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AN INTRODUCTION TO SOCIAL NEUROSCIENCE

The brain is the most complex organ in the known universe, and specifying the neural mechanisms underlying social structures and interactions has become one of the grand challenges for the neurosciences to address in the twenty-first century.[1] Such an endeavor is both exciting and daunting because it necessitates the integration of theories, methods, and data across levels of organization from multiple disciplines and social species. To meet this challenge, the field of social neuroscience has grown dramatically as an interdisciplinary science. Our goal in this book is to introduce you to this field.

1.1 The Evolution of Social Behaviors

Our journey begins with the question of how did social behaviors evolve? Social behaviors can be classified according to the fitness consequences for the actor and its social partners. Four types of social behaviors that are found in species ranging from bacteria to humans are:[2] (1) mutual benefit—a social behavior that benefits all involved in the interaction; (2) selfishness—a behavior that benefits the actor at the expense of the other(s) involved in the interaction; (3) altruism—a behavior that is costly for the actor but that benefits other(s); and (4) spite—a behavior that is costly for the actor and the other(s).[2]

Social behaviors that fall under the category of mutual benefit or selfishness have direct effects on the fitness of the actor and, therefore, are favored through natural selection. Social behaviors that fall under the category of altruism and spite reduce the fitness of the actor, but the same evolutionary processes can select for these behaviors when certain conditions set forth in Hamilton's rule are met.

According to Hamilton's rule, altruistic behaviors are favored when the cost to the actor is smaller than the product of the benefit to the other(s) and the relatedness of the other(s) to the actor, where genetic relatedness describes the genetic similarity between two individuals, relative to a reference population. For instance, positive relatedness means that two individuals share more genes than average, and negative relatedness means two individuals share fewer genes than average. By the same logic, spiteful behaviors are favored when the cost to the actor is smaller than the product of the cost to the other(s) and the negative relatedness of the other(s) to the actor, or when the mutually costly behaviors represent a cost to the actor that is smaller than the product of the benefit for a third party and the relatedness of the third party to the actor.[2,3]

It also follows from Hamilton's rule that genetic relatedness, which can be signaled by factors such as kin recognition, may play a larger role in the evolution of social behaviors that fall under the categories of altruism or spite than in the evolution of social behaviors that fall under the categories of mutual benefit and selfishness.

The evolutionary principles favoring social behaviors are the same across species, and social behaviors evolved long before the appearance of humans. The human brain shares many design features with those of other organisms, and both comparative studies and animal models play an important role in revealing the secrets of brain function. The human brain also differs from that of other species. Apparently uniquely, the human brain contemplates the history of the earth, the reach of the universe, the origin of our species, the genetic blueprint of life, and the physical basis of our own unique mental existence.[4] Two observations that arise repeatedly in our journey through social neuroscience are that (1) there are conserved neural, hormonal, cellular, and molecular mechanisms underlying social behavior; and (2) social connections (e.g., kinship), social complexity (e.g., possible interaction partners), and social and cultural learning are driving forces behind the evolution of the remarkable capacities of the human brain.

1.2 The Social Brain of the Desert Locust

Social species are so characterized because they interact frequently with members of their own species (or what is termed "conspecifics") to form structures (i.e., patterns of interaction such as pair bonds, mother-infant attachments, and teams) that extend beyond the individual. Frequent interactions with conspecifics introduces complexities, demands, challenges, dangers, opportunities, and benefits not faced by nonsocial species. As a result, not only does the brain underlie social processes and structures, but social structures and processes can influence brain function and structure. These influences are generally thought to occur over generations through evolutionary processes such as natural selection. However, the influence of the social environment on brain structures and function can also be seen within a lifetime.

At any single moment in time, an individual member of a social species may vary in terms of its position along a continuum of social integration (salubrious social connections and bonds) to social isolation (e.g., exclusion, neglect). Where an organism falls along this continuum can be studied longitudinally in natural settings or manipulated experimentally in the laboratory to investigate the causal effects of the social context. Research has shown that where an organism falls along this continuum can influence brain structures and functions.[5] We survey a number of such influences in chapter 2 but consider the desert locust (*Schistocerca gregaria*) as a case in point (figure 1.1).

The desert locust is found in Africa, Asia, and the Middle East. It is a voracious insect, eating its weight in fruit, leaves, seeds, flowers, stems, bark, and shoots. At 2 grams, the daily consumption of an individual insect is insignificant. However, in their gregarious state, desert locusts form swarms of fast flying insects numbering as many as 50 billion and consuming up to 200,000 tons of food per day. Swarms of desert locust have ravaged crops and spawned famine for centuries.

What makes the desert locust of special interest here is that it can switch back and forth between an asocial state and a social state. The asocial state is the more typical condition, during which period the locust generally avoids conspecifics. Under specifiable conditions (e.g., stimulation indicative of swarming), the locusts transform from a solitary state to a gregarious (social) state, at which point the brains of these locusts grow approximately 30% larger presumably to accommodate the additional information-processing demands of their now more complicated social environment (figure 1.1).[6]

The deprivation of these social connections leads to a return to the asocial state, along with a consequent reduction in brain volume. Importantly, the brains of these locusts do not grow generally, but rather the growth is in brain regions that are particularly important in the swarming phase (box 1.1).

