CHAPTER

19

Developmental Neuroscience of Social Perception

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19.1 INTRODUCTION

Within adult social psychology, the study of social cognition encompasses a range of phenomena including moral reasoning, attitude formation, stereotyping, and related topics. This definition includes the processes underlying the perception, memory, and judgment of social stimuli; the effects of social, cultural, or affective factors on the processing of information; and even the behavioral and interpersonal consequences of those cognitive processes. Social psychology has provided an arsenal of measurement techniques and theoretical models to inform efforts within social neuroscience to study the mature human brain. However, neuroscience has traditionally defined social cognition more narrowly as the ability to perceive the intentions, actions, and psychological dispositions of others (Brothers, 1990). Within developmental psychology, the study of social cognition and its development has focused most intensely upon 'theory of mind,' or a person's awareness that other individuals maintain thoughts, beliefs, and desires that are different from his or her own, and that the actions of others can be best explained with reference to their

individual mental states (Frith and Frith, 1999; Premack and Woodruff, 1978). Developmental psychologists have characterized the stages of development in theory of mind abilities but have yet to provide a mechanistic account of 'how' theory of mind develops in children. Such questions necessitate studies that bridge the gap between cognitive accounts of theory of mind and the underlying brain mechanisms and, thus, require measurement at both the behavioral and neural system levels. One definition that cuts across disciplines and levels of analysis dictates that *social cognition* refers to the fundamental abilities to perceive, categorize, remember, analyze, reason with, and behave toward conspecifics (Adolphs, 2001; Pelphrey et al., 2004a). Currently, very little is known about the neural correlates of social cognition in children or about the changes in brain structure, function, and connectivity that underlie normative development in this domain. Providing an understanding of brain development in relation to changes in social cognition is important to the field, as it will allow for the construction of normative 'growth charts' for the function of circuits supporting various aspects of social cognition. Additionally, this knowledge

may aid researchers in their search for genetic and environmental factors (and gene × environment interactions) related to suboptimal social cognitive development as observed in autism and related neurodevelopmental disorders.

This chapter focuses on the development of a critical aspect of social cognition – *social perception*. Social perception is the initial stage of evaluating intentions and psychological dispositions of others by analysis of gaze direction, body movement, and other types of biological motion (Allison et al., 2000). It is closely linked to *action understanding*: the ability to appreciate other people's actions in terms of the mental states that drive behavior. It has been argued that social perception is an ontogenetic and phylogenetic prequel to more sophisticated social cognition abilities, particularly theory of mind (e.g., Baron-Cohen et al., 1995; Frith and Frith, 1999; Pelphrey and Morris, 2006; Premack and Woodruff, 1978; Saxe et al., 2004a). A task analysis supports this argument and reveals that successful social perception involves a set of three distinct but interrelated social cognition abilities: (1) individuating and recognizing other people, (2) perceiving their emotional states, and (3) analyzing their intentions and motivations. Successful social perception, in turn, facilitates a fourth and more sophisticated aspect of social cognition: (4) representing another person's perceptions and beliefs, a core component of theory of mind. In this chapter, the five neuroanatomically and functionally dissociable neural circuits that underlie these aspects of social perception are elaborated on and what is known about the functional development of each circuit in infants, children, and adolescents discussed. The focus is on functional magnetic resonance imaging (fMRI) and developmental studies of social perception involving other neuroimaging techniques, for example, electrophysiology are not included. This focus was selected because of the interest in identifying the exact neural systems involved in distinct and dissociable (at the neural systems level) aspects of social perception. It must be noted, however, that fMRI is limited in that it is not yet practical to study awake, behaving infants and toddlers with this method. In contrast, electrophysiology can be readily applied to infants and toddlers. However, in even the best, most controlled conditions with adults, it is a challenge to make precise statements about the neuroanatomical origins of scalp-recorded electrical signals. See, for example, the ongoing debate concerning the origins of the N170 in response to faces (Halgren et al., 2000; Itier and Taylor, 2004). This inferential problem is compounded when one wishes to study the development of a brain system with electrophysiology because then one has to identify a developmental precursor to the well-characterized adult signals and then make inferences about the underlying neural generator. Following the review of the available literature, a model of social cognitive development has been put forward that aims to explain how an early developing social perception network can give rise to more sophisticated aspects of social cognition, including theory of mind.

19.2 NEUROANATOMICAL SUBSTRATES OF SOCIAL PERCEPTION

19.2.1 Ventral Occipital Temporal Cortex and the Recognition of Other People

Several areas located in the ventral occipitotemporal cortex (VOTC) support the basic representation and recognition of other people. These include the lateral fusiform gyrus (FFG), which contains the 'fusiform face area' (FFA), and the 'extrastriate body area.' The former has a clear role in face perception and recognition (e.g., Kanwisher et al., 1997; Puce et al., 1996), while the latter has been implicated in the visual perception of human bodies (e.g., Downing et al., 2001). These brain regions provide the basic representation of their specific visual category that supports both bottom-up visual processing of social information and top-down imagery of those categories.

In adults, there are well-defined expectations of how brain activity related to visual object processing should be organized (Dehaene and Cohen, 2007; Martin, 2007). Faces and letter strings are two visual categories that have been studied extensively and elicit distinct responses in VOTC. Faces evoke selective activity in the mid-FFG relative to other objects (Allison et al., 1994; Kanwisher, 2000; Kanwisher et al., 1997). In contrast, the lateral mid-fusiform/inferior temporal gyrus shows a bias for processing words, letters, and letter strings over digits and other objects (Allison et al., 1994; Baker et al., 2001; Cohen and Dehaene, 2004; Dehaene et al., 2002; Hashimoto and Sakai, 2004; Polk and Farah, 1998; Polk et al., 2002). Both categories are hypothesized to recruit specialized neural processes that best suit the features that define the category (Kanwisher, 2000; Polk and Farah, 1998). The developmental origins of their specializations, however, are presumably quite different.

