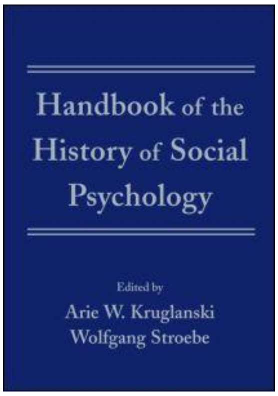

Handbook of the History of Social Psychology

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A History of Social Neuroscience

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6 A history of social neuroscience

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Psychological research during the 20th century championed psychoanalysis, behaviorism, and the cognitive sciences—all of which emphasized individualism. This research focus mirrored Western society, which saw advocates of individualism, such as Ayn Rand, Richard Dawkins, and Milton Friedman, elevated to celebrity status. In this context, it is easy to forget that humans are obligatorily a social species who, by definition, create emergent organizations beyond the individual—structures ranging from dyads and families to groups, communities, and cultures. These emergent structures evolved hand in hand with neural, neuroendocrine, cellular, and genetic mechanisms to support them because the consequent social behaviors helped these organisms survive, reproduce, and care for offspring sufficiently long that they too reproduced. *Social neuroscience* is an interdisciplinary field of research that has emerged over the past two decades to investigate these mechanisms and the social structures, factors, and processes with which they interface.

Why "social" neuroscience, and why now? Traditional neuroscience has for many years considered the nervous system as an isolated entity and largely ignored influences of the social environments in which humans and many animal species live. By the late 20th century, progress and new tools and methodologies in the neurosciences had brought this perspective to the doorstep of all areas of psychology. The Congressional declaration of the 1990s as the decade of the brain provided a clear signal to researchers, research institutions, scientific organizations, foundations and funding agencies, and the public that the neurosciences would be given the support to pursue more complex problems.

The new concepts, methods, and targets of investigations represented by the neurosciences were quickly embraced by the cognitive sciences, and the field of cognitive neuroscience threatened to replace the traditional field of cognitive psychology. Cognitive neuroscience and social neuroscience are related but represent complementary rather than redundant perspectives. If cognitive neuroscience metaphorically regards the brain as a solitary computer, social neuroscience metaphorically regards the brain as a mobile and broadband computer-node within a longstanding and evolving internet. This distinction is important because many of the most intriguing scientific problems facing humankind are, at least in part, social questions: What is the basis of a sense of the self and self–other distinctions; what are the processes underlying self-regulation, socialization, and acculturation; what situational and sociocultural factors optimize education and promote the development of excellence; what are the best means—individually, socially, and culturally—for dealing with life's stressors; how can we best promote positive health and health behaviors; how can we maximize social resilience; how can we develop and use technology in its various forms to best serve humankind; what is the basis of social inequality and how can we minimize if not eradicate it; and what is the place of humankind within the web of life? These questions, in turn, spawned questions about neural functioning, among them being what are the effects of social factors on brain and biological functioning, are there specialized circuits for social information processing, what is the nature of the interdependencies between genes and social environments, and what are the biological mechanisms underlying social cognition, social interactions, and group processes?

To make progress on these problems, something more is needed than a neuroscience focused exclusively on molecular, cellular, or even individual-level processes. In fact, we now recognize the considerable impact of social structures on the operations of the brain and body (e.g., see Anderson, 1998; Cacioppo et al., 2002). These social factors operate on the individual through a continuous interplay of neural, neuroendocrine, metabolic, and immune factors on brain and body, in which the brain is the central regulatory organ and also a malleable target of these factors. Social neuroscience emerged to investigate the nervous system and its manifestations at many interacting levels—from molecules to societies—and to bring together multiple disciplines and methodologies to define the emergent structures that characterize social species, generally, and that underlie human health and behavior, in particular.

When House, Umberson, and Landis (1988) published their finding in *Science* a quarter century ago that social isolation was as strong a predictor of broad-based morbidity and mortality as obesity, high blood pressure, and a sedentary lifestyle, they assumed that this association was attributable to the salubrious influence of friends and families on people's *health behaviors*. Something more interesting and more revealing appears to account for the biological effects of social isolation, however. The evidence suggests that the isolation of an individual member of a social species has direct, deleterious biological effects. Experimental studies in nonhuman social species, for instance, have found social isolation to decrease lifespan in the fruit fly (Ruan & Wu, 2008); promote obesity and Type 2 diabetes in mice (Nonogaki, Nozue, & Oka, 2007); exacerbate infarct size and edema and decrease post-stroke survival rate following experimentally induced stroke in mice (Karelina et al., 2009); delay the effects of exercise on adult neurogenesis (Stranahan, Khalil, & Gould, 2006); promote activation of the sympatho-adrenomedullary response to acute stressors (Dronjak, Gavrilovic, Filipovic, & Radojcic, 2004); and increase the growth of cancerous tumors in rats (Hermes et al., 2009); decrease open field activity, increase basal cortisol concentrations, and decrease lymphocyte proliferation to mitogens in pigs (Kanitz, Tuchscherer, Puppe, Tuchscherer, & Stabenow, 2004); increase the 24 h urinary catecholamine levels and evidence of oxidative stress in the aortic arch of rabbits (Nation et al., 2008); decrease the expression of genes regulating glucocorticoid response in the frontal cortex of piglets (Poletto, Steibel, Siegford, & Zanella, 2006); increase the morning rises in cortisol in squirrel monkeys (Lyons, Ha, & Levine, 1995); and profoundly disrupt psychosexual development in rhesus monkeys (Harlow, Dodsworth, & Harlow, 1965). These findings in nonhuman social species clearly cannot be explained in terms of friends and family motivating better health behaviors.

