Part I Fundamentals

1 Introduction to Behavior Genetics

Behavior genetics – the scientific study of heredity–behavior relations – has come of age. Since the middle of the twentieth century, accumulating scientific evidence has shown that genetic differences between individuals play a significant role in behavioral differences between them. In fact, it is now generally accepted that genetic variation is an important contributor to individual differences in behavior. Although the fundamental question about the role of inheritance in behavioral resemblance is not new, recent technological advances provide new ways to peek behind nature's curtain. It is easy to get excited about the potential for discoveries in behavior genetics. We appear to be entering a new era in which it may be possible to understand the biological mechanisms responsible for familial behavioral resemblance. However, we should enter this era with humility. The history of behavior genetics is full of periods of excitement followed by disappointment. It also contains sobering lessons of scientific hubris and state-sponsored human rights violations. There is a lot to be excited about, but it is important to remember history, and to understand the limitations of behavior genetics, especially when considering the application of behavior genetic findings to human beings.

This chapter provides a brief look at the history of behavior genetics and introduces some of its early influential thinkers. It goes on to discuss modern dog breeds because they are the outcome of applying practical knowledge about heredity–behavior relations. Dogs also provide a personal touchpoint to the material because many of us have had extensive interactions with them. Further, it introduces the use of non-human animals to understand human problems, which is an important feature of much behavior genetic research. This chapter considers our shared evolutionary history with other animals, which is the basis of their ongoing contributions to improving human health. It also sets the stage for the rest of the book by introducing the main behavior genetic research questions. Finally, the role of ethics oversight in the conduct of behavior genetic research is discussed. This chapter provides the context in which to consider behavior genetics concepts, methods, and findings.

1.1 A Brief History of Behavior Genetics

Officially, the field of behavior genetics was established in 1960, when its first textbook was published (Fuller & Thompson, 1960). Prior to that, efforts to understand the role of genetic differences in individual differences in behavior were mostly non-systematic, anecdotal, literary, philosophical, or focused on animal breeding, or evolution.

1.1.1 Familial Resemblance for Behaviors Has Been Observed Throughout History

It is likely that throughout human history people have noticed that some traits tend to "run in families." It is easy to see **familial resemblance** for physical traits, such as ear and nose shape, or

Figure 1.1. **Familial resemblance.** It is easy to see that members of families share physical similarities. Source: The Good Brigade / DigitalVision / Getty Images.

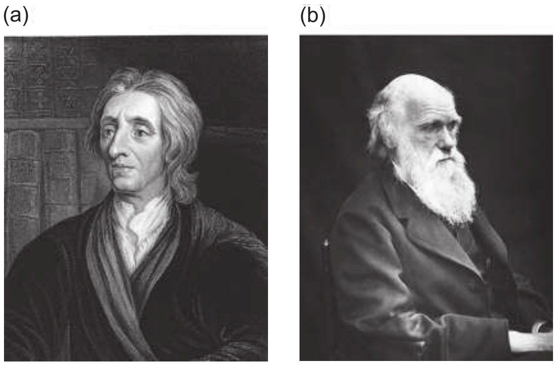

Figure 1.2. **Locke and Darwin.** (a) John Locke (1632–1704) developed the idea that humans are born as "blank slates" and experience is the main factor in individual differences in behavior. (b) Charles Darwin (1809–1882) focused on biological causes of behavior. He appreciated the role of behavior as a driving force of evolution and that behavioral traits can be the targets of selection. Source: (a) Hulton Archive / Staff / Getty Images. (b) Bettmann / Contributor / Bettmann / Getty Images.

eye and hair color (see Figure 1.1). You may have also noticed that some behavioral characteristics in children may resemble the behavior of their parents, such as having an outgoing personality, or suffering from anxiety, or even showing a tendency to abuse substances. Such resemblance is commonly recognized, and has inspired familiar phrases, such as "like mother, like daughter," or "the apple doesn't fall far from the tree."