To date, the most is known about the development of the face-sensitive area of the FFG. Current evidence indicates that face-selective neural processing is already present in the FFG by 6 years of age and becomes increasingly robust throughout adolescence (Aylward et al., 2005; Golarai et al., 2007; Grill-Spector et al., 2008; Libertus et al., 2009; Scherf et al., 2007; Tzourio-Mazoyer et al., 2002). Interestingly, the gradual refinement of face-related neural processing over development
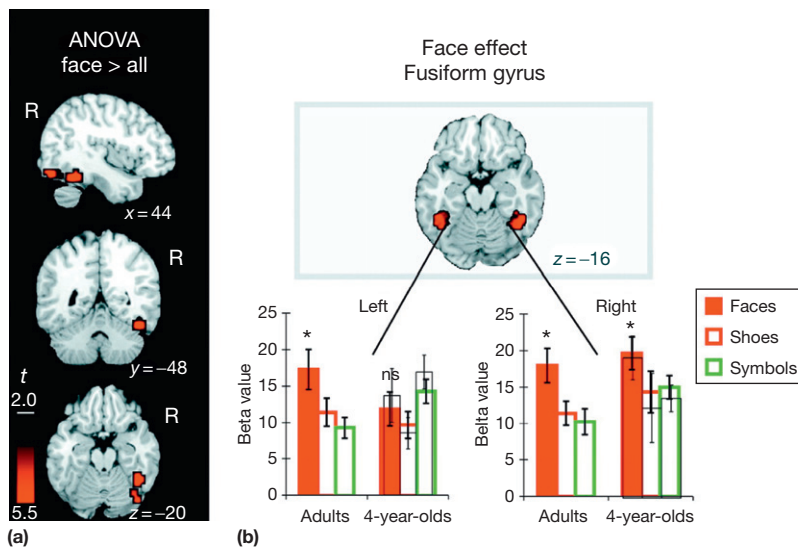
FIGURE 19.1 The right fusiform face effect. The right fusiform gyrus face effect for adults and children was evident in (a) a main effect of faces > all categories (shoes, letters, and numbers) in an ANOVA ($p < .05$, corrected) and (b) an ROI analysis in which voxels were selected based on their average response across all categories (faces, shoes, letters, and numbers) > scrambled. The light gray bars within the data from 4-year-olds represent children with motion estimates equal to those of adults (these data are equivalent to the full 4-year-old sample). The asterisks indicate significantly different from all categories at $p < 0.05$, corrected for multiple comparisons.

parallels the well-known changes in children's face recognition abilities (Carey and Diamond, 1994).

In order to differentiate the developmental origins of category-specific areas in VOTC, our group recently used fMRI to examine the organization of the ventral visual pathway for basic processing of symbols, faces, and nonface objects in 4-year-old children (Cantlon et al., 2011). We tested 4-year-old children's and adults' responses to faces, letters, numbers, and shoes in VOTC. As illustrated in Figure 19.1, children and adults exhibited a common pattern of face selectivity in the right mid-FFG at a locus consistent with previously reported face-selective sites in adults. This indicates that certain features of adult brain organization have already taken formed by 4 years of age (Cantlon et al., 2006; Grill-Spector et al., 2008; Mahon et al., 2009; Polk et al., 2007). This biased activity to faces in the right mid-FFG in overlapping regions previously reported as face selective in older children and adults (Grill-Spector et al., 2008) represents an early developing visual specialization for social information in VOTC.

Some evidence indicates that face selectivity in the FFG is related to face recognition memory in children (Golarai et al., 2007), where children who perform better on face recognition tasks exhibit a greater spatial extent of face-related activity. However, it is unknown whether the refinement of face-related processing hinges on 'increases' in the FF response to faces, 'decreases' in the responses to nonfaces, or 'both.' This question is critical for understanding the nature of the developmental process underlying category selectivity in the brain. In fact, a long-standing debate in the developmental literature concerns the question of whether neural development is driven by building up or pruning back representations in the brain (Bourgeois and Rakic, 2003; Changeux, 1985; Changeux and Danchin, 1976; Changeux and Dehaene,

1989; Dehaene-Lambertz and Dehaene, 1997; Purves et al., 1996; Quartz, 1999; Quartz and Sejnowski, 1997).

Faces have an evolutionary significance and spontaneously attract children's attention from birth, with research indicating that infants who are just days old prefer to look at images of faces instead of nonfaces, and familiar rather than novel faces (Johnson et al., 1991; Nelson, 2001). In the constructivist view, experience-dependent input specifies the connectivity and functions of cortical regions and thereby gradually builds up specialized cortical functions (Quartz, 1999). Selectionism, in contrast, postulates that redundant and irrelevant neuronal connections exist from birth and are gradually eliminated on the basis of experience-evoked activity in order to define specialized cortical functions (Changeux and Danchin, 1976). In principle, these two developmental processes can be distinguished in the category-selective brain responses of young children. For instance, in the case of face representation, a constructivist pattern of activity would predict an increase in face-related activity with increasing face recognition ability, whereas a selectionist pattern would predict a decrease in nonface activity with increasing face recognition ability. Naturally, both patterns are nonexclusive and may jointly occur, either simultaneously or at different ages.

In order to test these two theories, the relationship between children's developing category knowledge and their category-related brain activity was examined in the aforementioned study (Cantlon et al., 2011). The children were tested on a series of identification and naming tests with the same stimuli presented in the fMRI session. As illustrated in Figure 19.2, children's accuracy on the face-matching task was not correlated with an increase in the neural response to faces in the right mid-fusiform face-selective region of interest (ROI), as
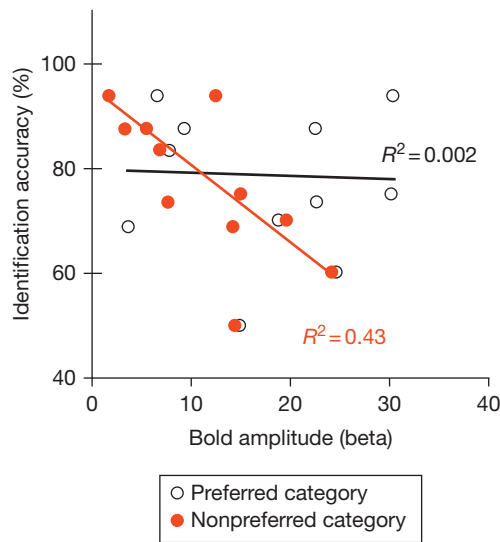
FIGURE 19.2 Scatterplot illustrating negative correlations between behavioral performance and the magnitude of the brain response to the nonpreferred category. In the brain region that showed the face effect, children's accuracy on a face identification task was correlated with a decrease in activity to the nonpreferred category (shoes) rather than an increase in activity to the preferred category (faces). Chance on the face identification task was 50%.

