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4 Sensation and Perception

Linda M. Bartoshuk

Any account of the history of sensation and perception must rely on the classic *Sensation and Perception in the History of Experimental Psychology* written by Edwin Boring (1886–1968) in 1942 as a companion piece to his monumental *History of Experimental Psychology* (Boring, 1929). Boring began with philosophy (“knowledge comes to the mind through the avenues of the senses”), took us through the Fall of Rome and the preservation of science by way of Arabic scholars, and led us through the labs of the nineteenth century that pioneered sensory physiology and psychology. This chapter relies on Boring’s book but updates and extends his observations and corrects a rare error of Boring’s that led to a decades-long myth about taste.

Sensation

Greek Philosophers

The identification of the Greek philosopher Thales (624–546 BCE) as breaking with the ancient tradition of explaining natural phenomena in terms of the supernatural is credited to Aristotle (Lloyd, 1970). Thales did not accept mythological explanations for natural phenomena but rather looked for explanations within the natural world.

Many of the Greek philosophers after Thales wrote about sensory experience. Unfortunately, only fragments remain of much of that work. The Greek philosophers we know best are Socrates (470–399 BCE), Plato (427–347 BCE), and Aristotle (384–322 BCE). Socrates’s contributions survive from accounts of him written by Plato, his student. Plato founded his Academy in Athens in about 387 BCE. The Academy was modest by modern standards; it was essentially a gathering of scholars outside the walls of the city. Importantly, it is known to have included women.

Aristotle, a pupil of Plato, tutored Alexander the Great. Aristotle commented on earlier scholars as well as providing his own observations in *De Anima (On the Soul)* and *De Sensu et Sensibilibus (On Sense and the Sensible)*. Theophrastus, a student of Plato and colleague of Aristotle, in his *De Sensibus (On the Senses)* also described and criticized the work of earlier scholars. Translations and discussions of the sensory ideas of these

Greek philosophers have been provided by Beare (1906) and Stratton (1917).

Some of the ideas of the Greek philosophers survived for a considerable time. In particular, one prominent idea was the suggestion that our senses provide an accurate picture of the world around us. For example, Empedocles (490–430 BCE) argued that objects give off effluences that enter pores in sensory organs. These effluences vary such that they can only enter a sense organ if they are the correct size and shape. This hints at a direct correspondence between an object and the sensation it generates; however, this is disputed by modern neuroscience. We now know that the peripheral and central nervous systems can alter information considerably while processing it.

Understanding of the nervous system was initially impaired because human dissections were culturally unacceptable to the ancients (dead bodies were thought to be a source of pollution) although animal dissections were not. However, Herophilus (335–280 BCE) and Erasistratus (304–250 BCE) did dissect human cadavers. Why? Heinrich von Staden, a classical scholar who is an authority on ancient science, argues that these two lived in Alexandria, a center of scientific learning where innovation and new philosophical thinking made human dissection culturally acceptable for a time. Herophilus and Erasistratus were the last to dissect humans for centuries, possibly because of the emergence of a new view of medical thought. Among other arguments, alterations due to death were said to alter the body and so make dissections useless. This new view of medicine concentrated on analyzing texts from the past and criticizing the views of earlier authors rather than doing original work (Von Staden, 1992).

Aristotle considered the study of animals crucial to the study of nature and he performed animal dissections. We associate Aristotle with the five senses (vision, audition, olfaction, taste, touch), but he actually believed in four; he included all the skin senses (touch, temperature, pain) as part of touch and included taste as part of touch as well since taste substances touch the tongue (Beare, 1906). Before Aristotle, Democritus (460–370 BCE) had argued for differences among the “atomic shapes” that make up taste stimuli. For example, he described sweet atoms as “round and large,” while bitter atoms were “small, smooth, and spherical . . . with hooks attached.” This is reminiscent of modern theories of sweet and bitter based on molecular structure.

Aristotle’s commentaries include observations that still fascinate psychologists. For example, he described a tactile illusion:

If we cross the fingers, one object placed between them so as to touch both their adjacent surfaces appears as if two. (Beare, 1906, p. 201)

This illusion is still discussed today (e.g., see Rogers-Ramachandran & Ramachandran, 2008; Tinazzi et al., 2013). In another example, Aristotle argued that there are two kinds of odors. One kind relates to foods:

Animals find the odour of food pleasant when they have an appetite for the food itself. When they are satisfied and want no more food, they cease to feel the odour of it pleasant. . . . But there is a different class, viz. that of

odours which are per se agreeable or disagreeable, as for example, those of flowers. . . . These latter odours are perceptible to man, and man only, as agreeable or disagreeable. Other animals perceive only those of the former kind. (Beare, 1906, p. 156)

Modern experts argue about whether or not all pleasure from olfaction is learned. Aristotle's observations hint that floral odors may not require learning but produce innate pleasure.

Theories of sensation among the Greek philosophers attempted to link the senses to the four elements (fire, water, air, earth) that were thought to make up all of nature, but there was considerable argument among them about how to do this. For example, as early as Alcmaeon (fifth century BCE), it was known that pressing on the eyeball produced a sensation of light. This led Alcmaeon to argue that the eye contained fire that played a role in how visual impressions entered the eye. The eye was also known to contain water and air, so others incorporated these into their theories of vision.

With regard to taste and smell, the Greeks made an error that was to reverberate for centuries. To them, food in the mouth stimulated taste and flavor. Inhaling odors from the environment stimulated smell. In reality, inhalation explains only part of olfactory experience; volatiles (gaseous compounds) emitted by odorous objects are inhaled with air and produce olfactory sensations. This is what we commonly call smell (orthonasal olfaction to be technical). However, the Greek observers did not realize that the volatiles in foods are released in the mouth by chewing. Those volatiles travel up behind the palate and into the nose from the rear. The modern term for this is "retronasal olfaction." Retronasal olfaction is responsible for flavor; taste and flavor are actually very distinct. Since this was unknown at the time, the Greeks attributed the retronasal olfactory sensations to the tongue. This mistake was not corrected until 1812 when William Prout (1785–1850), who was to become a famous physician but was then a medical student, wrote an anonymous essay (Prout, 1812). W. H. Brock, a historian of chemistry, identified Prout as the mysterious author of the essay (Brock, 1967).