Familial resemblance for behavioral traits has long been noted by writers, such as William Shakespeare, in lines like "Her dispositions she inherits" (*All's Well That Ends Well*, Act I:1) (Loehlin, 2009). Or when describing the character Caliban, "A devil, born a devil, on whose nature, nurture can never stick" (*The Tempest*, Act IV:1, Prospero) (Berg, 2001). In fact, this passage appears to have been the inspiration for a phrase that has long been used to characterize efforts to understand whether heredity or experience is more important in shaping behavior: "**nature versus nurture**."

Generally, philosophers have held that behavior is a result of some combination of nature and nurture, although there have been those who have taken stronger positions favoring one or the other. Contrasting views in this controversy are consistent with those of philosopher John Locke and naturalist Charles Darwin (Loehlin, 2009). Locke (see Figure 1.2(a)) developed the position that nearly all our capacities are produced by experience and suggested that we enter the world as "blank slates" on which experience writes. Darwin (see Figure 1.2(b)), on the other hand, made the argument that human beings are part of the biological world, which is shaped by the forces of

evolution, and that many of our capacities are rooted in biology. Darwin's argument was buttressed with systematic, data-driven observations that he had collected over decades of intensive study as a naturalist.

1.1.2 Behavior Is a Driving Force in Evolution

Charles Darwin's contribution to behavior genetics should not be ignored. Of course, his primary contribution to science was his development of and support for the theory of evolution via **natural selection**. Let us consider his oft used example of the finches of the Galapagos Islands that emphasizes **morphological** (i.e., physical structure) change made possible by the available genetic variation in populations and driven by **niche specialization**.

After returning home from his voyage on the HMS *Beagle* (1831–1836), Darwin studied the birds that he had collected on the trip and noted that on different Galapagos Islands there were finches that had substantially different beak morphology. On one island, ground finches had rather small beaks, whereas on another island, there were ground finches that had substantially larger beaks. In fact, he had collected many birds during his time on the Galapagos Islands, and kept careful records of where he collected them. It appears that Darwin collected approximately fifteen different species of finch on the Galapagos Islands. He postulated that at some point in the past, a small number of finches from the mainland (i.e., South America) arrived on a previously finch-less island, and subsequently spread out to colonize the other islands. He also hypothesized that the different islands provided different food sources, such as plants that produce either small or large seeds. On islands where small seeds predominated, finches with small beaks were better able to feed, and were therefore at an advantage in terms of both survival and reproduction. Similarly, on islands where large seeds were most plentiful, finches with larger beaks were more likely to thrive and multiply.

An important aspect of Darwin's finch example is that it shines a light on how *behavior* is a driving force in evolution (Thierry, 2010). Different islands provided different food supplies (e.g., small vs. large seeds), and it was differential success in feeding *behavior* that drove morphological change and the divergence of Galapagos finch species. Finding and consuming food has obvious implications for survival and successful reproduction. Even if a finch had a specialized beak, they would be an evolutionary dead end if they were not successful in finding and consuming the appropriate food (i.e., without appropriate behavior). In other words, it is behavior in combination with morphology in variable environments that drives evolution.

In addition, Darwin's theory of evolution provided a strong argument for shared evolutionary history across species, which is an important justification for the use of **non-human animal models** to investigate aspects of human behaviors and disorders (Thierry, 2010). We address the use of non-human animal models in behavior genetics later in this chapter.

1.1.3 Galton Studied the Inheritance Patterns of Mental Qualities and Talent in Families

Francis Galton (see Figure 1.3) is sometimes called the "father of behavior genetics" because of his contributions to the study of the inheritance of traits in families, and for his focus on "mental qualities" and "talent." He published his first analysis of the transmission of such traits in families in a two-part article in 1865 (Galton, 1865a, 1865b), and later in books such as *Hereditary Genius: An Inquiry into Its Laws and Consequences* (Galton, 1869), and *English Men of Science: Their Nature*

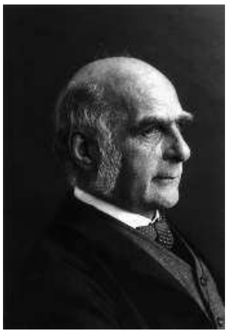

Figure 1.3. **Francis Galton.** Galton made contributions to many scientific areas including behavior genetics. Source: adoc-photos / Contributor / Corbis Historical / Getty Images.

and Nurture (Galton, 1874). In these works, Galton set out to show that talented people were found in higher proportions in some families than in others. Of note, Galton had a half-cousin named Charles Darwin. They were both grandchildren of Erasmus Darwin, who was a physician and natural philosopher in his own right. Quite a talented family, to be sure. Galton conceded that it is impossible to completely isolate the effects of heredity and environment by studying families because typically in families both are shared.