Born to the longest period of dependency of any species and dependent on conspecifics across the lifespan to survive and prosper, we do not fare well whether we are living solitary lives or we simply *perceive* we live in isolation (Cacioppo & Patrick, 2008). The properties of *Homo sapiens* responsible for success as a species are debatable, but it is clear that the number of genes and the size of the brain are themselves insufficient explanations. Estimates among biologists a decade ago were that 100,000 genes were needed for the cellular processes that are responsible for human social behavior, but it is now clear that humans have only a quarter that number of genes (Pennisi, 2005). The prefrontal cortex is thought to be particularly important for critical behaviors such as executive function, working memory and social emotions, yet the ratio of prefrontal to total cortical gray matter is no greater in humans than in nonhuman primates (Schoenemann, Sheehan, & Glotzer, 2005), and although humans may have more cortical neurons than other mammals, they have barely more than whales and elephants (Roth & Dicke, 2005). The specialized capacities of humans may result from increased number of synapses in the brain, greater cell packing density, and higher neural conduction velocities, raising the overall information processing capacity of the human brain (Emes, et al., 2008; Roth & Dicke, 2005). Other specialized capacities of humans range from hands with fingers and thumbs to social perception and cognition (e.g., imitation, theory of mind) and social bonding and language, which together promote complex and coordinated collective actions (Cacioppo et al., 2007; Calvin, 2004; Chicago Social Brain Network, 2010; Gazzaniga, 2008; Hrdy, 2005; Brothers, 1990b). Simply stated, we are biological as well as social animals, and biological as well as social factors need to be considered if comprehensive theories of human behavior and of human brain function are to be developed. Accordingly, over the past two decades, interest in the field coalesced across a wide range of scientific disciplines.

The historical roots of the field of social neuroscience run deep, however. Our goal in this chapter is to trace some of the major historical roots and survey selected branches that have sprouted in the field. Interested readers may also wish to consult Matusall, Kaufmann, and Christen (in press), who review the history of the emergence of social neuroscience as a new academic discipline and trace its origins to the early 1990s. When social neuroscience was first proposed, it was grounded in a conceptual framework termed the "doctrine of multilevel analysis" (Cacioppo & Berntson, 1992b). We begin our historical survey with this grounding.

The doctrine of multilevel analysis

Human behavior can be parsed into levels of organization; that is, different scales of representation, ranging from the molecular to the geopolitical. What constitutes a level of organization, at least at the lower levels, is often guided by knowledge of anatomy and physiology, but the ultimate criterion is the usefulness of the posited organization in shedding light on some designated behavioral phenomenon (Marr, 1982). The terms "social" and "neuroscience" refer to *sets* of levels of organization, and their use is entirely compatible with monism. The constructs developed by behavioral and social scientists, for instance, provide a means of understanding highly complex activity without needing to specify each individual action by its simplest components, thereby providing a cognitively efficient way of referring to components of complex systems. By analogy, chemists who work with the periodic table on a daily basis use recipes rather than the periodic table to cook, not because they think the recipes couldn't be expressed as chemical equations, but because doing so would be cognitively inefficient if their goal was simply to prepare a meal. The efficiency of expression is not the only issue, however. The concepts defining fine cuisine are not part of the discipline of chemistry. The theoretical terms of the behavioral and social sciences are similarly valuable in relation to those of biology, but can be informed and refined through integration with theories and methods from the neurosciences. This is so because theories provide hypotheses about the manifestation of behavior across levels of organization, methods permit these hypotheses to be tested, and the empirical tests can be used to support, reject, or refine these theories. These developments, in turn, can lead to a redefinition or refinement of what is meant by the constituent levels of organization.

A social interaction is the product of the operation of multiple psychological constructs, each of which represents a complex set of integrated component processes, each of which in turn can be further divided into specific information-processing operations (computations) performed by various regions of the brain. As a consequence, social interactions tend to be associated with strong activation of most regions of the brain, but this activation reflects the operation of so many different constructs, component processes, and computations that it is not a particularly useful scientific result. The development and application of neuroimaging methods offers a powerful means to study brain functions, but the resulting knowledge is more likely to be beneficial when these methods are combined with: (a) conceptual analyses that decompose complex psychological constructs into component structures, representations, processes, and computations; (b) converging measures that gauge neural events at different temporal and spatial scales; (c) behavioral measures that permit fine-grain analyses of brain–behavior associations; and (d) experimental (e.g., lesion, transcranial magnetic stimulation) and nonhuman animal studies that test the putative role of specific brain structures, circuits, or processes. In addition, quantitative meta-analyses are important to move beyond idiosyncrasies of individual studies, and neurodevelopmental investigations can contribute to our understanding of brain–behavior associations (Decety & Cacioppo, in press). When this is done in research, specific regions (e.g., the region of brain tissue surrounding the temporoparietal junction) are found to be associated with specific operations (e.g., attentional shifting and control) that are involved when an individual, for instance, takes the perspective of a person with whom they are interacting.

The goal of social neuroscience is to focus intellectual energy and unify scholarly activity across levels of organization to produce more comprehensive accounts of the human brain, mind, and behavior. Three specific principles articulated when the term "social neuroscience" was first introduced (Cacioppo & Berntson, 1992a, 1992b) outline the logic for the view that human functioning may be best captured by the confluence of social, behavioral, and neuroscientific endeavors. The first, the principle of *multiple determinism*, specifies that a target behavior at one level of organization can have multiple antecedents within or across levels of organization. On the biological level, for instance, researchers identified the contribution of individual differences in the endogenous opioid receptor system in drug use, whereas on the social level investigators have noted the important role of social context. Both operate, and our understanding of drug abuse is incomplete if either level is excluded, as the social context has been found to interact with individual differences at the level of receptors in the brain (Dalley, et al., 2007). Similarly, immune functions were once considered to reflect specific and nonspecific physiological responses to pathogens or tissue damage. It is now clear that immune responses are influenced by central nervous processes that, in turn, are affected by social interactions (Hawkley & Cacioppo, 2007). An understanding of human immunocompetence in everyday life will be inadequate in the absence of considerations of social and behavioral factors. An implication of this principle is that comprehensive theories of behavior will require a consideration of factors from multiple levels of organization. Accordingly, advances in the neurosciences and the social sciences may occur by increasing the scope of analysis to include the contributions of factors and processes from both social and neuroscientific perspectives.

