
C H A P T E R 1

The Brain in a Social Environment

Why Study Development?

MICHELLE DE HAAN
MEGAN R. GUNNAR

Recent years have seen a dramatic increase in the number of studies aimed at understanding the neural mechanisms underlying social behavior. This has led to the recognition of a new discipline, social neuroscience, and to the creation in 2006 of two new journals devoted to the topic: *Social Neuroscience* and *Social Cognitive and Affective Neuroscience*. Social neuroscience encompasses the study of a broad range of social abilities, including social-emotional perception, cognition, and behavior, which for the purposes of this chapter we collectively call “social processing.” This explosion of research has included investigation of how social and biological factors interact during development, resulting in the subfield of developmental social neuroscience. The aim of this chapter is to provide a brief background on the forces that have led to the rising popularity of social neuroscience, and to highlight why studying development is important for a full understanding of the neuroscience of social processing.

The Rise of Social Neuroscience

Psychological and biological explanations of social processing have historically been considered incompatible. Psychology has traditionally been seen as a “social science,” with a wide gulf separating it from the “natural sciences,” such as biology and chemistry. One important factor that has enabled researchers to establish a connection between the two levels of explanation is the emergence of tools allowing measurement of human brain activity. New tools, such as functional magnetic resonance imaging (fMRI), have allowed scientists to exam-

ine brain activity while healthy human participants actually engage in social processing. Before such tools became available, opportunities to study brain activation in humans were much more limited. For example, researchers might add tasks to clinical assessment of diseased or injured brains, such as recording responses to faces and objects directly from the cortical surface in patients undergoing such assessment for evaluation of epilepsy (Allison, Puce, Spencer, & McCarthy, 1999). Such studies are still valuable, but the availability of such tools as fMRI allows more widespread study of both injured and healthy brains, with scientists even making efforts to overcome the practical and technical difficulties of applying such tools to healthy young infants. For example, fMRI has been used to examine the infant brain's response to auditory social stimuli, such as language (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002) and emotional sounds (Sauter, 2008).

Advances in the application of more traditional tools have also been important. The advent of high-density recordings for electroencephalography (EEG) has been particularly useful for better understanding the spatial characteristics of brain activation in infants and young children, for whom alternate imaging modalities are either not appropriate or more difficult to use. For example, use of high-density event-related potentials (ERPs) together with source localization software has allowed scientists to consider the similarities and differences in patterns of brain activation in infants and adults in response to visual social stimuli, such as faces (Johnson et al., 2005). It is important to recognize, however, that brain imaging alone cannot fully reveal the biological mechanisms of social processing. Genetic, hormonal, biochemical, physiological, and anatomical studies, as well as comparative studies, all provide critical data, and advances in techniques for collecting these types of data have contributed importantly to the growing field of social neuroscience. Indeed, a general lesson emerging from the new discipline is that the relations between neural processes and social or cognitive processing must be studied at multiple levels of analysis.

Another force contributing to the emergence of social neuroscience has been the precedent set by the success of the related field of cognitive neuroscience. The growing body of research identifying the neural mechanisms underlying cognitive processes illustrates how it is possible to study the biological underpinnings of mental processes. The mind-brain complex need no longer be considered an unobservable "black box." Subjective experiences, such as moods and emotions, can be studied with scientific methods. Researchers in cognitive neuroscience have also increasingly acknowledged that social behavior and emotion influence cognitive processes and thus are themselves topics in need of investigation. This has led to an interest in understanding the neural bases of individual differences in these processes as they relate to such social-emotional constructs as personality. For example, recent studies have shown that children scoring lower on socialization show a reduction in an ERP component linked to the anterior cingulate cortex (Santesso, Segalowitz, & Schmidt, 2005), and that children scoring higher on trait anxiety show an augmented ERP response to novel, unexpected sounds (Hogan, Butterfield, Philips, & Hadwin, 2007).

These forces have contributed to shaping the growing field of developmental social neuroscience, and have allowed a preliminary picture of the developing social brain to emerge. The available data highlight similarities across age in the basic networks involved in social processing, but also pinpoint differences in the way in which such networks are activated. As outlined by Payne and Bachevalier (Chapter 3, this volume), a complex network of interconnected subcortical and cortical brain structures has been implicated as a substrate to social cognition in adults. This network includes the hypothalamus, amygdala, anterior temporal lobe, posterior superior temporal sulcus, orbital prefrontal cortex, and medial prefrontal cor-

tex. The limited information available so far suggests that a similar network is involved in children, but that it develops over an extended period from infancy until young adulthood, and that some components of the network (such as the amygdala) come online much earlier in development than other components (such as cortical regions). Functional imaging studies suggest that both the extent and pattern of cortical activation related to social processing change with age. For example, studies of the development of the cortical “fusiform face area” suggest that it is more diffuse and less specifically activated by faces in children than in adults (see Pascalis, Kelly, & Schwarzer, Chapter 4, this volume). Moreover, studies of the neural correlates of thinking about intentions suggest that although the same neural network is active in adults and adolescents, the relative roles of the different areas change, with activity moving from anterior (medial prefrontal) regions to posterior (temporal) regions with age (see Choudhury, Charman, & Blakemore, Chapter 9, this volume).