Galton attempted to disentangle nature from nurture by studying twins (Galton, 2012), and was the first to do so (Burbridge, 2001). Although he did not pioneer the comparison of **identical** and **fraternal twins** that has been a methodological standby for modern behavior genetics (see Chapter 3), he recognized that twins could be studied to address whether trait similarity changed across development. Galton stated that "nature prevails over nurture when the differences of nurture do not exceed what is commonly to be found among persons of the same rank of society and in the same country," which is a pretty strong statement given the flaws in his study design (i.e., the confounding of heredity and environment).

Galton coined the term **eugenics** to refer to "the science which deals with all influences that improve the inborn qualities of a race" (Galton, 1904), and was an outspoken proponent of its practice. We discuss eugenics in some detail in Chapter 15. But for now, let us just say that Galton's imprint on behavior genetics is still visible. His work is still with us more than a century later in other areas too, spanning from meteorology (e.g., weather maps), to statistics (e.g., regression), to forensic science (e.g., fingerprints), and even to cutting cakes (see Galton, 1906).

1.1.4 Modern Dog Breeds Are Largely the Result of Breeding for Behavioral Traits

An important type of evidence for the role of heredity in behavior has come from our relations with domesticated animals, especially dogs. Modern breeds of ***Canis lupus familiaris*** (the common dog) are the result of thousands of years of association with humans that has dramatically affected morphological and behavioral traits. No other land animal displays as much morphological and behavioral diversity as dogs. The modern concept of the **dog breed**, a line of dogs that share similar physical and behavioral traits maintained by selective breeding, formally originated in England in 1859 at the first modern dog show, and was subsequently institutionalized at the creation of the Kennel Club in 1873 (Pemberton & Worboys, 2015). The Fédération Cynologique Internationale (FCI), the world governing body of dog breeds, recognizes about 350 different breeds. It is easy to spot substantial physical variation in breeds of dogs from the small breeds like the Maltese that

Figure 1.4. **Morphological variation in dog breeds.** This illustration was first published in 1895 and shows substantial variation in height, weight, body conformation, muzzle shape, and other characteristics of 21 dog breeds. Source: THEPALMER / DigitalVision Vectors / Getty Images.

weigh about 6 to 8 pounds (2.7 to 3.6 kg), to the large like the Mastiff that can easily weigh over 200 pounds (90.7 kg; see Figure 1.4). Similarly, astonishing variability can also be seen in behavioral traits, with dogs that can be trained to herd other animals, use their sense of smell to track or find things, dig holes, run in races, hunt, fetch, fight, pull sleds, and so on.

Humans and dogs have been living in close proximity for hundreds of thousands of years, but true domestication of dogs is likely to have begun around 20,000 years ago. In that time, certain canine behavioral traits have been considered advantageous, and have been the targets of intentional **selective breeding** efforts. Behaviors that have been useful in hunting, farming, protection, and other areas in life, have been favored. Dogs that displayed the favored behaviors were nurtured and bred, whereas those that did not display them were not. In other words, humans have selectively bred dogs for *behaviors*. For the most part, the breeding efforts were not coordinated or systematic. But dogs that were useful and friendly were actively favored over those that were not. The selective breeding efforts became more systematic in the late 1800s when "dog fanciers" standardized descriptions of different breeds, began the practice of dog shows and keeping pedigrees, and codified the focus on "pure bred" dogs (Pemberton & Worboys, 2015).