might be expected. Instead, accuracy on the face-matching task correlated with a decrease in the response to shoes in the face-selective ROI. This finding suggests that as children in this age range become more proficient at recognizing faces, the mid-fusiform face-selective region reduces its response to other visual classes (as opposed to increasing its response to faces). These data suggest that brain regions that will eventually become selective for a particular category already produce a relatively strong response to their preferred category in early childhood, but they gradually decrease their responses to nonpreferred categories as knowledge is acquired. While adult category-selective brain regions show similar types of category biases in early childhood, there are undoubtedly developmental changes in the structure and function of those regions. For example, Golarai et al. (2007) reported that the spatial extent of activation in face-selective fusiform regions expands with increased memory for faces between 7 years of age and adulthood. The degree to which face-selective cortex expands over the course of early childhood (i.e., 0–7 years) remains in question. Our own findings suggest that one catalyst of those functional changes could be a decreasing representation of nonpreferred (i.e., nonface) entities in face-selective regions.

Many questions remain about exactly how the development of face specialization unfolds. One aspect of this process, evident in our fMRI results, is that neural responses in category-selective regions to nonpreferred

categories need to be pruned away. This is supported by the notion that learning proceeds by 'selection,' 'attrition,' or a 'use it or lose it' principle, which has long been proposed at the theoretical level (Bourgeois and Rakic, 2003; Changeux, 1985; Changeux and Danchin, 1976; Changeux and Dehaene, 1989; Dehaene-Lambertz and Dehaene, 1997; Purves et al., 1996) and has received empirical support in domains such as bird song acquisition or speech perception, both of which exhibit perceptual narrowing over development (Kuhl et al., 1992; Werker and Lalonde, 1988). Our data suggest a similar selectionist principle in the development of face-selective VOTC in human children.

It should be noted that our data are not inconsistent with a moderate form of the constructivist view (Sirois et al., 2008), which posits a selection process via lateral inhibition following category learning (for evidence of this phenomenon in adults, see Allison et al., 2002; Pelphrey et al., 2003). Under that hypothesis, however, one might expect preferred and nonpreferred category-related responses in VOTC to become increasingly anti-correlated over development. Although this pattern did not emerge in our data, longitudinal fMRI data on children's category-related visual responses at different points in their acquisition of category knowledge will help to further adjudicate among these hypotheses. Such data could reveal developmental periods during which representations are being constructed (with increasing responses to preferred categories) as well as periods during which a selection mechanism is engaged (with decreasing responses to the nonpreferred category). The degree to which selection or construction is observed at a given point in early childhood likely will depend on children's experience with the specific categories examined. At a single point in development, some categories could exhibit a pattern of increasing responses to preferred stimuli, while other categories exhibit decreasing responses to nonpreferred stimuli. Such a proposal is consistent with our data and with previously reported studies of VOTC activation in older children (Golarai et al., 2007; Grill-Spector et al., 2008; Libertus et al., 2009; Scherf et al., 2007).

A tentative biological mechanism for the reduction in high-level visual activity to nonpreferred categories over development may be the known reduction in synaptic density between 2 and 11 years of age (Chugani et al., 1987; Giedd et al., 1999; Huttenlocher and Dabholkar, 1997; Huttenlocher et al., 1982; Shaw et al. 2008). Synaptic density in visual areas steadily increases between birth and 1–2 years of age, reaches levels that are approximately 50–60% greater than adult levels, and then gradually decreases over the next several years. Some evidence indicates that vascular density parallels synaptic density in primary visual areas and thus blood supply might be related, at least in sensory areas, to neural

plasticity and synapse formation/elimination (Duvernoy et al., 1981; Logothetis and Wandell, 2004).

19.2.2 Limbic Circuitry and the Perception and Experience of Emotions

The limbic system is composed of a set of brain structures that support a variety of functions, including emotion. The amygdala is one such structure, and several fMRI studies have focused on its response to emotional (especially fearful) faces. Baird et al. (1999) first identified amygdala activation to fearful faces in adolescents aged 12–17 years. Thomas et al. (2001) later reported that adults demonstrated greater amygdala activation to fearful facial expressions compared to other expressions, whereas 11-year-old children showed greater amygdala activation to neutral faces compared to other expressions. One explanation offered by the authors is that the neutral faces were seen as more ambiguous than fearful facial expressions, resulting in increases in amygdala activation. In a cross-sectional study, Killgore et al. (2001) reported sex differences in amygdala responses in children and adolescents. They found that the left amygdala responded to fearful facial expressions in all children, although its activity decreased over the adolescent period in females but not in males. In a follow-up study, Killgore and Yurgelun-Todd (2004) compared children, adolescents, and adults during the perception of fearful faces. They reported that males and females differed in the right hemisphere – left hemisphere asymmetry of activation of the amygdala and prefrontal cortex (PFC) and this interacted with age. For boys, activation within the dorsolateral PFC was bilateral in childhood, right lateralized in adolescence, and bilateral in adulthood, whereas females showed a monotonic relationship with age, such that older females showed more bilateral activation than younger ones, but with significant bilateral activation at all ages. In contrast, amygdala activation was similar for both sexes, with bilateral activation in childhood, right-lateralized activation in adolescence, and bilateral activation in adulthood.

Lobaugh et al. (2006) reported that fear, disgust, and sadness recruit distinct neural systems both in 10-year-old children and adults. Two recent cross-sectional studies reported that adolescents display more amygdala activity in response to affective faces than either children or adults (Guyer et al., 2008; Hare et al., 2008). Further, adolescents also show less response to emotions in ventromedial PFC (vmPFC), a region whose functional connectivity with the amygdala is associated with habituation to emotional stimuli (Etkin et al., 2006; Hare et al., 2008). This suggests that teenagers may be more emotionally reactive and also less capable of relying on PFC for affect regulation (see also Grosbras et al., 2007; Lévesque et al., 2004).