An important corollary to this principle is that the mapping between elements across levels of organization becomes more complex (e.g., many-to-many) as the number of intervening levels of organization increases (Cacioppo & Tassinary, 1990a). One implication is that the likelihood of complex and potentially obscure mappings increases as one skips levels of organizations. This is perhaps one reason that going from the genotype to endophenotypes and from endophenotypes to phenotypes has proved to be more tractable than going directly from the genotype to phenotype (Cacioppo, Berntson, & Thisted, 2008).

The second principle is of *nonadditive determinism*, which specifies that properties of the whole are not always readily predictable by the simple sum of the properties of the parts. Consider an illustrative study by Haber and Barchas (1984), who investigated the effects of amphetamine on primate behavior. The behavior of nonhuman primates was examined following the administration of amphetamine or placebo. No clear pattern emerged between the drug and placebo conditions 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. The importance of this study derives from its demonstration of how the orderly mapping between the biological and social levels of organization would remain opaque until the analysis is extended across these levels of organization. A strictly physiological or social analysis, regardless of the sophistication of the measurement technology, would not have revealed the orderly relationship that existed.

The third principle is of *reciprocal determinism*, which specifies that there can be mutual influences between biological and social factors in determining behavior. For example, not only has the level of testosterone in nonhuman male primates been shown to promote sexual behavior, but the availability of receptive females influences the level of testosterone in nonhuman primates (Bernstein, Gordon, & Rose, 1983). This principle, too, implies that comprehensive accounts of behavior cannot be achieved if the biological or the social level of organization is considered unnecessary or irrelevant.

In sum, social neuroscience is characterized by its multilevel, integrative analyses. In the remainder of this chapter, we survey some of the roots of social neuroscience and the new branches that have sprouted. This survey suggests that the field is flourishing in part because of the increasingly sophisticated instrumental techniques that have furnished novel methods to map the functional anatomy of the brain, neural circuits, endocrine systems, and cellular and molecular processes. But the field is also flourishing because of our history. Social neuroscience, like other disciplines, is the product of cumulative knowledge. Contemporary scientists stand on the shoulders of those who went before. From this perch it is now possible to see that the bounded fields of the 20th century are related parts of the same landscape. This is a requisite step for bringing research on pieces of related problems together to address bigger questions and to develop more comprehensive scientific theories. The conceptual questions in social neuroscience have captured the imagination of a talented new generation of scientists (Adolphs, Baron-Cohen, & Tranel, 2002; Lieberman, Berkman, & Wager, 2009; Phelps, Rand, & Ryan, 2006). As Frith and Wolpert (2004) note, uncovering the biological mechanisms underlying social interactions is one of the major problems for the neurosciences to address in the 21st century. To address many of the big questions in the field requires larger and more interdisciplinary teams than were common in the prior century. Scientific teams of this sort are the rule rather than the exception in social neuroscience. The obstacles of geographical boundaries between scientists are diminishing, and the quality of scientific teams is no longer hostage to the quality of the faculty in a particular department, region, or nation. Social neuroscience is now an active area of research in every continent except Antarctica. In the next section, we trace illustrative roots of this field.

Roots of social neuroscience

A social approach that treats the individual as having no biological history or influence, or a biological approach that treats the individual organism as the broadest legitimate unit of organization, may be sufficient to illuminate some aspects of development and behavior but, as outlined above, neither is likely to provide a comprehensive account of human behavior. The study of the mind by biological, behavioral, and cognitive scientists in the latter half of the 20th century tended to focus on single organisms, organs, cells, intracellular processes, and genes. Social factors in this context were viewed often as noise to be ignored or, at best, as of minimal interest with respect to the basic development, structure, or processes of the brain and organism. To the extent that social factors were suspected of being relevant, their consideration was thought to so complicate the study of brain and behavior that they were not a priority (Llinás, 1989). The approach of social scientists throughout most of the 20th century was no less narrowly focused than that of biologists. World wars, a great depression, and civil injustices made it amply clear that social and cultural forces were too important to address to await the full explication of cellular and molecular mechanisms (Allport, 1947). Although exceptions can be found (Carter, Lederhendler, & Kirkpatrick, 1999; Kaplan & Bloom, 1960; Maclean, 1949; Matusall et al., in press; Shapiro & Crider, 1969), social factors were routinely ignored in the neurosciences, and biological events and processes were routinely ignored in cognitive and social sciences (Gilbert, Fiske, & Lindzey, 1998). This was not the case when the discipline of psychology was forming.

In 1808, Franz Joseph Gall argued that personality, mentation, and social behaviors were organized regionally in the brain and that the bumps on the skull corresponded to these localized functional organizations in the brain. Although naïve on a number of dimensions, Gall set the stage for theory and research on the localization within the brain of psychological functions. For instance, John P. Harrison led the arguments against Gall's phrenology by 1825.

Herbert Spencer's (1897) *Principles of Psychology* begins with the notion that many species, including humans, are social by nature. In this text, Spencer reasons that the tendency to affiliate with conspecifics serves an adaptive function, especially in the area of self-defense because of the safety provided by large numbers who stood together against threats and attacks. Spencer posited that these species developed feelings of pleasure in affiliation and feelings of displeasure when deprived of interaction with conspecifics. Together, this biological carrot and stick produced high levels of social contact and sympathy among members of these species.