Restricting mating between dog breeds reduces genetic variation within breeds, which has led to rather high prevalence rates of genetic disorders in certain breeds. On the bright side (for humans), the appearance of diseases in dogs that are also found in humans means that canines have an opportunity to serve humans in yet another way. Namely, certain canine genetic disorders serve as non-human animal models for diseases such as cancer, obsessive-compulsive disorder, narcolepsy, Alzheimer disease; or for behaviors such as aggression or anxiety (Ostrander, Wayne, Freedman, & Davis, 2017).

Breeding dogs *for* certain behaviors does not require a detailed understanding of heredity–behavior relations. It only requires a basic understanding that behavioral traits run in families and that mating together the animals that show the desired behavior increases the chances that the behavior will be expressed in later generations. There was, however, great interest in better understanding genetics in the late nineteenth and early twentieth century, primarily driven by those interested in agricultural applications.

1.1.5 Behavior Genetics Was Established in the Twentieth Century

Although Gregor Mendel delivered lectures describing his model of inheritance in 1865, which were later published (Mendel, 1866), his insights into heredity were not widely known or appreciated until they were "rediscovered" around 1900. Mendel's Laws were a scientific breakthrough that provided a framework for understanding the inheritance of any trait, including behavior. We cover Mendelian genetics in Chapter 2.

Early experimental work in heredity involved the examination of traits first in parents and then in their offspring, as Mendel had done. Thomas Hunt Morgan's group used Mendel's Laws and the common fruit fly, *Drosophila melanogaster*, to map the location of genes associated with specific mutations affecting eye color, wing shape, and other morphological traits (see Figure 1.5). The first quarter of the twentieth century also saw the genesis of systematic behavior genetic research, such as work by Edward Chace Tolman and Robert Choate Tryon into the inheritance of maze learning in rats (see Innis, 1992).

Enthusiasm for Mendelian genetics was also evident in those who were focused on human behavior. Francis Galton's ideas on eugenics were especially influential when Mendelian genetics represented the cutting edge of science (see Figure 1.6). The application of Mendelian genetics in combination with behavioral science, which was also in its infancy at the start of the twentieth century, produced an overly simplistic view of heredity–behavior relations that was ripe for misuse by those with a racist agenda (Chase, 1980). Such "scientific racism" was used to justify the legalization of involuntary sterilization across the United States, to restrict immigration into the

Figure 1.5. **Thomas Hunt Morgan.** T. H. Morgan won the Nobel Prize in Physiology or Medicine in 1933 for his contribution to the understanding of chromosomal inheritance. Source: THEPALMER / DigitalVision Vectors / Getty Images. Used with permission of Archives, California Institute of Technology.

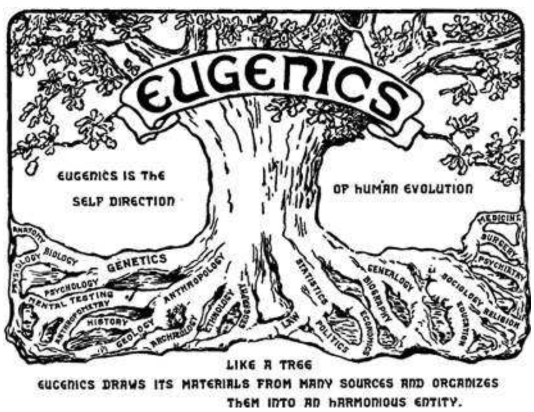

Figure 1.6. **Logo of the Second International Congress of Eugenics, 1921.** The meeting held at the American Museum of Natural History in New York had 53 scientific presentations on topics in sessions titled: "Human and Comparative Heredity," "Eugenics and the Family," "Human Racial Differences," and "Eugenics and the State." Source: Harry H. Laughlin, The Second International Exhibition of Eugenics held September 22 to October 22, 1921, in connection with the Second International Congress of Eugenics in the American Museum of Natural History, New York (Baltimore: William & Wilkins Co., 1923). Image in the public domain.

United States, and inspired Nazis in Germany to carry out the Holocaust. We tackle eugenics in Chapter 15. We mention it here to acknowledge that behavior genetics has had a profound and disturbing impact on world history, and to urge caution and careful consideration in any potential application of behavior genetic findings to human beings.