Although such results clearly make an important contribution to social neuroscience, applying neuroimaging techniques to developing populations is not simply a matter of taking the tools used with adults and using them to test children. Some brain imaging techniques used with adults are not usually applied to typically developing children, for ethical (e.g., positron emission tomography) and/or practical (e.g., fMRI) reasons. Even when techniques can be used with infants or children, important issues surrounding the analysis and interpretation of data need special consideration (see Gunnar & de Haan, Chapter 2, this volume).

The Components of Social Processing

Social processing includes our behavior as we interact with others, the thoughts and emotions we experience in relation to others, and our perceptions of others' social cues and behaviors. As outlined above and described in more detail by Payne and Bachevalier (Chapter 3, this volume), in adults a complex network of interconnected subcortical and cortical brain structures is believed to underlie social behavior, cognition, and emotions. Although a reasonable amount is known about the function of this network in adults, very little is known about its development and how it supports the progressive emergence of complex social abilities. A challenge is that social processes include such complex constructs as empathy, motivation, and theory of mind, which are difficult to map directly onto neural systems. For this reason, complex social processes are often broken down into more specific component processes. There are numerous examples of this approach in this volume. Carver and Cornew (Chapter 7) outline how the skill of social referencing can be broken down into the components of sharing attention, which is important for seeking social information; emotion recognition and associative learning, which are important for relating emotional information provided by others to novel events; and emotion regulation, which is important for using emotional information provided by others to govern one's own behavior. Similarly, Crone and Westenberg (Chapter 19) show how the use of social information to regulate decision making can itself be divided into the components of cognitive control, which keeps relevant information in an active state and exerts goal-directed behavior; future orientation, which involves anticipating consequences on the basis of reward and punishment; and perspective taking, which involves considering the thoughts and perspectives of other people. Mills and Conboy (Chapter 10) describe how language development in the first 3 years of life has been broken down into a set of skills including changes in the perception of phonetic contrasts in infants' native versus

non-native language, associating words with meanings, producing the first words, combining words into two- or three-word utterances, and speaking in full sentences. In a final example, Decety and Meyer (Chapter 8) argue that the complex construct of empathy can be deconstructed in a model that includes (1) bottom-up processing of shared motor representations, which are navigated by (2) parietal areas known to be crucial in differentiating the perceiver's own perspective from those of others; all of these can be regulated by (3) top-down executive processing, in which the perceiver's motivation, intentions, and self-regulation influence the extent of an empathic experience. This focus on studying subcomponents of more complex behaviors can be particularly useful from a developmental perspective, when it is often the case that only some components of or precursors to more complex behaviors are observable. Developmental studies can provide unique opportunities to see how the components of the system interact in ways not possible in adults, where all the components are fully mature and operational.

Perceiving and Communicating with Others

One basic component of human social behavior is the ability to perceive social signals from others, and to display social signals in turn. One very active area of research in this domain is the study of the development of face processing (see Pascalis et al., Chapter 4, and de Haan & Matheson, Chapter 6, this volume). Electrophysiological (ERP) studies have identified a face-sensitive ERP component, the N170, and have used this response to begin mapping how the cortical response to faces evolves from infancy to adulthood. These studies have generated intriguing results, demonstrating that the precursors of the N170 are present in infancy but are less face-specific at this stage, and that the neural processing of eyes matures earlier than processing of the whole facial configuration does (see Pascalis et al., Chapter 4). These studies also suggest that although the basic neural network responding to faces is similar in infants and adults, the relative contributions of the components within the network differ with age (Johnson et al., 2005)—a conclusion also supported by the limited data from studies using fMRI in children (see Pascalis et al., Chapter 4). Many questions still remain to be answered, as few developmental studies have focused on how the emotional content of a face influences the brain's response, and even fewer have focused on how the brain processes emotional signals in voices. The existing literature has focused mainly on the perception of static images of faces; these can be considered quite removed from the actual types of social signals normally available in the environment, which would involve multimodal, moving inputs.