Social processes in humans were once thought to have been incidental to human learning and cognition. However, there is growing evidence that this is not the case, and instead that the social complexities

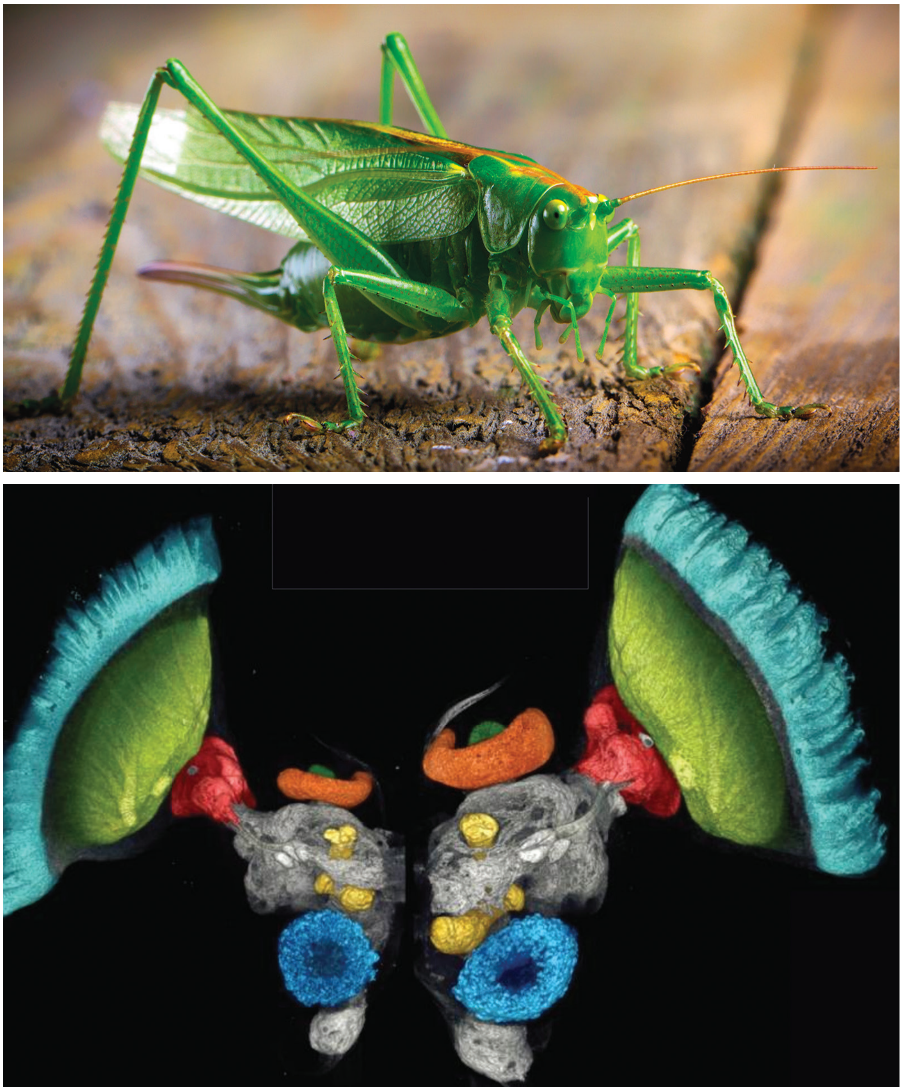

FIGURE 1.1. A. Top panel. The desert locust (*Schistocera gregaria*). iStock.com /MaYcal. B. Bottom panel. Half-brains of a solitarious locust (left) and gregarious locust (right) in frontal view to the same scale (scale bar, 1 mm). The locusts were of near-identical body size. This image shows the visual neuropiles of the optic lobe that include the medulla (lime), the lamina (cyan), and the lobula (red). Adapted from Ott and Rogers.[6] From Fig. 1 of Swidbert R. Ott and Stephen M. Rogers. Gregarious desert locusts have substantially larger brains with altered proportions compared with the solitarious phase. *Proceedings of the Royal Society B: Biological Sciences* http://doi.org/10.1098/rspb.2010.0694.

BOX 1.1. Use It or Lose It

Not the entire brain increases in size when submitted to complex social interactions. Because the brain is energetically expensive, it has been posited that specific brain regions should enlarge only when needed to meet functional demands.[46] In other words, the size of a neural region is related to its functional significance. If social connections/isolation follows the rule of "use it or lose it," regional neuroanatomical adjustments should occur contingent on the demands of social versus isolated living conditions. Consistent with this reasoning, experimental studies of social isolation or solitary states on brain size indicate that the effects are not uniform across the brain but instead are most evident in brain regions that reflect differences in the functional demands of solitary versus social living for that particular species. For instance, the gregarious locust has a larger midbrain to optic lobe ratio, and within both the visual and olfactory systems higher multimodal integration **centers** are disproportionately larger than the primary sensory neuropils.[6,48] The central complex, an important multimodal sensory and sensorimotor integration center, is also considerably larger in gregarious locusts. Despite the solitary desert locust having a smaller brain overall, the solitary locust has disproportionally large primary visual and olfactory neuropils, putatively due to the increased individual predation risk and the need for the solitary locust to detect visual stimuli at a greater distance.[48] Similar reductions in regional brain size in socially isolated animals have been found in other animals, including *Drosophila melanogaster*,[49] several species of honeybees,[(see 5 for review)] and mammals.[27] For instance, Technau[49] showed that socially isolated adult female wild-type Kapelle *Drosophila melanogaster* have fewer mushroom body fibers than do members of a control group—the mushroom bodies in *D. melanogaster* are involved in olfactory learning, multisensory integration, and memory.[(see 50 for review)] Other animals, like mice, that rely heavily on tactile inputs from whiskers have an enlarged sensory cortex. On the other hand, bats, which rely a lot on echolocation, have a large auditory cortex, and the highly visual short-tailed opossums have a large visual cortex.[27,51]

and demands of primate species have contributed to the evolution of the neocortex and to various aspects of human cognition.[7,8] For instance, cross-species comparisons have revealed that the evolution of large and metabolically expensive brains is more closely associated with social than ecological complexity.[9] Moreover, although human toddlers and chimpanzees have similar cognitive skills for engaging and interacting in the physical world, toddlers show more sophisticated cognitive skills than chimpanzees for engaging the social world.[10] We further address this topic in chapter 3.

1.3 Neuroscience and Social Neuroscience

The human brain is a surprisingly recent evolutionary development. If we compressed the 4.5 billion year–long history of the Earth into a 24-hour period, the first single-cell organisms would have emerged around 18 hours ago, the first simple nervous systems separating animals from plants would have emerged around 3.75 hours ago, the first brain would have emerged about 2.67 hours ago, the first hominid brain would have emerged less than 2.5 minutes ago, and the current model of the human brain would have emerged less than 3 seconds ago.