Fall of the Roman Empire, and Arabic Scholarship during the Middle Ages

Galen (129–c. 200 CE), a Greek physician who lived during the early part of the Roman Empire, dissected animals; as already noted, human dissection was culturally unacceptable at that time. He believed that dissection of the Barbary macaque monkey would provide information sufficiently similar to humans to be useful. He knew that nerves originated from the brain rather than the heart (as Aristotle believed). However, he believed that nerves were hollow tubes through which spirits moved.

As the Roman Empire declined, scientific thought transferred to Arabic scholars who translated the contributions of the Greeks and Romans but also translated works from India and China. All of these traditions informed their original work. Avicenna (980–1037), one of the most important scholars of that

age, wrote *The Canon of Medicine*. This text was used in universities up to the sixteenth century. An example of Avicenna's challenges to Galen is his treatment of pain. Galen argued that injuries were the only source of pain. Avicenna extended this to include changes in organs as well as injuries and described 15 types of pain with terminology that modern authorities (Tashani & Johnson, 2010) describe as similar to those in the McGill Pain Questionnaire (Melzack, 1983).

Reemergence of Human Dissections: The Beginnings of Sensory Anatomy and Physiology

Andreas Vesalius (1514–1564), a Flemish anatomist and physician, is considered to be the founder of modern human anatomy. He dissected human cadavers and his *De Human Corporis Fabrica*, published in 1543, was considered to be revolutionary in its accurate depictions of human anatomy. Interestingly, some of his contemporaries argued that any differences between the anatomy of Galen and that of Vesalius must mean that human anatomy had changed during the intervening years. Such an attitude is hard to imagine today. However, the progress in anatomy notwithstanding, the idea that nerve signaling depended on electricity was still a couple of centuries away.

Luigi Galvani (1737–1798), who discovered animal electricity, studied medicine and philosophy at the University of Bologna. He is famous for his (accidental) observation that an electric spark caused the leg muscles of a frog to twitch. Galvani used a variety of methods to produce the electric spark, but perhaps the most dramatic was lightning. He attached the nerve of a fresh frog corpse to a metal wire pointed to the sky during a thunderstorm. When lightning struck, the frog's leg twitched. This is said to have inspired the scene in Mary Shelley's famous novel where Doctor Frankenstein used lightning to animate his monster (J. P. Johnson, 2011).

Nineteenth-Century Sensory Physiology: The German Labs

By the nineteenth century, the spinal nerves were known to consist of thirty-one pairs (right and left) that branched off the spine and connected with specific parts of the body. The twelve paired cranial nerves were known to connect the brain with sensory organs. However, there was an important new discovery, dating to 1810, in a self-published book by Charles Bell (1774–1842). Each spinal nerve had two roots: one sensory and one motor. Francois Magendie (1783–1855) discovered this independently in 1822 without knowing of Bell's work. This discovery was not only of great importance for the study of sensation but also produced an acrimonious controversy over who was to get credit (e.g., see Berkowitz, 2014). Rather than declare Bell or Magendie the sole victor, the discovery is now called the Bell–Magendie law.

Johannes Müller (1801–1858) is the father of the doctrine of specific nerve energies. Müller was a physiologist. In 1826 he argued that sensory quality is

determined by the pathway by which the sensation is produced. Thus, no matter how you stimulate a sensory nerve, the experience is always the sensory quality typical for that nerve. One of the examples of this is the same phenomenon that the Greek philosophers used to argue for fire in the eye. Gently press your closed right eye near your nose; you will see a light on the upper right of your visual field. Another example: stimulate your tongue with an anodal electrical current and you will taste sour. Incidentally, Müller did not believe that the speed of a neural signal could be measured with typical lab apparatus because he believed it would be near the speed of light.

Hermann von Helmholtz (1821–1894) was interested in physics, but he initially trained as a surgeon since this training was free thanks to the army, and Helmholtz's family was not wealthy (Westheimer, 1983). Yet his interests motivated his research and he made very important contributions to the analyses of vision and audition. His breadth allowed him to examine the physics of the stimuli as well as the manner in which the physical energy was transduced by the sense organ. Helmholtz is credited with defining "modality" as "a class of sensations connected by qualitative continua" (Boring, 1942). In vision, colors fall along a wavelength continuum; in audition, sounds of different pitches fall along a frequency continuum. But what about touch, taste, and olfaction?

Incidentally, in 1850 Helmholtz first measured the speed of conduction of a nerve impulse using a frog. Helmholtz dissected the frog muscle with its sensory nerve attached. As we know from Galvani, shocking the nerve caused the muscle to contract. Helmholtz measured the conduction velocity of the nerve impulse by measuring the time the muscle took to contract when the nerve was stimulated in two different places. The difference in time between the two measures divided by the length of nerve between the two points gave the velocity. The value was about 25 metres (83 feet) per second, much slower than the speed of light.

The Emergence of Psychology

Wilhelm Wundt (1832–1920), called the first psychologist, studied briefly with Müller and then became an assistant to Helmholtz. Wundt founded the first laboratory devoted to psychology at Leipzig in 1879 and founded the journal *Philosophische Studien* in 1891. The last two volumes of that journal contained a Festschrift for Wundt's 70th birthday. The American contributors (Angell, Cattell, Judd, Scripture, Pace) show the influence of Wundt on American psychology.

Two students of Helmholtz (Wundt and Holmgren, a Swedish physiologist) in turn produced two students (Kiesow and Öhrwall, respectively) who debated whether or not taste was a modality. Öhrwall concluded that the classic four basic tastes are actually four separate modalities because they do not fall on a continuum. Kiesow argued that taste qualities are analogous to colors because there are taste phenomena that are analogous to color phenomena (e.g., contrast) and so taste should be considered a modality. In fact, Öhrwall made the

better argument, but Kiesow won, and we now consider taste a single modality. Kiesow's views found their way into psychology textbooks, possibly because so many early textbooks were written by psychologists who visited Wundt's lab in Leipzig.