In *Descent of Man*, Charles Darwin (1871) sought to address critics of the evolutionary theory he outlined in *Origin of Species* (1860). One such criticism was the perception that members of social species engaged in behavior that might be described as cooperative, altruistic, or mutual aid. Darwin proposed a form of natural selection that operated at the level of the group: "A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good would be victorious over most other tribes; and this would be natural selection" (Darwin, 1871). The principle of group selection was embraced and applied liberally until George Williams (1966) argued that traits (i.e., behavioral tendencies) that benefit the group at the expense of the individual would evolve only if the process of group selection was great enough to overcome selection within groups; and group selection is nearly always weak, so that group-related adaptations do not exist (Wilson & Wilson, 2008). Within a decade of Williams' influential paper, Richard Dawkins (1976) popularized the notion that traits that evolve are adaptive at the gene level through his use of the metaphor of the selfish gene. Genes serve their own selfish interests in the sense that whatever contributions are made by a gene, or set of genes, to an organism's structure and function are passed on to the next generation if and only if the gene made its way to the gene pool. If the genes acted selfishly, and if group selection did not exist, it was easy to reason that individuals also acted selfishly. This, in turn, appeared to provide a scientific rationale for focusing on the individual organism as the largest biological unit of analysis.

The notion of selfish genes is entirely compatible with the evolution in humans of a powerful "social brain"—a large cerebral cortex and an interconnected limbic lobule that together are sensitive to the complexities of physical and social environments (e.g., see Dunbar, 2011). Central to this complexity is the long period of dependency of the human infant and the interdependencies of adult humans for survival, especially in hostile environments (e.g., warfare). For the selfish gene to contribute its DNA to the ongoing gene pool, the individual must not only reproduce but also cooperate with others to assure that his or her offspring also grow to maturity and reproduce. Genetic selection in humans therefore appears to have resulted in a social brain that seeks meaning and connection with individuals and with social entities that extend beyond other individuals. Although concepts of genes and gene–environment interdependencies had not yet emerged in the 19th century, Francis Galton framed the contributions of heredity and environment to behavior as "nature and environment" in 1876.

A few well-publicized clinical cases in the 19th century provided early signs that the human brain acted more like an embodied, wirelessly connected broadband computing device responsible for social cognition, interpersonal processes, and behavior than a solitary computing device. The most famous is the case of Phineas Gage, a young American railroad construction supervisor who, in 1848, accidentally detonated a dynamite blast, rocketing a tamping rod through his eye and skull and decimating portions of the orbitofrontal and ventromedial cortex (Damasio & Grabowski, 1994). Gage was taken to a local physician, John Harlow, who treated his wound, blood loss, and subsequent infection (Harlow, 1868). He soon recovered from the life-threatening nature of his accident, but historical reports suggest that he did not recover his former self (Damasio & Grabowski, 1994; Haas, 2001). Prior to the accident, Gage was characterized as energetic, friendly, and reliable. Within a few months after the accident, Gage began acting in a fitful, irreverent, grossly profane manner, showing little deference to other workers. Described as impatient and obstinate yet capricious and vacillating, Gage was unable to proceed with any plans. He became incapable of holding a job or planning his future, and his friends complained that Gage was no longer the person they had known. He died penniless on 21 May 1860, thirteen years after the accident, more an abomination than a shadow of his former self.

In a second case, also around 1860, a patient who had suffered a neurosyphilitic lesion in the frontal part of his brain was institutionalized in Paris, France, and was attended by the physician Paul Pierre Broca. The patient, Leborgne, was known as "Tan" because this was the only word he was left able to speak (Schiller, 1979). In other respects, Leborgne was more normal. It was known by 1836 that damage to the left hemisphere could adversely affect speech, but Broca determined in the postmortem autopsy that Leborgne's lesion was in the third circumvolution of the frontal part of his left hemisphere (specifically, the posterior third of the inferior frontal gyrus). This area became known as *Broca's area* and was surmised to be the "speech center" of the brain, and such aphasias tend to have deleterious effects on patients' lives because of what they do to their ability to communicate with and relate to others.

The third is the case of an Italian peasant named Bertino, who suffered a head injury that left him with part of his frontal lobes exposed (Raichle, 2000). Angelo Mosso (1881), an Italian physiologist, observed sudden increases in the magnitude of the pulsations over the frontal lobes with the ringing of the local church bells and the chiming of a clock that signaled the time for required prayer. Mosso suspected that these changes in blood flow reflected Bertino's thoughts about prayer. When Mosso asked Bertino if this were true, he observed changes in blood pulsation as Bertino processed the question and answered "yes." Mosso further noted that the changes in brain pulsation were unrelated to any change in heart rate or blood flow to Bertino's forearm. When Mosso subsequently asked Bertino to multiply 8 by 12, he again observed an immediate increase in brain pulsation and another just before Bertino responded with an answer. These observations set the stage for contemporary functional brain mapping using hemodynamic measurements (Raichle, 2000).

Ideas about the anatomical basis of functional localization in the cortex have been debated for hundreds of years, but research on primary sensory cortices (Munk, 1900; Tunturi, 1952) and on somatosensory regions (Schaltenbrand & Woolsey, 1964) contributed to the refutation of the hypothesis that the brain was a homogeneous tissue that depended on total mass to carry out functions (Uttal, 2001). A fundamental assumption underlying many brain-imaging studies in social neuroscience is that there is a localization of information-processing components that bear on social cognition and behavior. The cases of Gage, Leborgne, and Bertino contributed to the view in the neurosciences that the lesion of circumscribed areas of the brain could cause the loss of very specific mental or nervous functions in humans, and to the complementary view that activity in circumscribed areas of the brain could reflect very specific mental or nervous functions in humans. Social affiliation and "swarming" in the locust, for example, appears to be controlled by a single transmitter (serotonin) acting within a circumscribed system (Anstey, 2009). In humans and other mammals, however, there is likely a limit to neurofunctional specificity, and distributed processing clearly exists within neural circuits involved in the orchestration of complex social cognition and behaviors. These celebrated case studies nevertheless stimulated research on the anatomical differentiation of social processes.