Despite the long evolutionary heritage, the human brain is not the most impressive looking structure. The average human brain measures about 140 millimeters (5.5″) wide, 170 millimeters (6.6″) long, and 90 millimeters (3.6″) high, and weighs about 1,300–1,400 grams (3 pounds). Yet the human brain is the most complex organ in the known universe. It consists of around 86 billion neurons, and each neuron is estimated to form around 5,000 synapses with other neurons, forming approximately 430 trillion synaptic connections for information transfer. If we were to develop a machine that could count all these connections at a rate of 1 per second, it would take more than 13.5 million years to complete the count for a single human brain. Moreover, these structures and transfers remain modifiable across the life span based in part on the environmental demands placed on the brain, including the demands placed on it through interactions with others.

The brain is the central organ of perceiving, identifying, and adapting to social and physical stressors via multiple interacting mediators from the cell surface to the cytoskeleton to epigenetic regulation and nongenomic mechanisms.[11,12] The brain has evolved to determine what is threatening to it, and to respond or adapt to the potential threat with a remarkable plasticity. By elucidating the underlying mechanisms of plasticity and vulnerability of the brain, social neuroscience provides a basis for understanding the efficacy of interventions for a broad variety of social disorders.[11–16] Social stressors cause an imbalance of neural circuitry that may alter one's cognitive or emotional state. This imbalance, in turn, affects systemic physiology via neuroendocrine, autonomic, immune, and metabolic mediators[14,17]. While acute vigilance or hyperattention to potential social threats may be adaptive, the chronic surveillance of the environment may be maladaptive and require intervention with a combination of pharmacological and behavioral therapies, as is the case for chronic loneliness.[17–19] While prevention is key, the plasticity of the brain gives hope for therapies that take into consideration individual differences, gender differences, and brain-body interactions.[11,12,17]

The scientific study of the structure and function of human brain plasticity is so complex that it requires a variety of basic, clinical, and applied disciplines.[20] It also requires comparative research across species as well as studies of healthy people, patients, and animal models to cover the terrain. Although scientific investigations of structure and function go hand in hand, differences in emphasis exist in this scientific frontier. The emphasis in some fields is on identifying constituent structures at different levels of organization, such as neuroanatomy. The emphasis on others is weighted more toward understanding the function of the brain and nervous system, such as the complementary fields of behavioral, cognitive, and social neuroscience.

Behavioral neuroscience, the oldest of these perspectives, replaced the black box between a stimulus and a response in behaviorism with the brain. Accordingly, the brain was viewed as an instrument of sensation and response, with representative topics of study including perception, learning, motivation, homeostasis, biological rhythms, and reproduction.

Cognitive neuroscience, which emerged in the early 1990s, grew out of the cognitive sciences to view the brain as the classic computer, with an operating system; input devices that were designed for selective input; output devices of various types; methods of representing, transforming, manipulating, and storing information; software programs that permitted incoming information to be combined with stored information to produce adaptable responses; and so forth. Accordingly, representative topics of study included attention, representations, memory systems, reasoning, decision making, executive functioning, and response inhibition and response selection.

Social neuroscience, which also emerged in the early 1990s, represents yet another broad perspective on brain function.[21] In social neuroscience, the human brain is regarded not as an isolated computer but metaphorically akin to a smart phone—computationally powerful, mobile, and broadband connected. The connection with other such devices—and sites that have been shaped or visited by other devices—is what makes our phones so powerful and so special, and the same is the case for the human brain.

The functions that are highlighted by this perspective go beyond the solitary computer to include the connections and coordination among interconnected computing devices as well as the structures and processes that were developed in the service of these devices (e.g., the existence and culture of social media). The brain functions that immediately come into focus from this perspective include communication, social perception and recognition, impression formation, imitation, empathy, competition, cooperation, pair-bonding, mother-infant attachment, bi-parental caregiving, social learning, status hierarchies, norms and cultures, social learning, conformity, contagion, social networks, societies, and culture.

The existence of connections between computing devices leaves them vulnerable to various forms of malware, including malicious software such as computer viruses, ransomware, spyware, Trojan horses, worms, adware, and scareware. The human brain is no different. Scientific investigations of the social brain have shown that humans are capable of altruism and salutary relationships and they are capable of deceptive, exploitive, and malicious interactions and relationships. Investigations discussed in this book are beginning to illuminate the biological mechanisms underlying salutary social interactions and relationships as well as protective mechanisms to reduce vulnerability to hostile interactions and exploitive interactions and relationships.

Behavioral, cognitive, and social neuroscience may look at the same construct or behavior but do so from different perspectives and interests. For instance, from the perspective of cognitive neuroscience, language is a system for the representation and processing of information within the brain; from the perspective of social neuroscience, language is a system for information exchange between brains, a system that promotes communication and coordination across discrete and sometimes distant organisms. This illustrates how each of these perspectives can provide important, *complementary* perspectives for understanding brain function.

In sum, social species are so characterized because through social recognition and interaction they form structures that extend beyond any individual member of the species. Social structures and processes differ across species but have evolved hand in hand with neural, hormonal, cellular, and genomic mechanisms because the consequent capacities and behaviors—such as communication, mutual aid, and mutual protection—helped these organisms survive, reproduce, and leave a genetic legacy. Social neuroscience is defined as the study of the neural, hormonal, cellular, and genomic mechanisms underlying social structures and processes. An important goal of social neuroscience is to identify these biological mechanisms and to specify the transduction pathways between neural and social structures and processes.

1.4 What Makes Us Human?

The question "what makes us human?" typically means, how are we different from other species? The debate over what differentiates humans from other species has a venerable history. Charles Darwin reasoned that the difference in mind between humans and the higher animals, great as it is, is one of degree and not of kind. For most of the twentieth century, research emphasized the similarities between the mind, brain, and biology of human and nonhuman animals, demonstrating that we are not unique in our use of language, tools, cultures, syntax, or even teachers.