In Boring's summary of important research contributions, he gave particular attention to the work of another of Wundt's students, David, P. Hänig (Hänig, 1901). Hänig, just as Kiesow, worked on the sense of taste. Hänig measured taste thresholds around the perimeter of the tongue. He was looking for different distributions for the thresholds of the four basic tastes. In that era, such a result would have been evidence for different physiological processes underlying the four tastes. Although this seems obvious to us today, it was not obvious in 1901. Hänig published the thresholds he measured in tables in *Philosophische Studien*. For some reason, Boring decided to plot Hänig's data, but he made a peculiar decision. Rather than plot the thresholds, he plotted their reciprocals (1/threshold) and labeled the results "sensitivity." In Hänig's tables, the thresholds for sweet were lowest on the tip of the tongue and for bitter were lowest on the back of the tongue. Thus, in Boring's plot the "sensitivity" for sweet was highest on the tip of the tongue and for bitter highest on the back of the tongue. Sadly, Boring's "sensitivity" was not labeled properly, and his graph seemed to suggest that sweet was tasted only on the tip and bitter only on the back (Bartoshuk, 1993a, 1993b). In reality, the threshold differences that Hänig found were very small. Over the years subsequent writers did not bother with Boring's plot and simply drew a tongue with sweet on the tip and bitter on the back. By the 1990s, the mistake was widely known. Nonetheless, in 1999 the bogus tongue map made it into the paper announcing the discovery of receptors for sweet and bitter, dimming what should have been one of the most exciting scientific discoveries in taste (Hoon et al., 1999).

William James (1842–1910), a Harvard professor, began teaching a psychology course in 1875 and set up a laboratory for teaching demonstrations. One of his students, G. Stanley Hall (1846–1924), was awarded the first PhD in psychology in America and did brief postdoctoral work with Wundt. Hall set up a psychology laboratory at Johns Hopkins University in 1883. Although it would seem that James deserves credit for the first psychology laboratory, most historical sources credit Wundt with the first laboratory because James's laboratory was devoted to teaching and not original investigation. Great figures in history do not always admire one another. James's letters are preserved in two volumes and are available through Project Gutenberg. On February 6, 1887, he wrote to his colleague Carl Stumpf about Wundt:

He aims at being a sort of Napoleon of the intellectual world. Unfortunately, he will never have a Waterloo, for he is a Napoleon without genius and with no central idea which, if defeated, brings down the whole fabric in ruin . . . whilst they make mincemeat of some one of his views by their criticism, he is meanwhile writing a book on an entirely different subject. Cut him up like a worm, and each fragment crawls . . . you can't kill him all at once. (James, 2012)

James is not widely associated with sensation and perception, but his classic text, *The Principles of Psychology*, has a famous quote about perceptual development:

The baby, assailed by eye, ear, nose, skin and entrails at once, feels it all as one great blooming, buzzing confusion. (James, 1890, p. 488)

William Dember (1928–2006), a psychologist known for his work in perception, sees this quote as evidence of James's interest in how the infant's initial elementary sensations differentiate into the array of different modalities that characterize perception. James was also interested in visual illusions, including the moon illusion. For those of you who have not experienced it, next time you have a chance, compare the apparent diameter of the moon when it is near the horizon and when it is overhead. The moon looks much larger when near the horizon. Although Dember takes issue with James's attempt to explain the illusion, he notes James's belief, shared by modern experts, that visual illusions hold clues to important principles (Dember, 1990).

Twentieth Century: Code for Intensity

Edgar Adrian (1889–1977) (Lord Adrian after 1955) won the Nobel Prize in 1932 for his discovery of how nerve fibers carry information. This was the key to all of the subsequent understanding of how our senses function. This work, published in three papers, concluded:

The frequency of the impulses varies with the intensity of the stimulus, but the size of the individual action currents does not vary. There is therefore an all-or-none relation between the stimulus and the impulse. (Adrian, 1926; Adrian & Zotterman, 1926a, 1926b, p. 483)

These impulses (called action potentials) convey sensory information. Intensity is determined both by the frequency of action potentials and by the number of nerve fibers carrying them.

Twentieth Century: Codes for Quality

The codes for sensory quality are different for each sense. For vision and audition, the two modalities for which the stimuli fall on a continuum, theories for how the stimuli were transformed into action potentials in the appropriate nerves, were first described very early, but the details of the processes were determined in the twentieth century. We begin with the senses for which stimuli do not fall on continua.

Touch. As noted earlier, Aristotle realized that the category “touch” contained several different qualitative sensations. Stevens and Green (1996) chronicled the development of thinking about touch. One of the most important developments was the discovery of sensory spots: some spots produced pain when touched with a needle, some produced pressure when touched with a stiff

hair, and some produced warmth or cold when touched with a brass cone that could be warmed or cooled. Maps of these spots over the body were independent of each other. Max von Frey (1852–1932) associated these spots with specific receptors in the skin, but his associations did not hold up well with more research. However, von Frey hairs (a set of filaments that produce a range of forces to test the skin) became very popular with scientists studying the skin and are still used today.