Finally, the 19th-century neurologist John Hughlings Jackson, in his essay "Evolution and Dissolution of the Nervous System," emphasized the hierarchical structure of the brain and the *re-representation* of functions at multiple levels within this neural hierarchy (Jackson, 1958/1884). Implicit in his message was the fact that information is processed at multiple levels of organization within the nervous system. Primitive protective responses to aversive stimuli are organized at the level of the spinal cord, as is apparent in flexor (pain) withdrawal reflexes to noxious stimuli. These primitive protective reactions are expanded and embellished at higher levels of the nervous system (see Bernston, Boysen, & Cacioppo, 1993). The evolutionary development of higher neural systems, such as the limbic system, endowed organisms with an expanded behavioral repertoire, including escape reactions, aggressive responses, and even the ability to anticipate and avoid aversive encounters. Evolution not only endowed us with primitive, lower-level adaptive reactions, but also sculpted the awesome information-processing capacities of the highest levels of the brain to permit the moderating influence of social and contextual factors. At progressively higher levels of organization, there is a general expansion in the range and relational complexity of social and contextual controls and in the breadth and flexibility of discriminative and adaptive responses (Bernston et al., 1993).

Adaptive flexibility of higher-level systems has costs, however, given the finite information-processing capacity of neural circuits. Greater flexibility implies a less rigid relationship between inputs and outputs, a greater range of information that must be integrated, and a slower serial-like mode of processing. Consequently, the evolutionary layering of higher processing levels onto lower substrates has adaptive advantage in that lower and more efficient processing levels may continue to be expressed. For example, pain withdrawal reflexes, mediated by inherent spinal circuits, can manifest in rapid protective responses to pain stimuli. At the same time, however, ascending pain pathways convey information to higher levels of the brain that mediate more complex affective, cognitive, and behavioral reactions such as fear, anxiety, avoidance, and aggression. Although reflex responses provide a rather rigidly organized prepotent response, they are not immutable, as higher neurobehavioral processes can come to suppress or bypass pain withdrawal reflexes (e.g., self-injecting insulin or recovering a billfold from a fire). Together, the heterarchical structure of the central nervous system envisioned by John Hughlings Jackson and detailed by Sherrington (1906) provides the neurobehavioral foundation for automatic and controlled information processing.

By the early 20th century, William McDougall (1911) was building on early views of the importance of biological and social factors in human behavior in his seminal text, *Introduction to Social Psychology*. Spencer's early views played an especially important role, as McDougall emphasized the biological predispositions that led to social behavior. Among the predispositions he described were innate mechanisms through which two individuals could come to share emotional responses. These mechanisms were largely descriptive rather than explanatory, however, as a growing list of instincts was posited to "explain" complex social behavior. As a consequence, this approach collapsed—an outcome that could be repeated if brain regions that are identified in neuroimaging studies simply replace instincts as "explanations" for social cognition and behavior (cf. Cacioppo et al., 2003). What might have rescued instinct models, and is now important for neuroimaging approaches, is the recognition of the principle of *multiple determinism*—that processes have determinants across levels. Although it is legitimate to work solely within a single level, the meaningful development of understanding will require that events and processes at one level of organization be understood or relatable to those at other levels. Ideally, the concepts and terms of distinct levels would ultimately be calibrated and refined by knowledge derived from other levels of analysis. In this fashion, patterns of neural activation may be even more informative to the extent to which they could be related to specific neurobiological processes and computations, as well as to psychological states.

Over the course of the 20th century, scientific disciplines in the biological and behavioral sciences, including psychology, began to diversify, as specialties emerged, and disciplinary, programmatic, and economic factors contributed to progressive insularity. In 1921, for instance, the American Psychological Association launched the *Journal of Comparative Psychology*, which combined the *Psychobiology* journal and the *Journal of Animal Behavior*. By the middle of the century, this journal had become the *Journal of Comparative and Physiological Psychology*. It was then divided again in the early 1980s to become (again) the *Journal of Comparative Psychology* and a new journal, *Behavioral Neuroscience*. Within the comparative literature, Konrad Lorenz's (1935) seminal work on imprinting in goslings caught the attention of John Bowlby (1969), who proposed that similar processes of attachment operated in humans. Although food is essential for survival, positive tactile contact has been found to be a stronger determinant of mother–infant attachment than is feeding, and its lack leads to devastating consequences for the individual and abnormal social behavior (Harlow et al., 1965). These works stimulated an area of research on the neurobiology of attachment and affiliation that remains active today (e.g., Hofer, 2009; Insel & Fernald, 2004; Meaney, 2003). The impact of this work was felt more in the field of social development than in the field of interpersonal processes, however, largely because the latter was so heavily influenced by cognitive approaches.

Behaviorism was already the dominant perspective when Watson and Rayner (1920) published their studies of Little Albert, the subject used in their work on the classical conditioning of fear. The polygraph was introduced shortly thereafter to distinguish lies from truthful verbal reports (see Committee to Review the Scientific Evidence on the Polygraph, 2003). Not coincidentally, the Rorschach inkblot test was introduced at this time for the purpose of assessing mental states and dispositions that people were unable or unwilling to report. Four decades later, Cook and Selltiz (1964) reviewed physiological measures for the purpose of achieving objective measures of states and processes people were unable or unwilling to report.