"What makes us human?" here means what in our evolutionary past has contributed to the human brain and nervous system. In this section, we introduce the human brain from this perspective, and we elaborate on the evolution of the human brain in chapter 3.

Although humans are a unique species, the human body and brain share many design features with those of other organisms. Many of the structures and associated functions of the human brain and body are related to antecedents in other animals (box 1.2). These similarities are not always evident because selective evolutionary pressures may produce a discontinuity in the form or function of a structure across species. As neuroscientist Michael Gazzaniga[22] noted: "Just as gases can become liquids, which can become solids, phase shifts occur in evolution, shifts so large in their implications that it becomes almost impossible to think of them as having the same components" (p. 3).

The human brain has evolved yet differs from nonhuman brains in more fundamental ways than simply the size of the brain. Differences have been found in gene expression across neocortical layers of the human, in contrast to the nonhuman primate, brain, suggesting substantial neocortical reorganization.[23,24] The predominant neural circuit underlying sensory-motor hierarchies in nonhuman primates, for instance, may have yielded to a form that spans the cortex, develops late, and promotes intermodal integration, abstract representation, manipulation, and storage of information.[25] Moreover, astrocytes, glia cells, neuronal synapses, and morphology of cortical minicolumns are not the same in all animals but instead show an evolutionary expansion to support increased computational capacities across regions of the brain.[23,26–28] As the behavior of species becomes more complex, more room is needed for the increase in the number of cells and intracellular connections in the brain. Real estate within the cranial vault is precious, so an evolutionary adaptation is an increased convolution (wrinkling) of the cerebral cortex[29] (figure 1.2). Each of these solutions to the need for computational power emerged in the mammalian brain long before the appearance of humans, and each contributes to what makes us human today.

The vertebrate brain is composed of three major components: (1) the hindbrain, the evolutionarily oldest part of the brain, which includes

BOX 1.2. Integration of Human and Animal Research

The basic structure of various brain systems has been conserved in vertebrate species throughout evolutionary time. There are not only similarities across vertebrate brains in neural structures, but also in the systems that control gene activity and in the neurochemicals that influence neuronal functions (e.g., glutamate, gamma-aminobutyric acid [GABA], norepinephrine, dopamine, serotonin, corticotropin releasing factor, oxytocin, vasopressin, endorphins).[23,52,53]

These similarities make animal models an important source of information about brain structures and brain function in the neurosciences, and these models provide an opportunity to study ancient aspects of social motivations (e.g., pair-bonding, response to isolation, parental nurturing) through experiments that include techniques such as optogenetics, electrophysiology, and gene manipulations that are not possible in humans. Neuroimaging techniques in humans are more focused on the role of cortical structures, whereas animal models involving rodents are more focused on the role of evolutionarily older subcortical structures in social behavior. Neurobiologists Damian Stanley and Ralph Adolphs from the California Institute of Technology summarized the relative strengths and weaknesses of four animal groups commonly used in social neuroscience.[54]

Differences in neural structures have also evolved across vertebrate species based on their unique needs and adaptations, which makes comparative studies across species possible. For instance, rodents, compared to humans, rely on olfactory cues for information about their environment, and their olfactory bulbs are relatively large and evolved. Humans, in contrast, rely more on visual cues, and their visual cortices and associated regions are relatively large and evolved compared to those in rodents. The oxytocin receptors in prairie voles are located within the dopamine-rich area of the striatum, whereas the oxytocin receptors in montane voles are not. These differences in receptor distributions are associated with differences in pair-bonding (prairie voles form pair bonds, montane voles do not), and experimental studies demonstrated pair-bonding depends on oxytocin acting on receptors within the striatum.[55]

The integration of knowledge from human and animal studies is especially important in social neuroscience, with findings in human studies providing insights for animal experimentation, and animal studies providing insights into the molecular, cellular, and circuit-level attributes of the social brain.

areas such as the cerebellum, pons, and medulla; (2) the midbrain, which includes areas such as the tectum (superior and inferior colliculi) and tegmentum (red nucleus, periaqueductal gray, and substantia nigra); and (3) the forebrain, generally the evolutionarily newest part of the brain, which includes areas such as the cerebral cortex, amygdala, thalamus, and hypothalamus.