One investigator, John Paul Nafe (1888–1970), argued against specialized skin receptors and suggested that skin sensations are produced by patterns across a population of nerve fibers. He argued that Helmholtz's definition of “modality” should be “abandoned” (Nafe, 1929). This minor rebellion did not last long. The accumulation of information clearly reveals specialized receptors in the skin, but the skin senses are not explained simply by discrete receptors. Rather, as a modern expert puts it,

The sense of touch produces a number of distinct sensory experiences. Each type of experience is mediated by its own sensory receptor system(s). (Klatzky, 2018, p. 460)

One of the fascinating features of the skin senses are the illusions that can be produced by interactions among them. One of the author's favorites was described by Barry Green, a leader in modern studies of the skin senses. This illusion can be performed with three quarters. Put two of them in the freezer and hold the third in your hand. Place the three in a row on a table with the body temperature quarter in the center and the two cold quarters on the outsides. Place your index finger, middle finger, and ring finger on the quarters. All will feel cold. This illusion of cold by the middle finger is called “referral of sensation.” As Green describes,

localization of thermal stimulation is subject to modification by tactile stimulation. (Green, 1977, p. 337)

Taste. The Greek philosophers recognized what we call the four basic tastes (sweet, salty, sour, and bitter), but throughout history some experts have suggested new taste qualities. For example, Wundt considered alkaline and metallic to be taste sensations. Even today there are advocates for a fat taste (oleogustus) and a protein taste (umami). Interestingly some of this debate stems from attributing a sensation to every receptor for chemicals that is in the mouth. We now know that receptors for chemical stimuli are found throughout the mouth and the gastrointestinal (GI) tract, but these receptors have different functions in different locations. For example, bitter receptors in the GI tract can slow down absorption and thus protect against the absorption of a poison (Jeon et al., 2008). With regard to fat and protein, fatty acids are components of fats, and glutamate is a component of protein. Although there are receptors for fatty acids and glutamate in the mouth, their real function is in the GI tract. Fats and proteins are broken down by digestion, which produces fatty acids and glutamate in the stomach where their receptors signal the brain

that fats and proteins were in the food recently consumed. The brain is programmed to value fats and protein in the diet and so makes us like the taste and smell of the foods containing these substances. This liking is called a "conditioned preference." That is, we learn to like fats and proteins. We do not learn to like the four basic tastes. We are born liking sweet and salty and disliking sour and bitter.

Carl Pfaffmann (1913–1994), working on his PhD in the laboratory of Lord Adrian at Cambridge University, was the first to record from a single taste nerve fiber (Pfaffmann, 1941). Pfaffmann got his master's degree in psychology from Brown University, and he valued behavioral research throughout his career:

Indeed it can be said that without behavioral study, hand in hand with physiological and anatomical methods, one gets only a partial insight; telling where! and to some degree how! but not for what! (Pfaffmann, 1974a, p. 420)

When Pfaffmann first recorded from taste fibers in the cat, he failed to find fibers responsive to the four basic tastes: sweet, salty, sour, and bitter. Rather, he found three types of fibers: (1) responsive to acid, (2) responsive to acid and sodium chloride (NaCl), and (3) responsive to acid and quinine. He found no responses to sugar. Pfaffmann concluded that taste quality must be coded as a pattern of responses across multiple nerve types. With time, Pfaffmann's across-fiber pattern theory of taste quality met an end similar to Nafe's pattern theory for touch. Additional data continued to show that taste fibers are not specific to a single taste quality, but they tend to respond best to one quality with lesser responses to others (Frank, 1973).

Pfaffmann dropped his pattern theory in favor of a labeled-line theory of taste quality. Frank's data plus behavioral data from the squirrel monkey changed his mind (Pfaffmann, 1974b). The squirrel monkey likes sucrose better than fructose. However, recording from its whole chorda tympani taste nerve shows that fructose produces a larger response than sucrose. Why would the squirrel monkey prefer sucrose to fructose if the fructose is sweeter? The answer came from single fiber recordings of two types of fibers from the squirrel monkey that respond both to sucrose and fructose. One type responds best to sucrose with lesser responses to fructose and almost no response to NaCl (sweet-best). The other type responds best to NaCl, also responds quite well to fructose, but responds only a little bit to sucrose (NaCl-best). Pfaffmann concluded that the taste experienced from the sweet-best fiber is sweet, while that from the NaCl-best fiber is salty. When fructose is the stimulus, the message is sweet from the sweet-best fibers with a moderate amount of saltiness from the salty-best fibers. When sucrose is the stimulus, the message is sweet from the sweet-best fibers with only a little saltiness from the NaCl-best fiber. The squirrel monkey prefers the purer sweet taste of sucrose to the sweet/salty taste of fructose. The whole nerve response for fructose was greater because it contained both responses from the sweet-best and salty-best fibers.

By the way, Pfaffmann failed to find sweet fibers in the cat because there are not too many of them, but they do exist (Bartoshuk, Harned, & Parks, 1971). It turns out that taste fibers can respond to water, depending on what was previously on the tongue. Cat saliva makes water trigger the cat taste fibers that respond normally to sour or bitter. Thus, cats taste pure (distilled) water as sour/bitter. In early cat experiments, sugar was dissolved in water, and the sour/bitter taste of the water masked the sweet taste. If sugar is dissolved in artificial cat saliva (mostly salt), cats can taste sugar, and we can record from their sweet taste fibers. We have some taste fibers similar to those in the cat, but the sour/bitter water taste is less strong to us. However, if you taste distilled water, you may be able to taste the sour/bitter taste (Bartoshuk, McBurney & Pfaffmann, 1964).

Olfaction. Several experts have tried to create a list of basic smells, but none of the lists are satisfactory. In fact, if you are a chemist, you can create a new molecule that has a smell that no one on the face of the earth has ever smelled before. How can our olfactory systems be flexible enough to handle this? Two early theories about the stimuli for olfaction were the vibration theory and the theory of molecular structure (size, shape, functional groups). The vibration theory dates back to 1938; the theory has had its ups and downs, but a recent attack may finally be the last (Vosshall, 2015). The vibration theory maintains that odor molecules give off molecular vibrations and that these determine olfactory quality. Part of the difficulty this theory poses is that few have the scientific background to understand it. Historically, the vibration theory was overwhelmed by the theory that molecular structure determines olfactory quality; the chemical structures of molecules are much easier to picture.

We do not know the exact number of compounds that emit odors, but it must be very large. How many we can identify is something else. Trygg Engen (1926–2009), one of the best-known olfactory investigators of the twentieth century, warned us to be careful about what we mean by "identify." For years various references claimed that experts could identify as many as ten thousand odors. Engen notes that such references are probably referring to discrimination: the ability to tell the difference between two odorants presented simultaneously. If we present odorants one at a time and ask people to name them, we quickly hit a limit. A chemist picked out forty-five odorants that he knew, and when they were presented in random order, one at a time, he identified sixteen correctly. Naming odors is hard. Learning to name odors is also hard. However, once learned, odors are hard to forget (Engen, 1982).