In a recent fMRI study, we examined the development of the neural circuitry supporting emotion regulation in school-age children (Pitskel et al., 2011). We focused on the circuitry supporting cognitive reappraisal, a particular approach to emotion regulation frequently utilized in behavioral psychotherapies. Despite a wealth of research on cognitive reappraisal in adults, little is known about the developmental trajectory of brain mechanisms subserving this form of emotion regulation in children. We asked children and adolescents to increase and decrease their emotional response to disgusting images (e.g., a picture of a person with mucus hanging from her nose) by either pretending it was real and right there in front of them (for the increase condition) or by pretending it was just make believe (for the decrease condition). Distinct patterns of brain activation were identified during successful up- and downregulation of emotion, as well as an inverse correlation between activity in vmPFC and limbic structures, particularly the amygdala, during downregulation, indicative of the regulatory role for vmPFC. Further, as illustrated in Figure 19.3, age-related effects on activity in the vmPFC and amygdala were discovered. Of particular interest, during downregulation of emotion, significant negative correlations with age in the amygdala were observed, consistent with more effective emotion regulation.

While this review highlights a number of findings from cross-sectional studies of age-related changes in brain function related to the perception and regulation of emotion, only one study has reported valuable longitudinal data on the neural circuitry underlying emotion processing. In a groundbreaking study, Pfeifer et al. (2011) reported longitudinal data from 38 neurotypical participants who underwent two fMRI sessions across the transition from late childhood (10 years) to early adolescence (13 years). Strikingly, responses to affective facial displays exhibited a combination of general and emotion-specific changes in ventral striatum (VS), vmPFC, amygdala, and temporal pole. Furthermore, VS activity increases correlated with decreases in susceptibility to peer influence and risky behavior. VS and amygdala responses were also significantly more negatively coupled in early adolescence than in late childhood while processing sad and happy versus neutral faces. Together, these results suggest that VS responses to viewing emotions may play a regulatory role that is critical to adolescent interpersonal functioning.

19.2.3 Lateral Temporal Cortex and the Perception of Biological Motion

Biological motion perception refers to the visual perception of a biological entity engaged in a recognizable activity. This definition includes the observation of
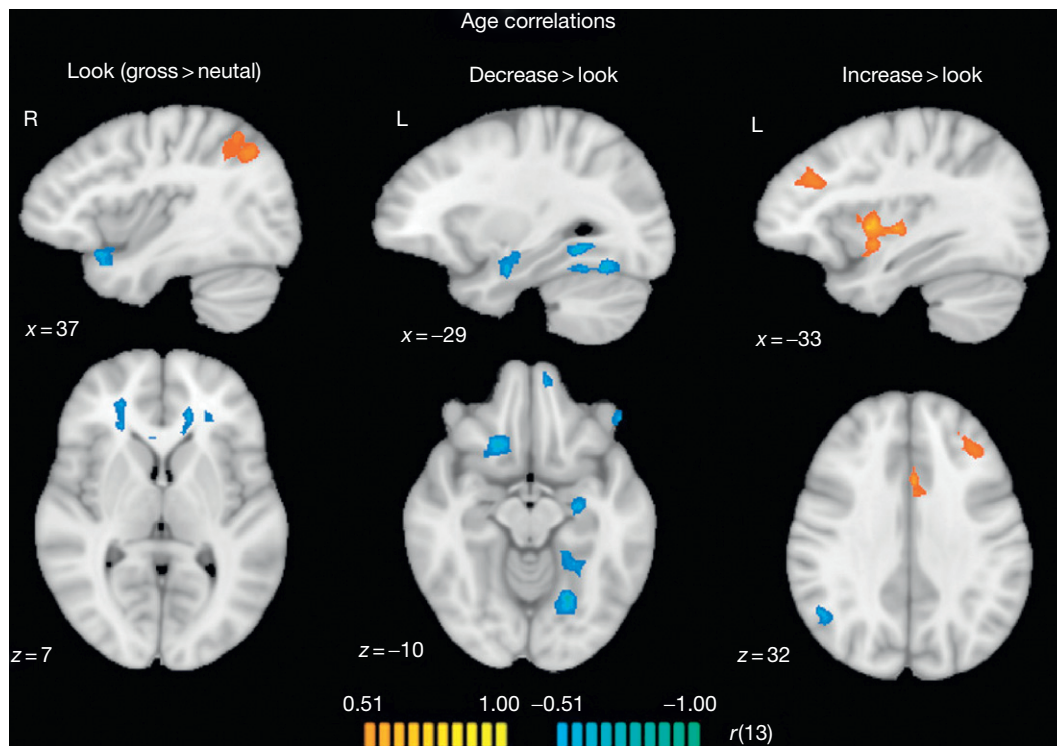
FIGURE 19.3 Activation correlated with age in each of three key contrasts, look-gross > look-neutral (reflecting the perception of disgust), decrease-gross > look-gross (reflecting efforts to downregulate emotion), and increase-gross > look-gross (reflecting efforts to increase emotion responses). Areas in orange are those that were positively correlated with age; areas in blue exhibited negative correlations with age. All activations are shown at threshold of $p < .05$. Images are displayed in radiologic convention.

humans walking and making eye and mouth movements, but the term can also refer to the visual system's ability to recover information about another's motion from sparse input. The latter is well illustrated by the discovery that point-light displays (moving images created by placing lights on the major joints of a walking person and filming them in the dark), while being relatively impoverished stimuli, contain the information necessary to identify the agent of motion and the kind of motion produced by the agent (Johansson, 1973). Biological motion is integral to social perception. The superior temporal sulcus (STS) region, particularly the posterior STS, has been implicated in the perception of biological motion including eye, hand, and whole-body movements (e.g., Bonda et al., 1996; Pelphrey et al., 2003). Specifically, it exhibits differences in activation to actions that are congruent with contextual factors relative to actions that are incongruent with the context. It is hypothesized that the STS plays such a role because intentions are used, chiefly, for predicting what people will do in the future. Since future actions are intrinsically dynamic biological motion, it seems reasonable that the STS, whose job it is to represent such motion, could be used for this role. However, it is currently unknown whether regions that represent intention for anticipation and prediction are distinct from areas that simply represent the current state of perceived biological motion.