Floyd Allport (1924, p. 31) presaged contemporary perspectives on the social brain in his text *Social Psychology*. Attention to biological as well as social determinants of human behavior was evident in Murchison's (Murchison & Allee, 1935) *Handbook of Social Psychology*, as well, but this *Handbook* was widely regarded as having missed the mark. In 1947, in the inaugural presidential address to Division 8 of the American Psychological Association, published in the *Psychological Review*, Gordon Allport argued that social psychology should reject developmental, comparative, and biological analyses of social behavior and focus instead on situational determinants. The subsequent editions of the *Handbook of Social Psychology* published in the 20th century give little attention to genetic or biological factors beyond the concept of arousal—a concept that emerged from the work of Papez (1937) on the limbic lobe, Moruzzi and Magoun (1949) on the reticular formation, Maclean (1949) on the triune brain, Campbell and Stouffer (1955) and Cooper (1959; Cooper & Singer, 1956) on racial attitudes, Lindsley (1957) on motivation, and Duffy (1957) and Malmo (1959) on the neurophysiology of activation. During this same period, research in the neurosciences was uncovering specific social and behavioral effects that could not be explained in terms of arousal. Among the significant discoveries were Egas Moniz (1937) and Freeman, Schoenfeld, and Moore's (1936) work on frontal lobotomy, Kluver and Bucy's (1937) research on bilateral temporal lobectomies, Olds and Milner's (1954) work on the rewarding effects of hypothalamic stimulation, Penfield and Rasmussen's (1950) reports on the specific sensory and motor effects of brain stimulation in humans, Karlson and Luscher's (1959) description of pheromones, and Luria's (1966) neuropsychological studies. It is not that the abyss between the social and biological sciences was too wide to be bridged, as illustrated by the work appearing during this period. Strong linkages spanning these broad fields were not constructed in part because the *Zeitgeist* in these fields did not favor interdisciplinary work, at least research that reached quite this far from the parent discipline, and consequently the work was either not read or not regarded as relevant to the problems that were being addressed at the time. It is worth noting that computers were still in their infancy. Quantifying and performing multivariate analyses of complex measurements across levels of organization represented a major obstacle, and digitized scientific literature and search engines were still a half century away. The field of social neuroscience would likely not have emerged in the late 20th century if not for these scientific innovations.

In 1962, Stanley Schachter and Jerome Singer published their paper, "Cognitive, social, and physiological determinants of emotional state." The thrust of their two-factor theory of emotion was that the sensations derived from a large and unexpected increase in physiological arousal could be experienced as widely different emotions, depending on the circumstances covarying with these sensations. Two years later, Leiderman and Shapiro (1964) published a small edited book on *Psychobiological approaches to social behavior* that depicted the impact that social factors such as conformity could have on biological processes.

The concept of arousal and its putative effects on cognition, emotion, and behavior played a central role in theories of social behavior for decades (e.g., Lanzetta & Kleck, 1970), but the emphasis was on perceived arousal or beliefs that had showed an arousal response rather than on an actual physiological arousal response (Valins, 1966; for a review, see Cacioppo, Berntson, & Crites, 1996). The subsequent work on nicotine and on the social and environmental influences on food intake by Schachter (1978) and his student, Judy Rodin (1980), represented an exception as it bridged to emerging work on the psychobiology of hunger and thirst (Berthoud & Morrison, 2008). Interestingly, Schachter (1978) did not envision or champion integrative research across multiple levels of organization which forms the basis for contemporary social neuroscience (Cacioppo, Berntson, Sheridan, & McClintock, 2000); he argued for substitutive reductionism:

> most complex behavior cannot as yet be understood in purely biological terms . . . when we do finally know enough biology and biochemistry, psychological kinds of explanations become superfluous.
>
> (pp. 433–434)

In contrast to Schachter's assertion, optimal reductionism does not entail substitutionism, but rather *calibrative reductionism* where events at higher levels of analysis may come to be understood at other levels of analysis, and to mutually enrich those lower-level understandings in the process. An example comes from the psychophysiological literature on stress-related ulcers. Since Brady's studies in the 1950s of gastric ulcers in "executive monkeys" whose actions were responsible for the delivery of aversive shocks, there has been a long history of investigation of the effects of psychological stress on the development of ulcers (Brady, 1958; Weiss, 1978). In the 1980s, this perspective was shattered. Barry Marshall's (for a review, see Marshall, 2002) work claimed that ulcers were the result of infection by the bacteria *Helicobater pylori*. Although it was initially scoffed at by the medical establishment, it is now clear that many cases of gastrointestinal ulcers are indeed bacterially induced. For his pioneering work, Marshall won the 2005 Nobel Prize in Physiology and Medicine. A secondary consequence of this development, however, was a strident devaluation by some of the decades of research on psychological stress and ulceration. This might be considered an illustration of Schachter's *substitutive reductionism*. However, over half the world's population harbors *H. pylori*. Why are they not all ulcerated? As it turns out, there are powerful influences of psychological stress on behavior, autonomic nervous system control, and neuroendocrine states that impact the ability of *H. pylori* to colonize and establish ulcers (Bosch et al., 2003; Gang et al., 2009; Saavedra & Benicky, 2007). This is an example of *reductive calibration*, where the medical understanding of ulcers was ultimately informed by psychological levels of analysis.

Adopting the perspective of reductive calibration, Cacioppo (1979; Cacioppo & Berntson, 1992) argued that basic biological structures and processes influenced (and could be used to track) social cognition and affect, and that biological structures and processes were influenced by the superorganismal structures and processes that defined social species. By the early 1980s, Richard Louttit, the Director of the Behavior and Neuroscience Division of the National Science Foundation, approached Cacioppo to discuss how to foster this interdisciplinary perspective. The result was a pioneering five-year program in which more than 40 accomplished scholars trained, a number of whom became editors of leading journals in the field. The level of theoretical and methodological sophistication expected of investigators increased. Several conceptual advances emerged from this program as well, including an edited volume (Cacioppo & Tassinary, 1990b) and the formalization of the problem of reverse inference and the mapping across social, cognitive, and biological levels of organization

(Cacioppo & Tassinary, 1990a), with a special emphasis on functional magnetic resonance imaging (fMRI; Sarter, Berntson, & Cacioppo, 1996). A number of the participants have made significant contributions to the field, including Blascovich and colleagues on threat/challenge appraisals (e.g., see Blascovich & Mendes, 2010; Blascovich, Mendes, Hunter, Lickel, & Kowai-Bell, 2001), Hatfield on emotional contagion (Hatfield, Cacioppo, & Rapson, 1994), Tesser on genetic influences on social attitudes (1993), and Gottman on relationship conflict (Gottman & Levenson, 1992). Subsequently, the establishment of the long-running Summer Institute in Cognitive Neuroscience, directed primarily by Mike Gazzaniga, contributed importantly to the training of generations of young scholars in human neuroscience.