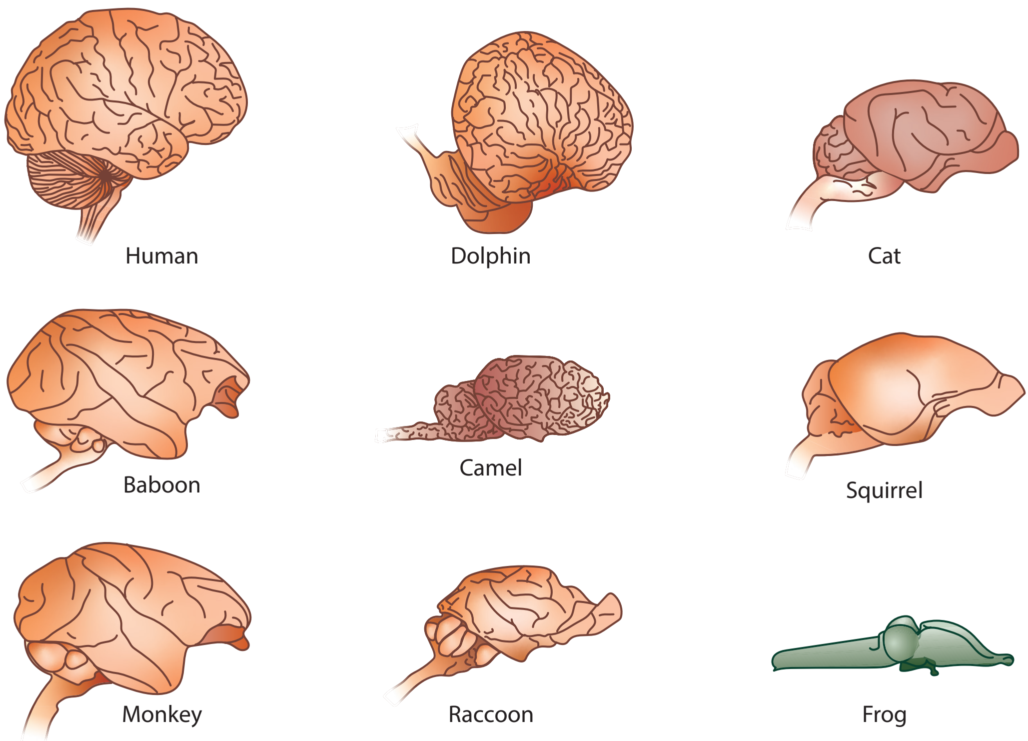

FIGURE 1.2. The gyrification (or wrinkling) of the cerebral cortex varies across species. Gyrification permits more brain mass to fit within a given volume. From https://serendipstudio.org/exchange/brains.

The cerebral cortex has two hemispheres (the right hemisphere and the left hemisphere), each in appearance the mirror image of the other. The surface of each of the cerebral hemispheres is characterized by gyri (ridges), sulci (shallow grooves between gyri), and fissures (deep grooves between gyri), which give the cerebral cortex its wrinkled appearance.

Major gyri and sulci divide each hemisphere into four lobes (figure 1.3): (1) the frontal lobe, the anterior portion of the cerebral cortex, which includes motor areas, supplementary, and premotor areas, areas involved in aspects of mentalizing and self-representation, language (e.g., Broca's area), planning, and executive functioning; (2) the parietal lobe, the middle portion of the cerebral cortex, which includes the somatosensory associative areas that interpret sensations as well as brain areas involved in visuospatial attention, mathematics, language comprehension, and abstract constructs (e.g., aspects of self-representation); (3) the temporal lobe, a lateral portion of the cerebral cortex, which includes the primary and associative auditory areas as well as areas

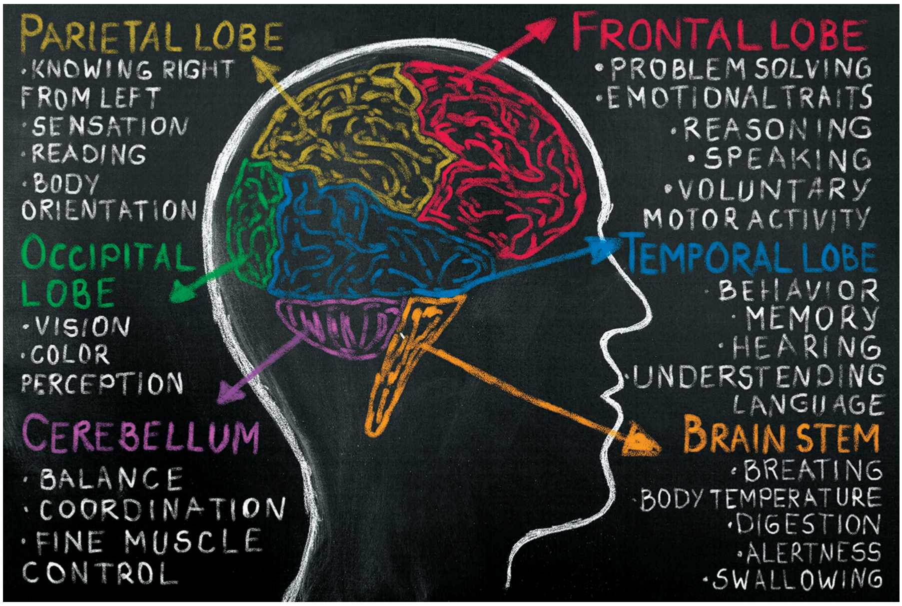

FIGURE 1.3. Each cerebral hemisphere consists of four lobes: the frontal lobe (red), parietal lobe (yellow), temporal lobe (blue), and occipital lobe (green). The cerebellum (purple) and brainstem (orange) are also shown here. Each lobe can have various functions (white). iStock.com/eli_asenova.

involved in memory, aspects of mentalizing, and social perception; and (4) the occipital lobe, the posterior portion of the cerebral cortex, which includes primary and associative visual areas. The left and right hemispheres are connected by a wide bundle of nerves called the corpus callosum.

The two hemispheres are central to a feat of the brain that appears to have emerged uniquely in humans. One function performed by the left hemisphere is to interpret events in a way that forms a coherent narrative. The interpretive function of the left hemisphere integrates information from the two hemispheres and associated operations of the brain to create this narrative.[30,31] These narratives may be confabulations—invalid narratives fabricated by the left hemisphere—but the resulting conscious experience is that the narrative is an accurate explanation for the observed events.[22] It is this left brain function that also provides for our unique ability to process vast amounts of contingently true information, which contributes to our unique social, cognitive, and environmental adaptability.

The notion that the left hemisphere functions like an Interpreter that fabricates a story—in many cases an erroneous story—to create a coherent personal narrative of events—past, present, and future—is contrary to the ancient notion that one can trust the accuracy of one's own conscious reasoning and interpretations. Indeed, this lay notion seems so beyond reproach that long ago common sense was given the mantle of being axiomatic—self-evident and unquestionable. And yet research on human brain function has shown that what seems self-evident or commonsense about one's own thoughts and behaviors cannot be taken as true any more than the commonsense notion that the sun and the stars circle around the earth can be taken as true.