Frith and Frith (1999) first suggested that the ability to distinguish between biological and nonbiological figures and their actions is one of the likely evolutionary and developmental precursors to theory of mind. They also noted that the STS region previously implicated in biological motion processing is adjacent to regions of the brain used for other, higher level aspects of 'mentalizing,' a concept closely related to theory of mind. The ability to infer goal states using the actions of an agent has been called an 'intentionality detector' and proposed as a component of the human mentalizing system (Baron-Cohen et al., 1994). By the age of 4 months, infants can detect biological motion from impoverished stimuli, 'point-light walkers,' and prefer these movies to those of nonbiological motion (Fox and McDaniel, 1982). A study of 8-month-old infants using ERPs suggested that there was activity in the right hemisphere in response to biological motion (Hirai and Hiraki, 2005). Lloyd-Fox et al. (2011) recently identified a more precise neurobiological basis for this very early developing social perception ability using functional near-infrared spectroscopy. In their pioneering study, 5-month-old infants watched videos of adult actors moving their hands, their

mouth, or their eyes, all in contrast to nonbiological mechanical movements. They observed that different regions of the frontal and temporal cortex responded to these biological movements and that different patterns of cortical activation emerged according to the type of movement watched. These findings demonstrate that from an early age, our brains selectively respond to biologically relevant movements, and further, selective patterns of regional specification to different cues occur within the lateral temporal cortex, including the STS region.

Only a handful of fMRI studies have examined the brain mechanisms for the perception of biological motion compared to nonbiological motion in children. In one fMRI study (Carter and Pelphrey, 2006), the functional development of the STS region was explored using a paradigm that was previously employed with a sample of adults (Pelphrey et al., 2003). In order to determine whether the STS region responded to biological motion more than to other types of complex, meaningful motion or to random motion, adult participants viewed a virtual scene that included four types of carefully matched, animated stimuli: a walking human (human), a walking robot (robot), a grandfather clock (clock), and a disjointed mechanical figure (mechanical) (see Figure 19.4). While the figures differed markedly in form, their movements were nearly identical. These figures allowed for the exploration of whether a biological motion pattern (walking) would be processed differently if made by a biological (human) versus nonbiological (robot) figure and whether there were differences in brain activation patterns for organized versus disorganized mechanical motion.

In adults, there were no significant differences between the human and the robot or between the clock and the disjointed mechanical figure in the posterior STS region. The posterior STS (right hemisphere > left hemisphere) responded more strongly to biological motion (robot and human) than to nonmeaningful but complex nonbiological motion (mechanical) or complex and meaningful nonbiological motion (clock) (Pelphrey et al., 2003). Importantly, not every brain region showed this pattern of effects. We observed a dissociation of function between the STS region and an area posterior and inferior to the posterior STS region corresponding to the motion-sensitive visual area MT or V5 (MT/V5, e.g., McCarthy et al., 1995; Tootell et al., 1995; Zeki et al., 1991). The STS region responded selectively to biological motion, whereas MT/V5 responded equally to all four types of motion.

As illustrated in Figure 19.5, 7- to 10-year-old children exhibited robust biological > nonbiological activity in the middle and posterior portions of the STS region. To examine possible age-related changes in these responses, it was assumed that higher levels of biological > nonbiological activity (i.e., greater biological−nonbiological difference scores) were indicative of a more maturely functioning system. Consequently, a positive correlation between the specificity of the STS region for biological motion and age was anticipated. Consistent with this prediction, the magnitude of the biological−nonbiological difference score was positively correlated with age in the right posterior STS region ($r=0.64$, $p=0.03$, two-tailed), with age accounting for approximately 41% of the variance in the biological−nonbiological difference scores. This finding highlights developmental changes in the functioning of the STS region during biological motion perception across middle childhood.

Much of what develops in regard to social cognitive abilities in childhood likely involves changes in connections among the various brain regions involved in social information processing. Increasing connections allow for increasingly sophisticated social perception and mentalizing abilities. Given the available research on the STS region, future research should aim to explore the development of structural and functional connectivity to and from this area. It could be the case that what appears to be a relative increase in differentiation in the STS region could represent changes in its inputs and outputs and
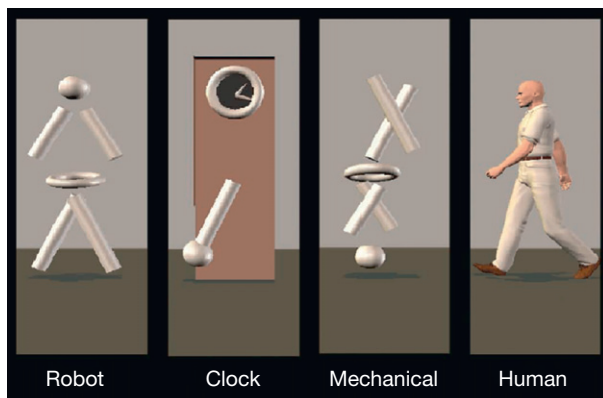

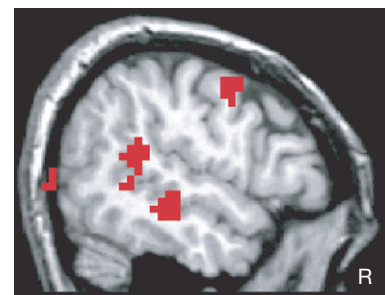FIGURE 19.4 Biological (robot and human) and nonbiological (clock and mechanical) motion stimuli.

FIGURE 19.5 The red-colored map indicates regions of significant biological > nonbiological motion activity in school-age children.

could thus either be a function of tuning of the STS response *per se*, or a development in the input by top-down regions to the STS. This could be examined using functional connectivity (to explore when regions work together) and diffusion tensor imaging (to determine the structural connections between these regions).

19.2.4 Medial PFC and the Representation of the Self and the Other

In adults, the medial PFC (mPFC) has been implicated in a wide range of social cognitive tasks, including making inferences about other people's intentions and mental states (Castelli et al., 2002; Gregory et al., 2002), the attribution of emotion to the self and others (Ochsner et al., 2004), self-reflection (Heatherton et al., 2006; Kelley et al., 2002; Northoff et al., 2006), and representing semantic knowledge about the psychological aspects of other people (e.g., Mitchell et al., 2005a,b). Additionally, the precuneus and posterior cingulate in the medial posterior parietal cortex (mPPC) are more active during self-knowledge retrieval than during other types of social or semantic tasks (e.g., D'Argembeau et al., 2010; Kelley et al., 2002). The capacity to perceive and reflect upon oneself as an individuated, unified, and stable entity with lasting qualities and traits (e.g., shy, intelligent, and kind) is a critically important and perhaps unique aspect of the human experience.