Beyond perceiving and displaying emotions, the abilities to communicate and to share affective experiences are also important for participating in the social world. Language allows young children to communicate their thoughts and intentions directly, and the development of language skills appears closely linked to that of other complex social skills, such as joint attention, empathy, and mentalizing. Less is known about the underlying neural bases of such complex skills in development, but the research described in this volume illustrates how even such complex areas are being tackled by innovative researchers. It has been established that a network including the temporal poles, the posterior superior temporal sulcus/temporoparietal junction, and the medial prefrontal cortex is involved in mentalizing. However, a puzzle for developmentalists is that some of these brain regions undergo very dramatic development into adolescence, even though the function of mentalizing appears to mature much earlier (see Choudhury et al., Chapter 9, this volume).

One important theme in much of the research investigating the neural correlates of perceiving and communicating social information has been the quest to understand how experience in the social world itself shapes the development of such abilities. For example, how do the faces that we see and the language that we hear affect the development of face- and speech-processing systems in the brain? Evidence suggests that at least in these domains, experiences in infancy have an important and lasting impact on how such social-perceptual information is processed (see Pascalis et al., Chapter 4, and Mills & Conboy, Chapter 10, this volume, for further discussion). A better understanding of the brain systems involved in these skills, and of the role experience plays in shaping their development, is important not only for the study of normative development; it may also provide insight into why these abilities sometimes do not develop normally and can also provide tools for earlier detection of disorders (see, e.g., Dawson, Sperling, & Faja, Chapter 22, this volume).

Relationships

Interpersonal relationships provide the context in which children construct a sense of who they are as individuals and social partners. Not only are relationships important for human development, but infants and parents are strongly motivated to form long-lasting relationships, termed “attachments,” to one another. The recognition that attachment is a species-typical human motivational system has had a profound impact on the field of social development. Understanding the neurobiology of the attachment motivational system has become a focus of research in developmental social neuroscience. The study of species in which adults form pair bonds is providing insights into the genetic and neurobiological processes that support the formation of long-lasting attachments (see Wommack, Liu, & Wang, Chapter 15, this volume). Not only has this work been applied to human adult romantic relationships (see Marazziti, Chapter 14, this volume); it has guided researchers interested in the formation of parent–child attachment relationships to focus on the roles of two neuropeptide hormones, oxytocin and vasopressin, in the formation and maintenance of these relationships (see Gonzalez, Atkinson, & Fleming, Chapter 12, and Bales & Carter, Chapter 13, this volume). The influence of these neuropeptides on dopaminergic activity in the nucleus accumbens appears to be important in supporting motivated approach to the object of attachment. However, animal studies have also revealed that the hypothalamic–pituitary–adrenocortical system and its neuroactive peptide, corticotropin-releasing factor, along with pain-alleviating opiate peptides, all play a role in regulating parent–offspring attachments, implicating regulation of the fear system as an important component of these relationships (see Bales & Carter, Chapter 13). An understanding of the neural systems that underlie the formation and maintenance of parent–offspring relationships also helps contribute to our understanding of why disruptions in these relationships can have such long-term consequences for the developing child, as reviewed in this volume by Reeb, Fox, Nelson, and Zeanah (Chapter 24) and by Sanchez and Pollak (Chapter 25).

Motivation and Emotion

Explicating the neurobiology of motivation and emotion is central to the study of social neuroscience and critical to our understanding of social-emotional development. Any observer of

young children quickly realizes that there are marked individual differences among children in their response to novel, strange, or unfamiliar events and in their emotional exuberance. Some of the earliest work in developmental social neuroscience has been directed at understanding the neural bases for these differences. As outlined by Schmidt and Jetha (Chapter 16, this volume), studies examining biases in EEG activity over the left and right frontal cortex provide evidence that processes influencing these biases are relevant for understanding both extremely inhibited or socially reticent children and those who are extremely uninhibited and socially outgoing. Not surprisingly, given the work on parent–offspring attachment and motivational systems, research on the approach/reward and avoidance/withdrawal systems more generally implicates the same neural systems that are discussed in work on parent–offspring attachment (see Ernst & Spear, Chapter 17, and Mayes, Magidson, Lejuez, & Nicholls, Chapter 18, this volume). Within the broader context of social neuroscience, interest in these systems reflects interest in understanding the neural bases of addiction and anxiety. From a developmental neuroscience perspective, these questions are motivated by an interest in understanding (1) why disturbances to the parent–offspring relationship increase the risk of substance abuse and depression; and (2) how individual differences in these systems may predispose children to different affective and behavioral pathologies, given exposure to adverse patterns of parenting.