Odor quality coding is combinatorial. Linda Buck and Richard Axel won the Nobel Prize in 2004 for their discoveries about how the olfactory system is organized. The olfactory system processes input in stages. Olfactory receptors are actually the peripheral ends of neurons distributed across the olfactory mucosa (tissue at the top of the nose). These neurons project to glomeruli (small clusters of cells) in the next stage, the olfactory bulb. Humans have about 350 different receptors. These receptors are tuned not to whole molecules but

rather to important functional groups (groups of atoms that give the molecule its properties). When an odorant enters the nose and stimulates the set of receptors that respond to it, all of the inputs from the same receptors find each other and project to specific glomeruli. Thus, the important functional groups of the odorant stimulate the set of glomeruli tuned to those groups and paint a crude picture of the chemical structure of that odorant across the glomeruli. That picture is stored in memory along with the appropriate affect resulting from previous encounters with that odorant. Eat something that makes you sick and you will learn to dislike the olfactory sensation associated with the pattern produced by that food. Eat something that makes you feel good and you will learn to like the olfactory sensation associated with the pattern produced by that food.

Color Vision. Light comes in different wavelengths that we perceive as different colors. There are two theories of color vision: the trichromatic theory and the opponent process theory. Thomas Young (1773–1829) proposed the trichromatic theory of color vision; however, Helmholtz is credited with refining it. Our retinas contain three types of photoreceptor cells (cones), each containing photopigments responsive to different frequencies of light. Light absorption sets in motion a cascade of events that result in action potentials in optic nerve fibers associated with each of these different photopigments.

Ewald Hering (1834–1918) proposed the opponent-process theory. This theory argues for excitatory and inhibitory responses that oppose one another. There are three of these processes: red-green, blue-yellow, and black-white.

In fact, both theories turned out to be correct. The function of the cones are as proposed by the Young–Helmholtz theory, but as input from the cones is processed, cells higher in the nervous system take on the properties attributed to them by the opponent process theory. Leo Hurvich (1910–2009) and Dorothea Jameson (1920–1998), a husband and wife team who collaborated on vision research, discovered that both theories were correct but operated at different points in the nervous system (Hurvich & Jameson, 1957).

White light results from the mixing of all the frequencies of visible light. We can also produce white light by combining red, green, and blue light. In fact, any three frequencies that when combined produce white can be considered primaries. Isaac Newton (1642–1726) created a color circle to illustrate the rules of colored light mixing. It is important to distinguish the mixing of colored lights from the mixing of colored paints. Paints absorb different colors of lights. When we look at a painted surface, we see the color left after the paints on the surface have absorbed colors. A mixture of paints of all colors will look black; all color has been subtracted out.

There is a phenomenon in olfaction that Noam Sobel and his colleagues have compared to white light and white noise. They created olfactory mixtures of around thirty odorants at concentrations that were of equal perceived intensities (Weiss et al., 2012). These mixtures produced smells that were similar even though the molecules in these mixtures were very different. The authors called this smell “Laurax” and suggested it may be an “olfactory white.”

Audition. Sound comes in different frequencies that we perceive as different pitches. Sound waves enter the ear and cause the eardrum to vibrate. That vibration is transmitted to three small bones in the middle ear and then to the basilar membrane in the cochlea of the inner ear. Helmholtz proposed that different areas of the basilar membrane are tuned to different sound frequencies and that this stimulates specific nerves that transmit pitch to the brain.

Georg von Bekesy (1899–1972) won the 1961 Nobel Prize for his work showing the details of how this worked. The cochlea is coiled like a snail. The basilar membrane travels the length of the cochlea, has fluid above and below it, and has hair cells on it that detect movement. The vibration transmitted by the bones in the middle ear causes a traveling wave in the fluid in the cochlea. The wave peaks at different points along the basilar membrane depending on the frequency of the sound. Those peaks are detected by the hair cells, which stimulate nerve fibers, which send messages telling the brain which frequencies were in the sound.

Distinction between Sensation and Perception

Jeremy Wolfe describes the distinction between sensation and perception in a modern text:

The ability to detect the pressure of a finger and, perhaps, to turn that detection into a private experience is an example of sensation. Perception can be thought of as the act of giving meaning and/or purpose to those detected sensations. (Wolfe, Kluender, & Levi, 2018, p. 4)

Distinguishing between sensation and perception now seems relatively easy given our sophistication about how the nervous system processes information. However, the distinction was not so easy when we knew much less about sensory nerves and the brain. Beare tells us about the Greek philosophers:

It has to be remarked that they failed for the most part to distinguish between sensation as the elementary fact and perception as the more complex and developed, implying objective reference. (Beare, 1906, p. 202)

By the middle ages, a theory of outer and inner senses had developed as part of Arabic philosophy. The theory had roots in Galen (Faruque, 1981). The outer senses were the traditional senses (touch, taste, olfaction, vision, audition). The inner senses were described as mental faculties thought to be located in the ventricles of the brain. Avicenna listed five inner senses. First was common sense; this was not common sense as we think of it today but rather the ability to combine the outer senses. Second was imagination. Third was the ability to receive meanings, a cognitive faculty. Fourth was the ability to understand intentions, e.g., hostility or danger. Fifth was memory, a retentive faculty (Knuuttila & Kärkkäinen, 2014). The progression from simple sensations to more complex associations as the input passes through different parts of the brain hints at our current view of the processing of information in the

nervous system. This theory was influential until accumulating information about the anatomy of the brain proved inconsistent with it.

Thomas Reid (1710–1796) is credited for his explicit distinction between sensation and perception. He wrote:

When I smell a rose, this involves both sensation and perception. The pleasant odor I feel, considered by itself and not in relation to any external object, is merely a sensation. . . . Perception always has an external object, and in our present case the object of my perception is the quality in the rose that I detect by the sense of smell . . . the act of my mind by which I have the conviction and belief in this quality is what in this case I call “perception.” (Reid, 1785, p. 100)

A century later, Wundt discussed what is often called “mental chemistry.” In his book *Outlines of Psychology*, he describes psychical elements (sensations, feelings of pleasure and pain) that combine to form psychical compounds (e.g., perceptions).