Many theoretical accounts of social cognition make self-referential processing a central component of processing others (Mitchell et al., 2005a,b; Spengler et al., 2009; Uddin et al., 2007), positing that one strategy for predicting the mental states of others is by referencing one's own thoughts, feelings, or behaviors in a similar situation. Recent studies have shown developmental changes from childhood to adulthood in activity in the frontoparietal network during self-perception tasks. To illustrate, Pfeifer et al. (2011) studied a sample of 12 children and 12 adults (average age = 10.2 and 26.1 years, respectively) using fMRI. The participants reported whether short phrases described themselves or a highly familiar other (Harry Potter). In both children and adults, the mPFC was relatively more active during self – than social – knowledge retrieval, and the mPPC was relatively more active during social – than self-knowledge retrieval. Direct comparisons between children and adults indicated that children activated the mPFC during self-knowledge retrieval to a much greater extent than adults. The particular regions of the mPPC involved varied between the two groups, with the posterior precuneus engaged by adults, but the anterior precuneus and posterior cingulate engaged by children. Only children activated the mPFC significantly above baseline during self-knowledge retrieval. This last finding suggests that the presence of a cortical, prefrontal-mediated, neural system supporting self-referential processing in children, is perhaps no longer needed in adults. Longitudinal data will be needed to more fully understand this pattern.

19.2.5 Posterior Parietal Cortex and Thinking About the Thoughts of Others

Thinking about the thoughts of others, or 'theory of mind,' has been studied most intensely using false belief tasks. In the typical design, a child watches while a puppet places an object in location A. The puppet leaves the scene and the object is transferred to location B. The puppet returns and the child is asked to predict where the puppet will look for the object. Three-year-olds think the puppet will look in location B, where the object actually is; older children think the puppet will look in location A, where the puppet last saw the object (Wellman et al., 2001). The 3-year-olds who fail the false belief task are not performing at chance, nor are they confused by the questions, but instead make systematically below-chance predictions with high confidence (Ruffman et al., 2001). The standard interpretation of these results is that 3-year-olds lack a representational theory of mind. That is, 3-year-olds fail to understand how the contents of thoughts can differ from reality (Gopnik and Astington, 1988; Wellman et al., 2001).

Although the false belief task has been used in literally hundreds of studies, it remains controversial whether success on this task depends on the deployment of a 'special' domain-specific mechanism for reasoning about other minds. As many researchers have noted (Bloom and German, 2000; Leslie, 2000; Roth and Leslie, 1998), children might pass or fail the false belief task for reasons having nothing to do with deficits in understanding other minds. In particular, the false belief task requires a high level of executive control – that is, the ability to plan and carry out a sequence of thoughts or actions, while inhibiting distracting alternatives. Thus, researchers have suggested that the false belief task underestimates children's ability to think about mental states (Bloom and German, 2000). Alleged shifts in children's theory of mind might reflect changes only in children's executive function – especially the abilities to select from among competing responses and to inhibit the tendency to respond based on reality (Carlson et al., 2004). Recently, an even bigger obstacle has arisen for the standard view: multiple reports that infants can make correct predictions on false belief tasks, when measured by violation-of-expectation looking time measured at 12–15 months (Onishi and Baillargeon, 2005; Surian et al., 2007) or predictive looking at 24 months (Southgate et al., 2007). These results have been taken as evidence for very early emerging, or even innate, cognitive mechanisms for theory of mind (Leslie, 2005).

Cognitive neuroscience provides a complementary route to address the same theoretical concerns. Are there cognitive and neural mechanisms selectively implicated in theory of mind, independent of executive demands? If so, do these brain regions' response profiles mature around age 4, the age when children reliably pass explicit false belief tasks, or early in childhood or even infancy?

Recent neuroimaging of adult brains has revealed a small but remarkably consistent set of cortical regions associated with thinking about other people's thoughts, or 'theory of mind' (Frith and Frith, 2003; Gallagher et al., 2000; Saxe and Kanwisher, 2003): bilateral temporoparietal junction (TPJ), mPFC, and posterior cingulate. The mPFC is recruited when processing many kinds of information about people (Amodio and Frith, 2006; Mitchell et al., 2005a; Ochsner et al., 2005), whereas the right TPJ is recruited selectively for thinking about thoughts (Saxe and Kanwisher, 2003; Saxe and Powell, 2006). Many functional neuroimaging studies have borrowed paradigms from the rich, older tradition of studying theory of mind in children, though few have directly investigated the development of these neural mechanisms in childhood (Kobayashi et al., 2006, 2007). In two initial studies, Kobayashi et al. (2006, 2007) reported that unlike adults, 9-year-old children did not show activation in the right or left TPJ during belief-reasoning tasks. These results suggested the tantalizing possibility of surprisingly late developmental changes in the neural mechanisms for theory of mind. However, many important questions remain opened. For example, if the TPJ, bilaterally, is not recruited for theory of mind in 9-year-olds, when do these regions develop adult-like selectivity? Are these brain regions involved in some other social cognitive function in the younger children? Or are these brain regions perhaps involved in domain-general functions in younger children and acquire a social role only later in life?

Another important question concerned the developmental relation between theory of mind and the perception of human body actions. Basic perception and understanding of human action are very early emerging, with preverbal infants demonstrating their ability to attend to human action and interpret human body movements in terms of pursuit of goals (Gergely et al., 1995; Johnson, 2003; Meltzoff and Brooks, 2001; Woodward, 1998; Woodward et al., 2001). A longitudinal study found that infants' early action understanding predicts their later success at age 4 years on explicit false belief tasks, suggesting that early perceiving and later reasoning about other people may rely on common cognitive mechanisms (Wellman et al., 2004). But how are the neural mechanisms for action perception and theory of mind related?