Gary Berntson had long applied neuroscientific methods to the study of social signaling and communication in nonhuman primates and severely brain-damaged humans (Berntson & Boysen, 1990). By the end of this program, Cacioppo and Berntson began a long-term collaboration that, among other things, led to their focus on multilevel neurobehavioral organizations (Berntson et al., 1993), and their proposal of the doctrine of multilevel analyses (Cacioppo & Berntson, 1992a, 1992b).

Klein and Kihlstrom (1998) championed a neuropsychological approach to the study of social processes and behavior, but most of the physiological work on human social cognition and behavior during the 20th century relied on noninvasive peripheral measurements (e.g., see reviews by Cacioppo & Tassinary, 1990b; Klein & Kihlstrom, 1998; Landis, 1929). The use of electroencephalography (EEG) to investigate social behavior dates back to the late 1930s and early 1940s, when Solomon, Jasper, and Braley (1937) used it to study behavior problems in children, and Frederic Gibbs and colleagues used it in a study of candidates for military service (Harty, Gibbs, & Gibbs, 1942) and aggression and criminal behavior (Gibbs, Bloomberg, & Bagchi, 1942). Although EEG was occasionally used in social psychological investigations (Cacioppo, Petty, Snyder, & Quintanar, 1979; Davidson, Ekman, Saron, Senulis, & Friesen, 1990), it was not until event-related potentials (ERPs) were derived from EEG to investigate social processes (Cacioppo, Crites, Berntson, & Coles, 1993) and to contrast implicit and explicit social cognition (Ito & Cacioppo, 2000) that measures of brain activation began to be used more broadly to investigate component processes underlying social categorizations (e.g., see Harmon-Jones & Winkielman, 2007).

Developments in the 1990s in electrophysiological recording, brain imaging, and neurochemical techniques made it possible to investigate the role of neural structures and processes in humans. Prior to these developments, studies of the neurophysiological structures and functions associated with social psychological events were limited primarily to animal models, postmortem examinations, and observations of the occasional unfortunate individual who suffered trauma to or disorders of the brain (Damasio & Grabowski, 1994). Paralleling these advances were developments in genetic and microbiological approaches and assays that opened up new possibilities for investigating social influences on hormonal, cellular, and molecular processes in roaming human and nonhuman animals (e.g., see Insel & Fernald, 2004).

Social issues have shaped theory and research in the social sciences. The dramatic increase in life expectancy realized in developed nations in the 20th century represents one of the greatest cultural and scientific advances in our history, but also a major challenge to the societal status quo (Olshanky, Goldman, Zheng, & Rowe, 2009). Forecasts are for the US population to rise from its current level of approximately 300 million people to almost 400 million in 2050. During this same period, the population 65 years or older will rise from approximately 39 million to about 100 million. Perhaps more importantly, the ratio of those over versus under retirement age will more than double, growing from 15% in 2008 to about 33% in 2050. The emergence of an aging world is not a transient "age wave" that will disappear once the baby boomers have passed on, but rather we are well on our way toward a fundamentally new, permanent, and older age structure in our society (Olshanky et al., 2009). This, coupled with rising rates of obesity and chronic disease, led to concerns about the costs of social security and medical care. Work in social epidemiology (House et al., 1988) and health psychology (Anderson, 1998; Taylor, Repetti, & Seeman, 1997) underscored the importance of understanding the role of social factors in health and disease.

By the beginning of the 21st century the barriers between the social sciences and the neurosciences were falling, and the fields of cognitive neuroscience and social neuroscience were rising (Matusall et al., in press; Raichle, 2000). Distinct branches of social neuroscience emerged (see next section), books on social neuroscience began to appear regularly, and a book series on social neuroscience was introduced by MIT Press; social neuroscience came to be regarded as a priority area at federal extramural funding agencies; special issues on social neuroscience appeared in journals including *Journal of Personality and Social Psychology, Neuropsychologia, Political Psychology*, and *Social Cognition*; two new journals were launched—*Social Neuroscience* and *Social, Cognitive, and Affective Neuroscience*; the first interdisciplinary center for social neuroscience was established at the University of Chicago; the *Handbook of Social Neuroscience* was being prepared for publication (Decety & Cacioppo, in press). The Social and Affective Neuroscience Society grew out of premeetings at the Society for Personality and Social Psychology, and the Society for Social Neuroscience grew out of associated meetings at the Society for Neuroscience: The former represents social cognitive neuroscientists using primarily fMRI, whereas the latter represents scientists from a large number of disciplines investigating the neural, hormonal, cellular, and genetic mechanisms underlying the emergent structures that define social species using a wide variety of methods in studies of animals as well as humans, and patients as well as normal participants. As such, these societies are complementary and reflect the needs, demands, and diversity of the field.

Broadside attacks on the value (Kihlstrom, 2006) and methods (Vul, Harris, Winkielman, & Pashler, 2009) of the field also began to appear. Kihlstrom (2006), for instance, argued appropriately that social neuroscience is not useful to address some if not many questions in social psychology, whereas Vul et al. (2009) argued that some of the most visible fMRI findings in the field were attributable to the use of inappropriate statistical analyses. Although those whose research was implicated by Vul et al. argued the point (e.g., Lieberman, et al., 2009), these criticisms had the positive effect of increasing the rigor and skeptical analysis in the field. Like any new field, social neuroscience faces problems and challenges that must be confronted and addressed. When one considers how far the field has come in a relatively short period of time, the questions facing it are to be expected and will need to be addressed if progress is to continue to be made toward providing more comprehensive accounts for the basic structures, processes, and behaviors of humans and other complex social species. Nevertheless, social neuroscience has opened areas of research that have not traditionally fallen under the rubric of social psychology, including the social regulation of gene expression and health, the origins of language and consciousness, and the mysteries of brain function.