Advances in our understanding of the nervous system now permit us to describe the events by which sensations become perceptions. One interesting result concerns the accuracy of the information we receive from our environments. Contrary to the view of the Greek philosophers like Empedocles, we do not necessarily receive accurate information about the world.

Throughout each sensory system, from the peripheral receptors to the cerebral cortex, information about physical stimuli is transformed in stages according to computational rules that reflect the functional properties of the neurons and their interconnections at each stage. . . . A major goal of cognitive neural science is to determine how the information that reaches the cerebral cortex by means of parallel pathways is bound together to form a unified conscious perception. (Kandel et al., 2013, Part 5, Introduction)

However,

perceptual systems . . . perform inferences about the world. . . . The brain uses information it has extracted previously as the basis for educated guesses. (Kandel et al., 2013, Part 5, Introduction)

How Do We Measure Sensations?

Science requires measurement. Measurement of sensations requires units. We must be able to add up these units to describe varying intensities of sensation. Gustav Fechner (1801–1887) created psychophysics, the branch of psychology that measures the association between physical stimuli and the sensations they produce. In addition, Fechner gave us a unit of sensation. He began by measuring the absolute threshold: the lowest intensity of a stimulus that can be detected. Then he increased the intensity until he could just perceive an increase. That increase in intensity is the “just-noticeable difference” or “jnd.” The jnd is our unit of sensation. We can specify any sensory intensity by counting the number of jnds from the threshold to that intensity. Fechner’s

Elemente der Psychophysik (1860) laid out the methods by which one could determine absolute thresholds and jnds. This view dominated psychology for a century.

S. S. Stevens (1906–1973) started a revolution by noting a problem with the jnd as a unit of sensation. Consider jnds for loudness. If the jnd is a proper unit, then a sound that is 8 jnds should be twice as loud as a sound that is 4 jnds. But it is not. Rather, the 8 jnd sound is more than twice as loud as the 4 jnd sound as if the subjective size of the jnd for loudness is growing as the sound gets more intense.

Stevens created a new set of psychophysical methods called direct scaling methods. Magnitude estimation has proved the most popular (e.g., see S. S. Stevens, 1955). With this method, we ask a subject to estimate the magnitude of a sensation (let’s stick with loudness) by choosing a number to represent the intensity. Now, if the next sound is twice as loud, the subject is to assign it a number twice as large. If it is half as loud, the subject is to assign it a number half as large. In his autobiography Stevens describes a fascinating interaction with Richard Held. Held (1922–2016), who spent most of his distinguished career studying vision at MIT, got his PhD at Harvard (his thesis committee consisted of Boring, Stevens, Newman, and Bekesy). Stevens (1974) says,

One day during a coffee break Richard Held accused me of acting as though a person has a built-in loudness scale from which values can be read. That was an interesting idea. Why not try it? I presented a series of sound intensities in irregular order, and Held assigned numbers to them, apparently with no trouble at all. That method, magnitude estimation, which calls for the matching of numbers to perceived intensity, was soon to transform psychophysics. (p. 415)

Stevens called the resulting loudness scale the sone scale.

In 1932 the British Association for the Advancement of Science formed a committee chaired by A. Ferguson (a physicist) for the purpose of considering whether or not sensations could be measured. The committee was composed of psychologists and physicists including N. R. Campbell, a strong opponent of psychophysical measurement. The deliberations of this committee are delightfully summarized by Joel Michell (1999).

As an exercise in critical inquiry, the deliberations of the Committee were a sham. Both the interim and final reports (Ferguson et al., 1938; Ferguson et al., 1940) consisted largely of set pieces: the big guns of a confident, intellectually dominant, Campbell camp, and the pea-shooters of an intellectually limp psychophysics camp. (p. 144)

Perhaps the best thing Ferguson’s committee did for psychology was to attack Stevens’s sone scale. Stevens was no pushover. He responded by writing one of the classic papers on measurement: “On the theory of scales of measurement” (S. S. Stevens, 1946). The Ferguson committee is long forgotten; Stevens’s classification of scales into nominal, ordinal, interval, and ratio now dominates our view of measurement. *Nominal* scales are the most primitive. Values on

such a scale simply identify (e.g., numbers assigned to football players). *Ordinal* scales rank. For example, we might rank beverages in terms of how sweet they are. For *interval* scales, the distances between two ranks are the same. *Ratio* scales are those common to the physical sciences (e.g., length). There is a zero, and the ratings on the scale have the ratio properties of a ruler.

S. S. Stevens spent his career at Harvard. As a young psychologist he made history not only by taking on the august Ferguson committee, but also by taking on the august Society of Experimental Psychologists (SEP). SEP was founded in 1904 by E. B. Titchener (1867–1927). The young Stevens and five cohorts objected to the advanced age of the members of SEP and created a new younger group (the Society of Experimenting Psychologists) with the following invitation:

A few of the boys want to get together for a little give and take and we want you with us. (Benjamin, 1977, p. 542)

Boring, who was Stevens's mentor, was offended by the "ing" and pressured the group to choose a new name. Benjamin tells us that one of the members, William A. Hunt (1903–1986) (one of the earliest scientist/clinicians in psychology), had a token for the Philadelphia Rapid Transit in his pocket. The PRT token suggested the name "Psychological Round Table," and that became the society's new name (Benjamin, 1977).

Incidentally, Titchener opposed admitting women to SEP (the group voted to admit women the year after he died), and PRT also failed to admit women initially, finally admitting them around the 1970s.