Psychopathology

Studies of the neural bases of social processing can make an important contribution to our understanding of developmental disorders in social processing. The development of brain systems involved in social processing is shaped both by genetic information and through interaction with the environment, and disruption of either of these forces can lead to psychopathology. Children with genetic disorders that affect brain development may have atypical social behavior as a direct result of the genetic influence. Skuse and Gallagher (Chapter 23, this volume) outline work linking genotypes and phenotypes in the context of genetic developmental disorders, and highlight the need for the collection of more detailed information on the cognitive and behavioral phenotypes of brain structural anomalies observed in such disorders. Disordered social behavior in children with genetic disorders can also arise indirectly, as their atypical brains lead them to experience the world differently. For example, Dawson et al. (Chapter 22, this volume) describe how early genetic and environmental risk factors for autism can lead to abnormalities in brain development, which in turn alter children's patterns of responses to and perception of the environment. This view highlights the importance of identifying such early risk factors, in order to minimize their negative influence on further development. Finally, disordered social behavior can also result from negative environmental influences on brain development that otherwise would have occurred normally. In this volume, Reeb et al. (Chapter 24) and Sanchez and Pollak (Chapter 25) both discuss how complex sets of neural circuitry are shaped and refined over development by children's social experience. These studies of children who have experienced extreme social environments involving abuse, neglect, or deprivation are important not only for clarifying the processes through which social development goes awry in those cases, but also for providing a more general understanding of the interplay between social experience and brain development.

Summary and Conclusions: The Importance of Developmental Social Neuroscience

As noted earlier, a complex network of interconnected subcortical and cortical brain structures has been implicated as a substrate to social behavior. The limited information available to date suggests that the neural structures in this network develop over an extended period from infancy until young adulthood. Importantly, some structures (such as the amygdala), come online much earlier in development than other (e.g., cortical) structures, which become specialized for processing social stimuli over a more protracted period. An important goal for future studies is to provide a more comprehensive picture of which specific social skills functionally mature at which points in development, and to determine which parts of the social brain network are mediating these skills.

One key question in social neuroscience has been whether the general cognitive processes involved in perception, language, memory, and attention are sufficient to explain social competence, or whether over and above these general processes there are specific processes that are special to social interaction. Developmental studies can be useful in this regard, as they allow study of the earliest periods when infants are first experiencing social stimuli, and they potentially allow the study of dissociations among skills that are not observable in adults as different skills emerge at different ages. Although brain structures mature at different tempos, they become increasingly integrated during infancy and adolescence to support the progressive emergence of complex social abilities.

Further developments in technology, and researchers' innovations in using these tools, will also be important for developmental social neuroscience. For example, applying fMRI to young infants provides information about the spatial pattern of brain activation that is more detailed than the data available from more commonly used measures, such as EEG/ERP. However, currently this type of work is very challenging and involves assessment of responses in sleeping children; this excludes certain types of studies, such as research on activation during visual processing. Better integration of the multiple levels of research—genetic, neurophysiological, neurohormonal, and neuroanatomical levels—within developmental social neuroscience is also an exciting prospect for the future.

Finally, better understanding and assessment of social environments will prove important as well. For example, evaluating children's exposure to different emotions during development can prove very challenging for researchers, yet data on such exposure would be very valuable to obtain. Given evidence that experience can have a very rapid (Maurer, Lewis, Brent, & Levin, 1999) as well as a lasting (Maurer, Mondloch, & Lewis, 2007) impact on human development, advances in this area not only will be important for understanding typical and atypical neurosocial development, but also may be very valuable for establishing evidence-based interventions for preventing or ameliorating disorders.

References

- Allison, T., Puce, A. L., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception: I. Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex*, 8, 415–430.
- Dehaene-Lambertz, G., Dehaene, S., & Hertz-Pannier, L. (2002). Functional neuroimaging of speech perception in infants. *Science*, 298, 2013–2015.

- Hogan, A. M., Butterfield, E. L., Phillips, L., & Hadwin, J. A. (2007). Brain response to unexpected novel noises in children with low and high trait anxiety. *Journal of Cognitive Neuroscience, 19*, 25–31.
- Johnson, M. H., Griffin, R., Csibra, G., Halit, H., Farroni, T., de Haan, M., et al. (2005). The emergence of the social brain network: Evidence from typical and atypical development. *Developmental Psychopathology, 17*, 599–619.
- Maurer, D., Lewis, T. L., Brent, H. P., & Levin, A. V. (1999). Rapid improvement in the acuity of infants after visual input. *Science, 286*, 108–110.
- Maurer, D., Mondloch, C. J., & Lewis, T. L. (2007). Sleeper effects. *Developmental Science, 10*, 40–47.
- Santesso, D. L., Segalowitz, S. J., & Schmidt, L. A. (2005). ERP correlates of error monitoring in 10-year-olds related to socialization. *Biological Psychology, 70*, 79–87.
- Sauter, D. (2008, May). *Brain imaging studies: Theoretical issues and methodological challenges*. Paper presented at the pre-IMFAR workshop Progress in the Study of Brain Functions in Infants At-Risk for Autism, London, UK.