Branches of social neuroscience

The growth in interest in social neuroscience has been seen in multiple disciplines. Among the most active areas of research are brain imaging studies in normal children and adults in psychology and economics; animal models of social behavior in neurobiology, genetics, neurophysiology, and psychology; studies of stroke patients in neurology; imaging studies of psychiatric patients in psychiatry, genetics, and psychology; computational analyses of regional brain activity in psychology, computer science, neurobiology, and genetics; and research on the social determinants of peripheral neural, neuroendocrine, and immunological processes in psychology, endocrinology, molecular biology, immunology, epidemiology, and medicine. Many of these areas of research are proceeding along largely independent trajectories and, therefore, various branches of social neuroscience are now identifiable. These include social cognitive neuroscience (e.g., Adolphs, 2003b; Gallagher & Frith, 2003; Ochsner & Lieberman, 2001), computational social neuroscience (Behrens, Hunt, & Rushworth, 2009; Frith & Wolpert, 2004), cultural neuroscience (e.g., Chiao, in press; Han & Northoff, 2008; Wexler, 2006), social developmental neuroscience (De Haan & Gunnar, 2009; Decety & Michalska, 2010), clinical social neuroscience (Cacioppo et al., 2007; Simon et al., 1999) and comparative social neuroscience (Carter et al., 1999; Hofer, 2009; Insel & Fernald, 2004).

Although social neuroscience is defined conceptually, some of its branches are defined primarily by the methods, participants, or general quantitative approaches that are used. Social cognitive neuroscience seems to be characterized by the use of fMRI in studies of social cognition (Ochsner & Lieberman, 2001), whereas comparative social neuroscience is defined by cross-species comparisons (Carter et al., 1999). The richness and variety of these subareas reveal the broad field of social neuroscience to be a new paradigm that embraces animal as well as human studies, patient as well as nonpatient studies, computational as well as empirical analyses, neural as well as behavioral research, and a wide range of methodologies that have been deployed to investigate the lawful relationships and mechanisms spanning levels of organization ranging from the molecular to the molar.

Conclusion

Throughout most of the 20th century, the neurosciences emphasized cellular processes and neural substrates and production mechanisms for behavior, largely rejecting or ignoring mentalist and functionalist theories, whereas the social sciences emphasized multivariate systems, situational influences, and applications. These differences resulted in very different subject samples, research traditions, and technical demands, leaving what some regard as an impassable abyss between social and biological approaches (Scott, 1991). The notion that billions of neurons can give rise to the human mind also inclined many neuroscientists to regard the social aspects of the mind as unimportant in the search for basic principles or as too complicated to sustain scientific progress. As a result, some of the most distinguishing human behaviors—ranging from the self and morality to social identity to culture—were left unstudied. This oversight is interesting in light of the intimation from the cases of Gage, Leborgne, and Bertino that the brain is more than an information-processing organ: that the human brain also organizes information in a form that distinguishes self from others, biases information processing in ways that protect the self from actual and symbolic threats to support reproductive success, and promotes social identity, cooperation, and civil social discourse.

By the end of the 20th century, evidence began to accumulate showing that social factors have profound implications for basic development, structure, or processes of the brain or mind, and that comprehensive theories of the human mind and behavior may require the integrative study of behavior across multiple levels of organization ranging from the biological to the social (Cacioppo & Berntson, 1992b; Cacioppo et al., 2000). For instance, Brothers (1990b), referring primarily to neurophysiological recordings in nonhuman primates, proposed that the superior temporal sulcus is involved in integrative processing of conspecifics' behavior, and the amygdala and orbitofrontal cortex are subsequently involved in specifying the socioemotional relevance of social information; Kanwisher (2000; Kanwisher, McDermott, & Chun, 1997), using fMRI data, emphasized the role of the fusiform gyrus in face processing; and Damasio and colleagues (Adolphs, et al., 1999; Damasio & Grabowski, 1994), focusing primarily on data from humans with brain lesions, have emphasized the role of the frontal (ventromedial prefrontal, orbitofrontal) cortex, amygdala, and somatosensory cortex (insula, SI, SII) in social perception, cognition, and decision making. Reviews of the functions associated with specific brain regions and of the neural substrates of social information processing are available in Adolphs (1999, 2001, 2003a), Allison, Puce, and McCarthy (2000), Cacioppo et al. (2002), Frith and Frith (2001), Klein and Kihlstrom (1998), Ochsner and Lieberman (2001), Rizzolatti, Fogassi, and Gallese (2001), Scholl (2001), and Scholl and Tremoulet (2000). These reviews represent the emergence of new theoretical arenas, often housing conflicting views, on the precise anatomical definition of a brain region (Brierley, Shaw, & David, 2002; Merboldt, Fransson, Bruhn, & Frahm, 2001) or the precise nature of the information-processing operations being performed by a brain structure or system (e.g., fusiform area and face processing; cf. Kanwisher, 2000 vs. Tarr & Gauthier, 2000)

Social psychology has much to gain from studies of the neurobiology underlying social processes, and neural and medical sciences have much to gain from a deeper understanding of the powerful impact of social factors on physiological systems and health outcomes (Berntson & Cacioppo, 2004). Although the social psychological and neuroscience perspectives may have emerged from distinct historical origins, disciplinary perspectives, and theoretical frameworks, it is increasingly clear that a comprehensive understanding of the relations between social and biological phenomena will require attention to both domains. Fortunately, an inexorable shift toward a transdisciplinary social neuroscientific destiny is currently under way that will benefit all of science.

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