Long before the measurement theory of Fechner and Stevens, scholars in different fields needed measurements of sensory intensities for a variety of reasons. Consider a scale for the brightness of stars. Hipparchus (190–145 BCE), a Greek astronomer, ranked the stars by brightness. Ptolemy (100–170 CE), a Greco-Roman astronomer, created the *Almagest*, which includes a star catalog listing the brightness in six categories (1 = brightest, 6 = faintest); each magnitude was twice as bright as the next (Stevens called such a scale a "logarithmic interval scale" (S. S. Stevens, 1957)).

Stellar brightness played a crucial role in the determination of the size of the universe thanks to the observations of Henrietta Leavitt (1868–1921) working at the Harvard College Observatory (G. Johnson, 2005). Leavitt observed Cepheid variable stars pulsing in brightness and deduced that the pulsation was related to their absolute brightness (i.e., the brightness right at the star). The apparent brightness of a star seen from earth is related to the absolute brightness and the distance of the star from earth (the inverse square law). Thus, observing the pulsation can tell us the distance of the star from earth.

A category scale was devised for the army to test the preferences of soldiers for various foods (Meiselman & Schutz, 2003; Peryam & Pilgrim, 1957). This scale has nine categories (1 = dislike extremely, 2 = dislike very much, 3 = dislike moderately, 4 = dislike slightly, 5 = neither like nor dislike, 6 = like slightly, 7 = like moderately, 8 = like very much, and 9 = like extremely). This scale has become one of the most widely used scales to measure food acceptability.

Similarly, a category scale (0 = no pain, 10 = worst possible pain) is widely used to assess pain intensity (Krebs, Carey, & Weinberger, 2007). This scale is commonly used in hospitals to decide whether or not to medicate patients.

By the 1960s, category scales had morphed into visual analogue scales (VASs). Typically, the VAS is a line labeled in terms of the maximum and minimum intensities for a given sensation (e.g., see Hetherington & Rolls, 1987). For example, early VASs were used to assess hunger (Silverstone & Stunkard, 1968; Spence & Ehrenberg, 1964). Silverstone and Stunkard asked subjects to rate their hunger on a line with the label "Not at all hungry" underneath the line on the left and "As hungry as you have ever felt" on the right. The VAS was given a vote of confidence by the prestigious British journal *Proceedings of the Royal Society of Medicine*. That journal introduced a new section in 1965: the Section of Measurement in Medicine. Perhaps not surprisingly, given the British Ferguson Report, the inaugural essay discussed only measurement as seen by the physical sciences (Cohen, 1965). Yet in 1969, Aitken published, "Measurement of feelings using visual analogue scales." The VAS is now used widely to measure sensations.

Category scales rank stimuli; as we noted earlier, the numbers on category scales do not have ratio properties. For example, on the pain 10-point scale a pain rated "8" is not twice as intense as a pain rated "4." That was an issue that worried a variety of investigators. For example, Lasagna (1960) asked patients to consider the categories of pain classification: slight, moderate, severe, or very severe. He found that "a drop of pain from severe to moderate was, on the average, considered most important, and a drop from slight to none least important." One reason that the VAS was considered to be an advance over category scales is that it does have ratio properties (Price et al., 1983).

Could we give category scales ratio properties by spacing the categories appropriately? The answer is yes. For example, Green and his colleagues used magnitude estimation to rate typical intensity descriptors and used the resulting spacing to create the Labeled Magnitude Scale (LMS) for oral sensations (Green, Shaffer, & Gilmore, 1993).

Problem: Category Scales, VASs, and Stevens's Magnitude Estimation All Fail to Compare Different Groups of People

The measurement scales already discussed were devised to compare different stimuli. However, with time, investigators began to get interested in comparing sensations across different people (or groups of people). This introduced a new dilemma. When two different sensations are to be compared, each subject can experience both sensations; this is a within-subject comparison. However, when the sensations of two different people are to be compared, we have an across-subject comparison. Two different people cannot share sensory experiences. How can we compare their sensory experiences? Initially, some investigators simply used the available scales without realizing that they were implicitly assuming that the intensity labels on the scales denoted the same perceived

intensities to all subjects. Early on, a few investigators realized this would not provide valid comparisons. Aitken wrote,

The same word used by different people need not convey that they experience the same feeling, neither does comparable positioning of marks on lines. (Aitken, 1969, p. 989)

Other investigators made similar points (Bartoshuk, Duffy, Fast et al., 2002; Biernat & Manis, 1994; Birnbaum, 1999; Narens & Luce, 1983). One way to solve this problem is with a new method, called "magnitude matching" (Bartoshuk, Duffy, Green et al., 2004).

Using a within-subject scale to make across-subject comparisons can do real harm. Consider the impact on women of the common practice in hospitals of asking subjects to rate their pain on the 10-point pain scale (or its VAS counterpart). But first, let us compare the pain of women and men with a method that permits valid comparisons across groups: magnitude matching. We asked women and men to rate a variety of everyday sensations using Stevens's magnitude estimation (Bartoshuk, Duffy, Green et al., 2004). Among those everyday sensations we included "the most intense pain ever experienced" (and asked subjects to name the source of the pain) and the brightest light ever seen (usually the sun). We selected the female subjects who named childbirth as their most intense pain and compared their average pain to the brightest light they had ever seen. The childbirth pain was about 20 percent more intense than the brightest light. We looked at all of the male subjects. Their most intense pain was about equal to the brightest light. Thus, if there is no systematic difference in the perceived intensity of the brightest light between women and men, we can conclude that childbirth (for those women who named it as their worst pain) was 20 percent more intense than the most intense pain experienced by the men. Note that a few men rated kidney stone pain to be much more painful than the brightest light was bright. However, since more women have babies (experiencing very intense pain in the process) than men have kidney stones, we have a systematic difference between women and men for the most intense pain they have ever experienced. This means that the "10" on the pain scale denotes a more intense pain for those women than it denotes for most men. Hospitals tend to medicate patients with pain ratings above "4" on the pain scale. Do we really think it is a good idea to make women suffer worse pain than men to get an analgesic?