In a classic series of experimental investigations, psychologists Richard Nisbett and Timothy Wilson[32] found that "when people attempt to report on their cognitive processes, that is, on the processes mediating the effects of a stimulus on a response, they do not do so on the basis of any true introspection" (p. 231). The results of their studies—and many that have since been conducted—indicate that self-reports of processes of this form tend to be invalid because (1) people can be unaware of the existence of a stimulus that influences a response, (2) they can be unaware of the existence of the response, (3) they can be unaware that the stimulus has affected the response, (4) they may have developed a false belief about the cause for a response, and (5) they may have overgeneralized a belief about a cause for a response. In short, these self-reports reflect the operation of the Interpreter within us trying to make sense of the world.

Self-reports of current conscious states or behaviors depend on our willingness to report what we are experiencing at a given moment in time. These are not equivalent to self-reports of the narratives or explanations we generate for our conscious states or behaviors—a conscious state that typically reflects the work of the Interpreter. For instance, when people are asked to rate what they feel after having been exposed to an advertisement, they are able to report on their conscious state. (Whether or not they are *willing* to report this state accurately is a different question.) However, when people are asked to rate how their exposure to an advertisement influenced what they feel, they typically feel able to do so but their reports depend on the operation of the Interpreter and are generally invalid. Nisbett and Wilson showed that even when such reports are accurate, the accuracy is the result of a lay theory of the effects of some stimulus being correct, not the result of people having access to the process on which they are reporting. People are willing to say more than they can know in large part because the brain functions to form coherent narratives from past and present events, resulting in people often having no clue about what they think they know versus what they can actually know. This issue will emerge throughout the book.

All the ways in which our brains differ from other brains and with what consequences is a story that has only begun to be written. What is clear is that the final story will not be self-evident and that, given the importance of our interactions with others, it is a story that social neuroscience will likely have a significant hand in writing.

1.5 Doctrine of Multilevel Analysis and the Golden Triangle

Social organisms are constituted at various levels of organization. Although not an exhaustive list, these levels include: (1) individual cells (e.g., nerve cells), which are an important unit of structure in living organisms and may serve a specific function(s); (2) tissues (e.g., nerves), which are made up of cells that are similar in structure and work together to perform a specific function(s); (3) organs (e.g., brain), which consist of tissues that work together to perform a specific function(s); (4) organ systems (e.g., nervous system), which consist of two or more organs that work together to perform a specific function(s); (5) individual organisms (e.g., humans), which refers to the entirety of a living thing that carries out basic processes such as taking in materials, releasing energy from food, releasing wastes, growing, sensing and responding to the environment, and reproducing; (6) dyads (e.g., mother-infant), referring to a pair of organisms who together perform social processes such as communication, coordination, mutual aid and protection, bonding, imitation, nurturance, cooperation, social influence, and social learning; (7) groups, which refers to sets of three of more organisms who operate together to perform social processes; and (8) society, which refers to a large group involved in persistent social interaction who share institutions and a distinctive set of beliefs and knowledge (e.g., norms, practices, and behaviors) transmitted through social learning (i.e., culture).

Mapping across systems and levels (from genome to societies and cultures) requires interdisciplinary expertise, comparative studies, innovative methods, and integrative conceptual analyses.[33,34] The *doctrine of multilevel analysis* in social neuroscience provides one such framework for the scientific investigation of social structures or processes across multiple levels of organization.[21] The doctrine includes three principles for formulating and interpreting investigations along the continuum of organizational levels.

The first is the *principle of multiple determinism*, which specifies that social behaviors may have multiple antecedents (causes) within or across levels of organization. For instance, one might consume a considerable quantity of pizza in an effort to remedy a low blood-sugar condition (biological determinant) or to win a food-eating contest (social determinant). Biological responses can also be multiply determined. Although immune response was once thought to reflect only physiological responses to pathogens or tissue damage, a more complete understanding of immunity has led to demonstrations of how a person's perceptions of his or her close personal relationships may impact inflammation and immunity.[35] Psychosocial stress, operating through the brain's perception of the meaning of events, can also increase proinflammatory cytokine production in the absence of infection or injury. Animal research has revealed related findings in mice: exposure of mice to two weeks of social isolation enhances tumor liver metastasis in part via its suppressive effect on the immune system of the host.[36] An important implication of the principle of multiple determinism is that *comprehensive* theories require a consideration of multiple factors, often from various levels of organization—for example, from the biological through the organismal to the social level.

The *principle of nonadditive determinism* specifies that properties of the whole are not always readily predictable by the simple sum of the (initially recognized) properties of the parts.[21] For instance, the behavior of nonhuman primates was examined following the administration of amphetamine or placebo.[37] No clear pattern emerged until each primate's position in the social hierarchy was considered. When this social factor was taken into account amphetamine was found to increase dominant behavior in primates high in the social hierarchy and to increase submissive behavior in primates low in the social hierarchy. A strictly biological (or social) analysis, regardless of the sophistication of the measurement technology, might not have unraveled the orderly relationship that existed.

Finally, the tendency is to think that biological factors determine social structures and processes, but the *principle of reciprocal determinism* specifies that there can be mutual influences among biological and social factors.[21] For example, it is unsurprising that the level of testosterone in nonhuman male primates has been shown to promote sexual behavior. However, it has also been shown that the availability of receptive females in a colony influences the level of testosterone in the male primates.[38,39] That is, the causal pathway between the biological and social level is bidirectional or reciprocal. There are numerous other such examples, such as maternal behavior altering the expression of genes in female rodent infants through a process of deoxyribonucleic