The neuroimaging findings reviewed above indicate that action perception (including watching hand, body, and head movements) recruits a region near the right TPJ, in the right posterior STS (Allison et al., 2000; Pelphrey et al., 2003, 2005; Puce et al., 1998). Critically, the posterior STS response depends not only on the pattern of biological motion but on its relation to the environmental context, suggesting that these regions are involved in interpreting human behavior in terms of intentions and goals (Brass et al., 2007; Pelphrey et al., 2004b,c; Saxe et al., 2004b). Early reviews of the adult neuroimaging literature proposed the existence of a single neural substrate (sometimes called posterior STS/TPJ) 'for detection of the behavior of agents and analysis of the goals and outcomes of this behavior' (Frith and Frith, 1999). However, more recent research has revealed that, at least in adults, these two regions are functionally distinct (Gobbini et al., 2007). The posterior STS shows a high response during action observation, and the TPJ shows a high response during reasoning about beliefs, but not vice versa. The possibility remained that theory of mind and action perception initially depend on a single region in posterior STS and TPJ, which then differentiates into two separate regions with distinct functions, later in development. In order to test this hypothesis, Saxe et al. (2009) compared the patterns of brain activation associated with perceiving biological motion (see Figure 19.4) and thinking about thoughts, in the same children.

Children's brains differentiated, within ongoing stories, sections that described the characters' thoughts from sections describing the physical context. Regions in precuneus and bilateral TPJ showed significantly higher responses during the mental rather than physical sections, as did mPFC, but at a lower threshold. To investigate selectivity for thinking about thoughts, the responses to people versus physical and mental versus people subsections in each ROI were compared. All the regions showed a significantly higher response for people rather than physical sections as well as a higher response for mental rather than people sections, except the mPFC, in which this latter difference did not reach any significance. That is, we did not find evidence that the mPFC reliably differentiated information about characters' thoughts from any other facts about people, although the average response in the mPFC was also not significantly different from that observed in the other regions in a direct comparison. These results suggest that in children, unlike previous results in adults, the right TPJ is not significantly more selective for mental state facts, relative to other social facts, than the mPFC. In order to determine whether this difference reflected a developmental change, changes in response patterns with age were examined. A selectivity index was calculated for each brain region, used to measure the difference (in units of percent signal change from rest) between the mental and people sections, relative to the difference between the mental and physical sections, for each individual: $100 \times (mental - people)/(mental - physical)$.

Only one brain region showed a significant correlation between age and the selectivity index: the right TPJ. Critically, the brain regions implicated in theory of mind did not overlap with those recruited during perception of biological motion.

This finding of age-related change in brain activation raises as many questions as it answers. There is a broad consensus among developmental psychologists that theory of mind is largely mature well before age 6 years (Onishi and Baillargeon, 2005; Southgate et al., 2007; Wellman et al., 2001). The above neuroimaging results, in contrast, suggest that a key component of the neural organization underlying theory of mind is still changing 3 years later, around age 9 years. So what are the cognitive (and behavioral) correlates of the increased neural specialization? The observed changes are hypothesized to reflect changes in neural organization, specifically in the selectivity of the right TPJ neural response, and are consistent with the pattern of anatomical development of human cortex as revealed in longitudinal MRI studies (e.g., Gogtay et al., 2004). Additionally, a longitudinal study found that gray matter does not reach mature density in 'higher order association areas,' including regions near the TPJ, until early adolescence (Gogtay et al., 2004). The aforementioned findings suggest that the strong selectivity observed in adult brain regions for social perception is not innate but emerges gradually over many years in childhood. In particular, regions showing the most selective response profiles in adulthood show late developmental change (the right TPJ in this study), whereas regions with more general response profiles in adulthood show less developmental change (the mPFC in this study). For both perceiving and reasoning about other people, these results suggest that the basic cognitive signatures of domain specificity may be in place long before the brain systems underlying these processes have reached an adult-like state. The implications of this conclusion are as yet unclear. But one conclusion does seem clear: the finding of late-emerging cortical selectivity undermines the interpretation of category-selective brain regions in adults as evidence for innate and early-maturing domain-specific cognitive or perceptual modules. In particular, our results in the right TPJ are challenging for theories of cognitive development that emphasize an innate and early-maturing domain-specific module for theory of mind.

19.3 A DEVELOPMENTAL MODEL OF SOCIAL PERCEPTION

To date, the field of developmental social neuroscience has begun to dissect some of the neurobiological mechanisms underlying key aspects of social perception and social cognition in infants, children, and adolescents.

This initial work and associated methodological developments have provided the exciting opportunity to address a number of fascinating theoretical questions including: (1) Do later-developing social cognition abilities colonize the systems engaged by earlier-developing abilities? Or, as development proceeds, are new regions recruited into a more basic underlying network? (2) How do the components of the social brain come to interact with each other and with other brain circuits involved in such activities as executive function and language? (3) What are the constraints for specific regions to take on aspects of social perception and social cognition (e.g., proximity and connectivity to motion and speech decoding)?

As our review has illustrated, there is a diverse set of brain regions that contribute to the complex set of social information processing tasks that we call 'social perception.' Given principles of division of labor in the brain, we would expect that each of these regions would show functional specialization. However, social perception emerges from the joint activity and connectivity of each brain region as it contributes to information processing. Early in development, the main source of social input comes from looking at faces and actions of others. Panel (a) of Figure 19.6 depicts this early social network. External input is processed for its basic social components – emotionality in the limbic areas, static faces and body information in the VOTC, and dynamic biological motion in the STS. This information can be used to anticipate other actions and guide social exploration, but only if it is integrated across these individual domains and sensory modalities. We know that in school-age children and adults, the integration of information for the understanding of action takes place in the STS, but we do not know when this begins to happen (Mosconi et al., 2005).

This early circuit relies on sensory input available to even young infants and probably does not require sophistication on the part of the child in terms of their ability to represent complex environmental knowledge or knowledge about others' mental states (Senju et al., 2006). However, it is the very simplicity that provides the child with their first abilities to perceive and anticipate the actions of others and to reap the positive rewards of being able to do so. With this early success, the child (and their social perception system) would be motivated to dedicate more resources to the problem of predicting and understanding others.