Hedonic Sensations: Pleasure and Pain

Hedonism, an ethical philosophy maintaining that pleasure should be maximized, dates back to Aristippus (435–356 BCE), a student of Socrates. Robert Bolles (1928–1994) traced hedonism from the Greek philosophers to modern animal studies (Bolles, 1991). Bolles credits John Locke (1632–1704) for the shift of hedonism from moral philosophy to the psychological principle

that we are motivated to act by pleasure and pain. Jeremy Bentham (1748–1832), the English founder of utilitarianism, argued for both the moral philosophy and the psychological motivation. He maintained that maximizing pleasure and minimizing pain is good. To measure the amount of pleasure or pain, he invented hedons (units of pleasure) and dolors (units of pain). These were only theoretical units, Bentham did not actually try to measure pleasure and pain. Bentham also recognized motivation. One of his most famous quotes is:

Nature has placed mankind under the governance of two sovereign masters, pain and pleasure. It is for them alone to point out what we ought to do, as well as to determine what we shall do. (Bentham, 1876, p. 1)

One early argument concerned whether or not pleasure and pain should be on a continuum. John G. Beebe-Center (1897–1958), a Harvard professor famous for his hedonic studies, believed that the existence of the continuum had been empirically demonstrated, and he described what he considered to be the most convincing experiment. Graduate students at Clark University ($N = 15$) were presented with pairs of colors. In the first series, they were instructed to judge which of the two was the more pleasant. In the second series, they were instructed to judge which of the two was the more unpleasant. The results showed that the choices of "more pleasant" were essentially the inverse of the choices of "more unpleasant." The conclusion: "pleasantness and unpleasantness are true psychological opposites" (Fernberger, 1914). Describing this experiment, Beebe-Center concluded,

Pleasantness and unpleasantness are concepts characterizing experience. They are quantitative variables so related to each other that they may be represented respectively by the positive and negative values of a single algebraic variable. This single variable we shall call hedonic tone. (Beebe-Center, 1932, p. 7)

Today we might find it difficult to conclude that pleasure and pain are on a continuum from a study utilizing fifteen subjects, but the concept of a hedonic continuum is now generally accepted nonetheless.

Another early argument was whether or not pleasure and pain should be considered to be sensations. In the 1890s, Wundt and his student Titchener considered sensations and affect as different elements of immediate experience (Titchener, 1896; Wundt, 1897). Paul T. Young (1892–1978), a student of Titchener, studied affect empirically with animal studies (Young, 1959). He argued for a "hedonic continuum" and was particularly interested in temporal changes (e.g., decline in pleasure associated with eating over time). In particular, Young distinguished between sensory and hedonic intensity using NaCl as an example. As concentration rises for NaCl, saltiness rises, but the hedonic intensity first rises with concentration and then falls.

The neural structures mediating pleasure and pain have influenced thinking in this field. Some early authors argued that for pleasure and pain to be sensations, nerves would have to exist to carry those sensations, and no such nerves had yet been discovered (Marshall, 1892). This argument was weakened

with the discovery of pain nerves and with the discovery of pleasure centers in the brain.

With increasing sophistication in the study of the nervous system and with advances in learning theory, changes in pleasure and pain have become a focus of interest. Michel Cabanac introduced the concept of "alliesthesia"; the pleasure a stimulus evokes can change based on physiological changes in the body (Cabanac, 1979). For example, the pleasantness of sugar declines after consumption of sugar (called the Cabanac effect). Carl Pfaffmann, an academic descendant of Wundt (Bartoshuk, 1978), noted the ease with which neutral stimuli can be made pleasant or unpleasant by conditioning. The area within psychology that studies how affect is transferred from one stimulus to another is called "evaluative conditioning."

The argument about whether or not pain and pleasure should be considered to be sensations was never really settled. In the modern era, we tend to think of sensations as having attributes: quality, intensity, and affect (Cabanac, 1979).

Overview

The twentieth century has seen explosive progress in our understanding of sensation and perception, documented in a variety of texts on both psychological and neurophysiological studies. Our earliest insights about sensation came from simple observations. The Greek philosophers lacked the science and (for the most part) the cultural permission to dissect human cadavers and so learned little about what is inside our bodies. As time passed and science advanced, we came to understand how our nervous systems process primitive sensory information into our understanding of the world and how we interact with it. We do not know how accurate our pictures of the world are. Information about the world not only passes through sensory filters but also is processed further as it moves through the nervous system. For the most part, evolution and personal experience shape that processing so that the picture of the world that ultimately results helps us survive. But our senses are not perfect. Hopefully, as our understanding of sensation and perception advances, we will get better at understanding where our senses can mislead us.

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5 Attention: Awareness and Control

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Definition

Attention is a central link in understanding how the complex activity of our environment leads to the more limited world of which we are aware.¹ Attention mechanisms are also central to our interface with the world and with our own feelings and thoughts. Attention is a means of self-control through selection of those actions consonant with our current goals. As a consequence of its importance, the study of attention has a long history both within and outside of scientific studies of psychology.

The most commonly quoted definition of attention was written by the American psychologist and philosopher William James at the turn of the twentieth century. James (1890) said:

Everyone knows what attention is. It is the taking possession of the mind in clear and vivid form of one out of what seem several simultaneous objects or trains of thought. (p. 403)

Taking possession of the mind clearly meant that attention was the entry to consciousness, where consciousness is here identical with awareness and is usually signified by the ability to report the event during or immediately after its occurrence. Every aspect of James's definition has been discussed, and it remains important as a way of looking at the phenomena under study in the name of attention. James's distinction between attention to objects and to trains of thought was particularly prescient. In modern experimental work on attention, orienting to sensory information dominates, but attending to information stored in memory is also crucial.

Most current definitions of attention are taxonomies of the chief methods used to measure it – sustained attention, divided attention, selective attention, attention span, orienting, etc. Because most experiments measure attention to

¹ This chapter draws upon a four-volume set of classic papers on attention edited by M. I. Posner, *The Psychology of Attention* (2016), London: Routledge. Many of the papers cited here are available in those volumes for further research into the topics discussed in this chapter. I appreciate the work of Professor Mary K. Rothbart and of Ashley Dresen in reading and helping improve the chapter.