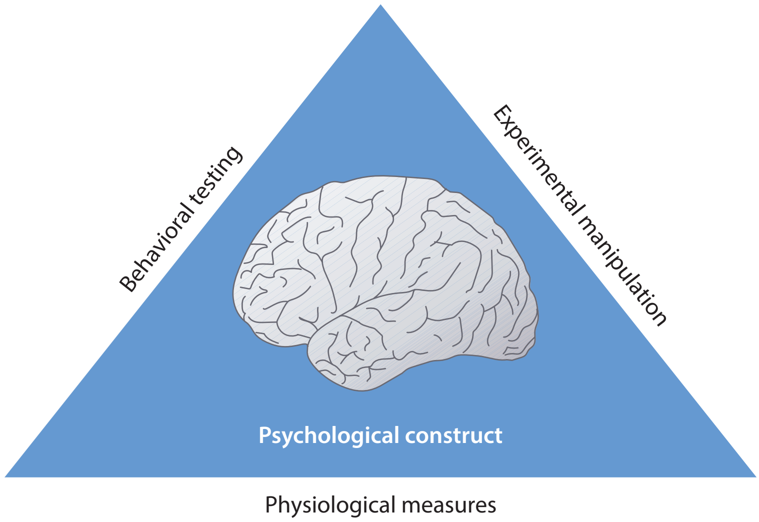

FIGURE 1.4. The golden triangle of social neuroscience research. This equilateral triangle represents the equal importance of three angles (behavioral testing, experimental manipulation, and physiological measures) to perform sound research on brain–behavior relationships. Based on Cacioppo & Cacioppo.[42]

acid (DNA) methylation, and the genes altered in this way later affecting the maternal behavior of these female rodents.[40] That is, the effects of social and biological processes can be reciprocal. One important implication is that comprehensive accounts of social behavior may not be achieved if the biological, cognitive, or social level of organization is considered unnecessary or irrelevant.

These principles point to the importance of multilevel analyses, but how might scientists use these principles in the design of their investigations? We have suggested a golden triangle approach.[41,42] The equilateral triangle in figure 1.4 represents the equal importance of three converging approaches that contribute to an understanding of the neural, hormonal, cellular, and genetic mechanisms underlying social structures and processes.

First, behavioral analyses and assessments are important. According to this approach, the functional consequences of a social phenomenon are decomposed into component representations and processes. These, in turn, may be decomposed into the computations that are likely to be implemented by the brain. What these component processes (or computations) might be will change with advances in theory, methods, and evidence. Evidence from functional or electrical neuroimaging is not necessary in such studies, but it may prove useful either as a source of hypotheses about what these constructs, components, or computations might be or as a means of performing a crucial test between competing hypotheses. Tasks can then be defined that permit the isolation of one or more specific component processes, as verified by behavioral analyses, which in turn permit finer grain analyses of brain function in subsequent research.

Because neuroimaging is noninvasive, it can have an important role to play in the development, testing, and refinement of theories of (and component processes underlying) social phenomena that are difficult to study in nonhuman animals. Correlative evidence from the waking brain using a variety of measurement techniques, therefore, constitutes a second leg of the golden triangle. The brain does not operate exclusively at the spatial level of molecules, cells, nuclei, regions, circuits, or systems, nor does it operate exclusively at the temporal level of milliseconds, seconds, minutes, hours, or days. Any single neuroimaging methodology provides a partial view of brain activity within a very limited range of spatial and temporal levels. Therefore, converging measures that gauge neural events at different temporal and spatial scales can be used to provide a more complete picture of brain function (figure 1.5).[42,43] The neuroimaging studies can then be designed to investigate one or more specific component processes or computations that were isolated in behavioral analyses.

Finally, the third leg of the golden triangle represents experimental evidence from animals and humans. Neuroimaging is a correlative methodology, so random assignment and experimental manipulations including reversible lesions and pharmacological interventions in humans and nonhuman animals are essential to further elucidate the causal role of any given neural structure, circuit, or process in a given task. The term *animal model* can refer to the assay or experimental procedure by which a treatment is produced or measured,[44] but we use it here to refer to investigations in which the participants are nonhuman social animals. We are not the first or the only social species, and the similarities and differences between humans and other social species make comparative, experimental, and mechanistic studies of nonhuman animals an important source of information regarding the role of specific neural, hormonal, and molecular mechanisms in social neuroscience. The protection and ethical treatment of these animals is therefore of paramount importance and is governed by the same ethical principles as is research on human participants.

Each of the legs of the golden triangle has limitations, but yield from the combination of the three is greater than the sum of the parts. Thus, for instance, functional and electrical neuroimaging represents an important part of the methodological armamentarium, but the resulting

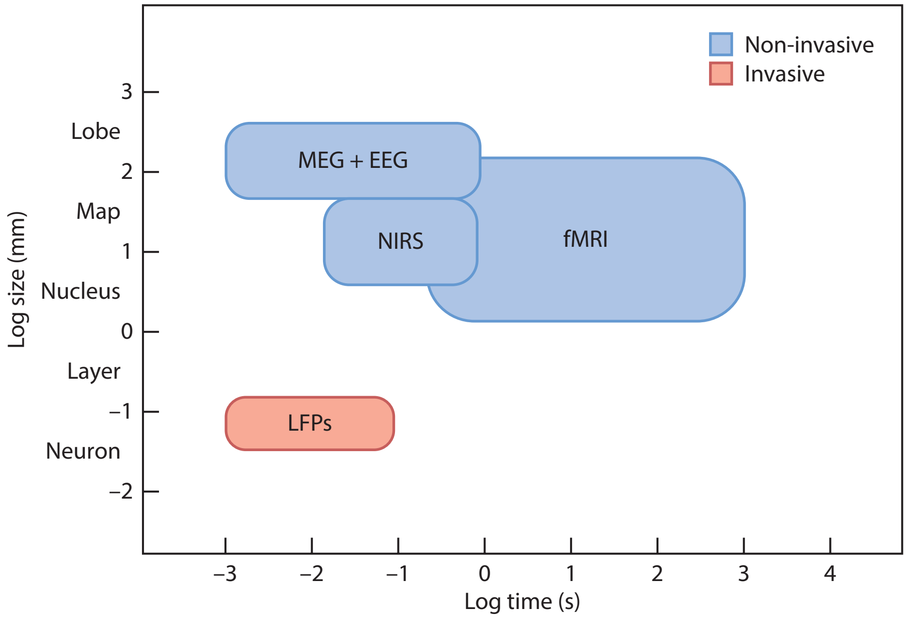

FIGURE 1.5. Illustration of functional neuroimaging and neurophysiological techniques showing comparison of spatiotemporal resolution and penetration depth of neurometabolic optical techniques. The *x*-axis (time in seconds today or size of object/animal/patients) and the *y*-axis (distance from neuron to lobe) are scaled logarithmically. Penetration depths are color-coded from noninvasive (blue) to invasive (red). LFPs = local field potentials, NIRS: near infrared stimulation, fMRI = functional magnetic resonance imaging, MEG + EEG = magneto-encephalography and electroencephalogram. Image is inspired from Van Gerven et al. (2009).[43]