Indeed, this simple circuit, while probably remaining critically important throughout life, can only make very temporally limited predictions. For example, while smiling and reaching may provide information enough to anticipate actions over the next few seconds, it probably cannot be used to predict what a person will be doing an hour from now. To predict this longer scale of actions,
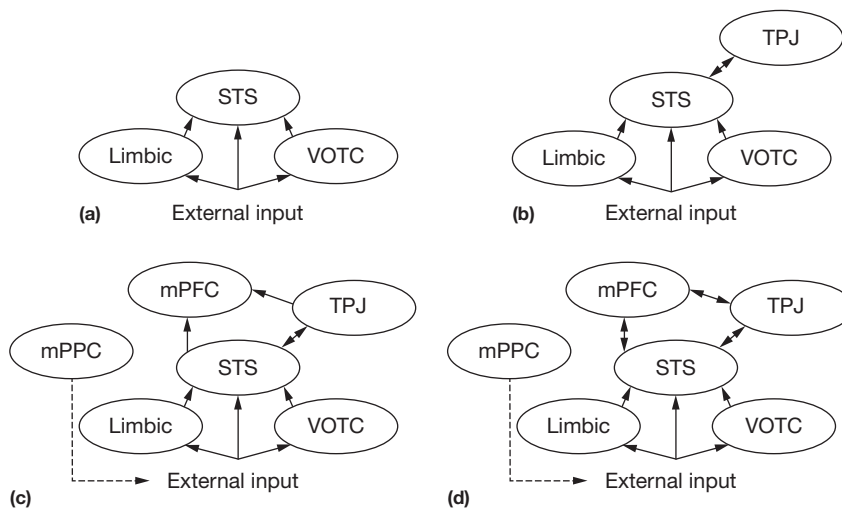
FIGURE 19.6 A developmental model of social perception development.

more sophisticated and enduring constructs about others need to be built. At this point, the TPJ is recruited (panel (b)) to allow the attribution of more abstract mental states, most likely by communicating with other areas representing language and semantic knowledge (not shown). It also must communicate with the STS, with initial projections from the STS to the TPJ needed to keep the latter informed about the current state of action, as it is perceived. Reciprocal connections from the TPJ back to the STS would allow the system to take advantage of the knowledge about how intentions (and more sophisticated representations) can unfold into action.

Further development of the system (panel (c)) would bring online prefrontal areas. It is well known that prefrontal regions and connections to the prefrontal regions from the posterior portion of the brain continue to develop well into adulthood. Thus, in early stages, the prefrontal contribution to social perception is probably limited and impoverished. However, as these regions develop, children gain the ability to reason and simulate social interactions, albeit with limited capacity. Additionally, mPPC regions such as the precuneus may begin to allow the child to switch between internal and external foci, instead of being driven completely by external stimuli. Behaviorally, this likely manifests in and is strengthened by pretense (the capability to make believe or to act 'as if'), which could be thought of as a precursor to adult-like abilities to deliberately ruminate and ponder. Indeed, pretense may be critical for adult-level performance for two reasons. First, pretense allows the child to generate scenarios, including social situations, which can be reprocessed for additional learning. Second, by reducing the dominance of external factors, the frontal-executive control of posterior areas, which may be relatively weak, can be developed.

In the final stage (panel (d)), the child develops adult-like control over posterior areas representing social information. These regions can still provide bottom-up processing of social information but can now also be activated by top-down mechanisms. One consequence of this is that social events that are separate in time can be brought together for the purposes of deliberate social reasoning. For example, we might be able to recollect an expression we perceived our friend make earlier in the day (via top-down reactivation of limbic and FFA regions) and couple that with body language we are perceiving now (via the STS) and reach a conclusion about her mental state.

19.4 FUTURE DIRECTIONS

The work reviewed in this chapter has set the stage for critical research to inform our neural systems level understanding of autism spectrum disorder (ASD). ASD is a common, early-onset neurodevelopmental disorder characterized by difficulties in social interaction and communication and repetitive or restricted interests and behaviors. ASD displays great phenotypic heterogeneity and etiological diversity, but social dysfunction is its hallmark and unifying feature. This social dysfunction is revealed by abnormalities in both simple behaviors, such as sharing gaze, and more complex social behaviors, such as triadic attention sharing. Anomalies of social perception, unlike communication problems or repetitive behaviors that are present in numerous disorders (such as anxiety or expressive language impairment), are unique to ASD and are documented across sensory modalities. Autism is a developmental disorder; early deficits derail subsequent experiences, thereby canalizing development toward more severe dysfunction and creating sequelae in additional domains of function. Consequently, the lack of reliable predictors of the condition during the first year of life has been a major

impediment to the effective treatment of ASD. Without early predictors and in the absence of a firm diagnosis until behavioral symptoms emerge, treatment is often delayed for 2 or more years.

A significant body of research has already informed our understanding of the brain basis of ASD via research on the development of systems for social perception in children and adults with and without autism (for a recent review of this research, please see McPartland et al., 2011). There is, however, a noticeable lack of information about the very early development (e.g., the first 2–3 years) of brain systems for social perception in infants and toddlers with or without ASD. This is because of the enormous challenge involved in successfully conducting this research. However, a recent study by Elsabbagh et al. (2012) illustrates the great potential for neuroimaging to contribute to our understanding and early diagnosis of ASD. They tested the hypothesis that neural sensitivity to eye gaze in early infancy would predict development of ASD in toddlerhood. The study involved a prospective longitudinal sample of infants at high familial risk for ASD and a comparison group of infants at low risk. The researchers recorded electrophysiological brain responses (event-related potentials; ERPs) while 6–10-month-old infants viewed faces with dynamic eye gaze directed either toward them or away from them. Approximately 18–30 months later, these children were clinically evaluated for the presence of an ASD. Strikingly, neural responses to dynamic eye gaze shifts during the first year predicted clinical outcomes at 36 months, despite similar patterns of gaze as measured by eye tracking. The authors conclude that ERP responses to eye gaze in the first year of life reflect developmental processes leading to the later emergence of ASD.

As the field strives for earlier methods of detecting autistic development, these remarkable findings offer hope for future clinical practice, suggesting the possibility of noninvasive, brain-based screening methods that could detect differences prior to behavioral emergence. Of course, prior to realization of such clinical benefits, it will be critical to investigate the specificity of this biomarker to autism, its presence in an unselected, population-based sample, and, most importantly, its viability in individual patient data. Given historical difficulty parsing heterogeneity in ASD, these findings suggest the potential power of systems neuroscience approaches to identify meaningful subtypes of ASD to inform treatment and predicting outcome. For the future, a strategy of deep behavior and brain phenotyping over longitudinal development is envisioned to offer a detailed profile of brain–behavior performance for a given individual for the purpose of detection of atypical development, subcategorization (e.g., for genetic analysis), treatment selection, and prediction of treatment response (see Rubenstein and Rakic, 2013).

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