The twentieth-century horrors conducted in the name of eugenics have cast a long shadow on the field of human behavior genetics. Efforts to understand the role of genetic variation in human individual differences in behavior were also limited because of the dominant role in psychology played by behaviorism, which focused on the primacy of environmental influence and learning and de-emphasized the role of biologically based individual differences in behavior. In addition, the potential toolbox of genetic methods was relatively bare thereby limiting scientific inquiry into human behavior genetics. The technological barrier persisted until the end of the twentieth century when the breakthrough technology of polymerase-chain reaction (PCR) was developed (see Chapter 5).

Through much of the twentieth century, important advances in behavior genetics were achieved in research using non-human animals. Fruit flies (*D. melanogaster*), mice (*Mus musculus*), and rats (*Rattus norvegicus domesticus*) were the species that made the largest contribution, although dogs, monkeys, zebra fish, honeybees, roundworms, and other species have been and continue to be used to investigate heredity–behavior relations. Although the state of genetic methods was also a limiting factor to progress, more experimental genetic methods will always be available to those who work with non-human animals compared to those who work with humans. For instance, it is ethically unacceptable to conduct controlled breeding experiments or to induce genetic change in humans, but such approaches are routine in studies using non-human animals.

Check-up

- Who were the two cousins who made important contributions to understanding heredity–behavior relations in the late 1800s, and what were their contributions?
- What can dog breeds reveal about heredity–behavior relations?
- What is eugenics and how was science used to advance eugenic policies in the early twentieth century?

1.2 Behavior Genetics Focuses on Understanding Individual Differences in Behavior

The focus of behavior genetics is on understanding the role of genetic *variation* in ***individual differences*** in behavior. Researchers do not seek to identify genes that "cause" behaviors, or to find genes "for" behaviors.

It is easy to see that in a population not everyone behaves the same. Researchers also recognize that individuals are genetically unique, except for identical twins. In other words, there are genetic differences between people. So, the focus is on understanding how genetic differences between people are associated with behavioral differences between them. In that sense, behavior genetics focuses on diversity. Without both genetic and behavioral diversity, there would be no need for the field of behavior genetics.

1.2.1 Reliable and Valid Measures of Behavior Are Necessary

The importance of properly measuring behavior in behavior genetic research cannot be overstated. To be useful in behavior genetic research, behavioral measurements must be both reliable and valid. **Reliable** measures are those that show consistency. If you step on a scale and it indicates that you weigh 155 pounds (70.3 kg), and then you step on it a second time a minute later and it indicates that you weigh 160 pounds (72.6 kg), then it is not a reliable scale. **Valid** measures are those that measure the intended construct. If you are interested in measuring height, you should use a ruler with inches (or centimeters), not a scale with pounds (or kilograms). Although it is true that on average taller people tend to be heavier than shorter people, weight is not a valid measurement of height.

Psychologists have developed and tested quite a large toolbox of reliable and valid behavioral measures to study human and non-human animal behavior. Commonly used types of behavioral measures to study human behavior in behavior genetics include self-report questionnaires, reaction-time tasks, and neuroimaging. Commonly used behavioral measures to study non-human animal behavior in behavior genetics include spontaneous activity (e.g., running wheel), beverage preference (e.g., two-bottle choice), and attack latency (e.g., resident-intruder paradigm). This text focuses significant attention on reliable and valid behavioral measurement because without it, genetic analysis is meaningless (see Box 1.1).

Box 1.1 Critical Concept: Measuring Behavior

Although it is easy to get excited about the spectacular technological advances in molecular genetics, it is important to keep in mind that the goal of behavior genetics is to understand the causes of individual differences in *behavior*. Therefore, in addition to being experts in genetics, behavior genetics researchers must also be experts in measuring behavior. Behavior genetics is a subfield of psychology that uses the tools and methods of genetics to better understand individual differences in behavior.

Psychologists have been diligently developing tools for measuring behavior for over a century. In some cases, the best way to learn about a person's behavior is to ask them questions. Such **self-report** can be done verbally during an interview or in writing by using a questionnaire.