knowledge is more likely to be beneficial when combined with conceptual analyses that decompose complex constructs into component structures, representations, processes, and computations; converging measures that gauge neural events at different temporal and spatial scales; behavioral measures that permit fine-grain analyses of brain–behavior associations; and experimental studies that test the putative role of specific brain structures, circuits, or processes.

1.6 Concluding Remarks

Social species are so characterized because through regular social recognition and interaction, structures (e.g., pair bond, group) are formed that extend beyond any individual member of the species. Social structures and processes differ across species but have evolved hand in hand with neural, hormonal, cellular, and genomic mechanisms because the consequent capacities and behaviors helped these organisms survive, reproduce, and leave a genetic legacy. Social neuroscience is defined as the study of the neural, hormonal, cellular, and genomic mechanisms underlying social structures and processes.

Social neuroscience is built on studies across levels of organization in which variables are measured and/or manipulated to determine the pathways and mechanisms operating within and between each of the levels of organization underlying a phenomenon. Teams of scientists who are investigating brain function in neurological patients, animal models, and healthy individuals are increasingly common. These interdisciplinary collaborations have capitalized on a variety of methods and techniques ranging from behavioral studies, neuroimaging techniques (e.g., magnetic resonance imaging, functional magnetic resonance imaging, high density electroencephalography, optogenetics, receptor autoradiography) to experimental manipulations of neural mechanisms (e.g., transcranial magnetic stimulation, optogenetics, viral vector gene transfer) across scales of neural organization in chimpanzees or healthy humans to cellular and molecular techniques. Even well-traveled techniques such as meta-analyses and electrophysiology have seen upgrades that, for instance, permit investigations of the source and chronoarchitecture of neural structures and processes. The development of experimental manipulations of neural processes in humans through, for instance, the use of transcranial magnetic stimulation and neurotransmitter agonists and antagonists has also helped determine the causal significance of specific neural regions in social cognition, emotion, and behavior. Finally, increases in computational speed and capacities are increasingly simplifying the problem of addressing questions across levels of organization that involve large datasets and/or previously computationally prohibitive simulations or analyses.

Moreover, the twenty-first century presents its own unique array of questions. The development and accessibility of the Internet have transformed major aspects of the social environment, including how and where people study, meet, shop, and interact. Understanding how online interactions are similar to and different from face-to-face social interactions and how they might best be performed to benefit users across the life span is of particular relevance to a world growing more and more dependent upon the Internet and social networking sites for social interactions. And the century is still young. What the short history of social neuroscience has shown is that the number of social neuroscience papers that are appearing in multidisciplinary science journals has grown dramatically since the field was first defined in 1992 (figure 1.6), and the field continues to attract some of the best and

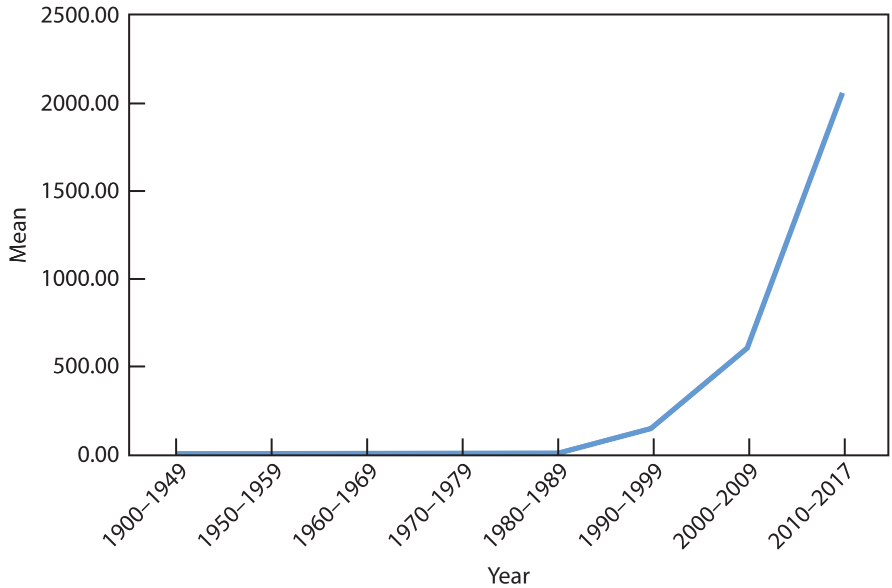

FIGURE 1.6. Mean number of scientific articles published per year on social neuroscience, based on a Web of Science literature search on the topic (social AND neuroscience) OR (social AND brain) for the periods of 1900–1949, 1950–1959, 1960–1969, 1970–1979, 1980–1989, 1990–1999, 2000–2009, and 2010–2017.

brightest young scientists across a wide range of disciplines, with high rates of citation of social neuroscience articles in their dominant disciplinary journals.[45]

The successes that social neuroscience has already met in its first few decades of existence suggest a promising future as it opens a critical avenue for better understanding the neural mechanisms underlying social structures, cognition, interactions, and behavior. A multilevel integration of the social, biological, and cognitive factors underlying behavior should also contribute to the development of new therapeutic interventions to address acute and chronic individual, communicative, and social disorders such as autism, psychopathy, and social phobias. The road ahead is replete with conceptual challenges and methodological issues, but it also promises exciting scientific discoveries. In short, the twenty-first century is an exciting time in which to be a social neuroscientist.

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