. All parts of the tongue are sensitive to all five tastes.

21. Taste projection fibers are contained in several cranial nerves. Taste information is conveyed first to the brainstem and then to the thalamus and the somatosensory cortex.

22. Humans can possibly discriminate 1 trillion odors. Other species that have a higher dependence on olfactory signals have olfactory systems that are much more sensitive.

23. The 6 million olfactory receptor neurons of the human are contained within the olfactory epithelium lining the nasal cavity. Additional cells include supporting cells and basal cells. Olfactory neurons that die can be replaced by basal cells that differentiate into neurons. Olfactory neurons extend cilia into the olfactory mucosa and project very fine unmyelinated axons that contact glomeruli with the olfactory bulbs.

24. The cilia of olfactory neurons are studded with specialized odorant receptor molecules; the human genome contains hundreds of genes for different receptors, all of which employ a particular G protein for signal transduction.

25. Outputs from the olfactory system are transmitted directly to prepyriform cortex, the amygdala, and the hypothalamus, and then processed by other brain regions.

26. The vomeronasal system is a complementary olfactory system specializing in the detection of pheromones. Evidence suggests that although this system is vestigial in humans, we may nonetheless be sensitive to certain pheromonal cues via trace amine-associated receptors (TAARs) embedded in the main olfactory epithelium. Further research is needed, however.

**REFERENCES FOR LECTURE DEVELOPMENT**

***Books and Articles***

Beauchamp, G. K., Bartoshuk, L., and Carterette, E. C. (1997). *Tasting and smelling: Handbook of perception and cognition*. San Diego, CA: Academic Press.

Buck, L. B. (1996). Information coding in the vertebrate olfactory system. *Annual Review of Neuroscience*, 19: 517–545.

Burkey, J. M., and Daniels, R. L. (2015). *The hearing loss guide: Useful information and advice for patients and families*. New Haven, CT: Yale University Press.

Evans, C., and Stoddart, M. (2003). *Vomeronasal chemoreception in vertebrates: A study of the second nose*. London: Imperial College Press.

Fernández, L., Breinbauer, H. A., and Delano, P. H. (2015). Vertigo and dizziness in the elderly. *Frontiers in Neurology*, 6: 144.

Finger, T. E., Silver, W. L., and Restrepo, D. (Eds.). (2000). *The neurobiology of taste and smell* (2nd ed.). New York: Wiley-Liss.

Furman, J., Cass, S., and Whitney, S. (2010). *Vestibular Disorders: A Case Study Approach to Diagnosis and Treatment* (3rd ed.). New York: Oxford University Press.

Hayden, S., and Teeling, E. C. (2014). The molecular biology of vertebrate olfaction. *Anatomical Record*, 297: 2216–2226.

Hildebrand, J. G., and Shepard, G. M. (1997). Mechanisms of olfactory discrimination: Converging evidence for common principles across phyla. *Annual Review of Neuroscience*, 20: 595–631.

Jiang, Y., and Matsunami, H. (2015). Mammalian odorant receptors: Functional evolution and variation. *Current Opinion in Neurobiology*, 34:54–60.

Liman, E. R., Zhang, Y. V., and Montell, C. (2014). Peripheral coding of taste. *Neuron*, 81(5): 984–1000.

Müller, U., and Barr-Gillespie, P. G. (2015). New treatment options for hearing loss. *Nature Reviews, Drug Discovery*, 14: 346–365.

Musiek, F. E. and Baran, J. A. (2018). *The Auditory System: Anatomy, Physiology, and Clinical Correlates* (2nd ed.). San Diego, CA: Plural Publishing.

Rouby, C., et al. (Eds.). (2002). *Olfaction, taste, and cognition*.Cambridge, UK: Cambridge University Press.

Small, D. M. (2012). Flavor is in the brain. *Physiology and behavior*, 107: 540–552.

Wiest, G. (2015). The origins of vestibular science. *Annals of the New York Academy of Science*, 1343: 1–9.

***Online Resources***

[National Institute of Deafness and Other Communication Disorders (NIDCD)](http://www.nidcd.nih.gov) (Part of the National Institutes of Health)

Information on auditory conditions and disorders, including current research on them.

[Ménière’s Society](http://www.menieres.org.uk/)

Information and support for Ménière’s disease, a long-term disease that affects balance and hearing.

[Association for Chemoreception Sciences (AChemS)](http://www.achems.org)

Recent advances in chemical senses research and directory of chemosensory researchers.

[Monell Chemical Senses Center](http://www.monell.org/)

Dedicated to research on taste and smell, the Monell Center’s website provides information about their current research and fact sheets/primers on the chemical senses.

[Tour the Tongue (NOVA, PBS)](http://www.pbs.org/wgbh/nova/body/tongue-taste.html)

How does our sense of taste work, and why did it evolve?

[The mystery of motion sickness – Rose Eveleth (Ted-Ed)](https://ed.ted.com/lessons/the-mystery-of-motion-sickness-rose-eveleth)

Ted-Ed feature discussing motion sickness.

[How do we smell? – Rose Eveleth (Ted-Ed)](https://ed.ted.com/lessons/how-do-we-smell-rose-eveleth)

Ted-Ed feature discussing the olfactory system.

**ANIMATIONS & VIDEOS**

***Companion Website Animations & Videos***

**Video 6.1 Inside the Ear**

This video is a 3D animated reconstruction of the structures of the human ear and the process of detecting and encoding audio stimuli. Sound waves are followed form their arrival at the outer ear through to their encoding as nerve impulses.

*Textbook Reference*: Introduction: Hold the Phone

**Animation 6.2 Brain Explorer**

The Brain Explorer allows students to review the brain regions relevant to the structures and processes discussed in each chapter, with descriptions, in both surface and cross-sectional views.

*Textbook Reference*: Hearing: Pressure Waves in the Air Are Perceived as Sound

**Animation 6.3 Sound Transduction**

*Textbook Reference*: Hearing: Pressure Waves in the Air Are Perceived as Sound

**Animation 6.4 Mapping Auditory Frequencies**

*Textbook Reference*: Hearing: Pressure Waves in the Air Are Perceived as Sound

**Animation 6.5 The Vestibular System**

*Textbook Reference*: Balance: The Inner Ear Senses the Position and Movement of the Head

**Animation 6.6 The Human Olfactory System**

*Textbook Reference*: Smell: Chemicals in the Air Elicit Odor Sensations

**KEY TERMS**

amplitude

ampulla

amusia

basilar membrane

central deafness

cochlea

cochlear implant

cochlear nuclei

conduction deafness

cortical deafness

deafness

decibel (dB)

ear canal

flavor

frequency

fundamental

glomerulus

gustatory system

hair cell

harmonic

hearing loss

hertz (Hz)

inferior colliculi

infrasound

inner ear

inner hair cell (IHC)

interaural intensity difference (IID)

interaural temporal difference (ITD)

medial geniculate nucleus

middle ear

motion sickness

odor

olfaction

olfactory bulb

olfactory epithelium

organ of Corti

ossicles

outer hair cell (OHC)

oval window

papilla

pheromone

pinna

place coding theory

primary auditory cortex

pure tone

scala media

scala tympani

scala vestibuli

semicircular canal

sensorineural deafness

spectral filtering

stereocilium

superior olivary nucleus

T1R

T2R

taste

taste bud

tectorial membrane

temporal coding theory

timbre

tinnitus

tonotopic organization

trace amine–associated receptor (TAAR)

transduction

tympanic membrane

ultrasound

umami

vestibular nuclei

vestibular system

vestibulocochlear nerve

vomeronasal organ (VNO)

word deafness