CHAPTER

18

The Neural Architecture and Developmental Course of Face Processing

G. Righi[1], C.A. Nelson III[2]

[1]Boston Children's Hospital, Boston, MA, USA; [2]Harvard Medical School, Boston, MA, USA

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18.1 INTRODUCTION

Faces are ubiquitous in our environment and convey information that is used extensively in all social interactions. For example, human adults can easily classify faces on the bases of their gender, race, and identity and thus recognize quickly whether they have come across a friend or a foe (Bruce and Young, 1986). Moreover, faces also convey information that can assist an observer in gaining insight into the internal state of another person; for example, slight changes in facial features are related to different emotional states, from happiness to sadness, from anger to fear, from surprise to disgust (Ekman, 1993). Even though for most adult

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observers, gathering information from a face is a relatively seamless process, this skill undergoes a lengthy developmental trajectory that has its origins in infancy and continues well into adolescence. Throughout development, both the behaviors that accompany face processing and the neural underpinning of these behaviors undergo substantial modification. The bias brought to this chapter is that we cannot fully understand the mature face-processing system unless we make a parallel effort to understand the development of this system. The goal of this chapter is to provide an extensive overview of the research on face processing from infancy to adulthood. In each of the sections, the results of both behavioral and neurophysiological research that examines different aspects of face processing, including facial identity, facial categorization (e.g., of gender, race), and the discrimination and recognition of facial expressions are reviewed. The various sections that follow are organized chronologically with the exception of the first section. In the first section, face processing in adults is discussed in order to provide the reader with a framework on which to understand the results of the developmental work, which is presented in chronological order from infancy through adolescence. The last section of this chapter discusses impairments in face development that result from either traumatic brain injury or neurological syndromes.

18.2 FACE PROCESSING IN ADULTS

Despite the chronological organization of the majority of this chapter, the discussion of face processing in adults is dealt with first. This will provide the reader with an illustration of the mature face-processing system, including its neural architecture, which in turn will serve as a template against which to compare the development of this system. In this first section, primarily experimental evidence is reviewed, but the methodological tasks most commonly used to measure face processing are also discussed, as they apply to both the study of adults and the study of developmental populations.

18.2.1 How Adults Process Faces

Most people can recognize hundreds of individual faces by the time they reach adulthood, and their ability to memorize facial identities remains more or less intact throughout their lifespan. Moreover, face recognition is surprisingly robust. For example, it has been shown that recognition performance is relatively impervious to physical transformations including blurring (Harmon, 1973; Yip and Sinha, 2002), changes in lighting conditions (Braje, 2003; Braje et al., 1998), and changes in viewing angle (Hill et al., 1997; O'Toole et al., 1998). The resilience to these transformations is something that any observer has experienced as these variations make the recognition of identity more challenging but nevertheless successful. One of the reasons behind the robustness of face processing is that faces are not identified by focusing on specific features in isolation; rather, human observers rely on both specific facial features and on the relations among them and perform what has been termed 'holistic processing' (Tanaka and Farah, 1993; Young et al., 1987). More recently, several authors have suggested that there are three different types of holistic processing that all come into play during face processing but that can be specifically tested using different experimental manipulations (Gauthier and Tarr, 2002; Maurer et al., 2002). Aside from differences in terminology, both Gauthier and Tarr (2002) and Maurer and colleagues (2002) suggest that when viewing faces, observers process (1) the specific special arrangement of features in a face (i.e., two eyes above nose and mouth), (2) the specific spatial relations among features in a face (i.e., distance between the eyes, length of the forehead, etc.), and (3) a face gestalt in which all facial features are integrated into a representation. Healthy adults are also very proficient at detecting facial expressions, regardless of whether they are familiar or unfamiliar with a specific face. There are several well-established behavioral demonstrations of these specific types of processing strategies. The sensitivity to facelike configurations is such that adults excel at detecting the presence of faces even in very degraded situations such as in extremely blurred images or even when they are presented with highly schematic faces (Diamond and Carey, 1986). Adults are also very good at detecting variations in the spacing of features within a face, such that they can recognize different identities even when they vary only in spacing among facial features (Le Grand et al., 2001). This sensitivity to the 'configural' properties of a face has also been shown by using the 'face inversion' paradigm (Yin, 1969), which has revealed that the ability to recognize faces is greatly hindered by picture plane inversions and even more so when the distinctions between the experimental stimuli are created by spacing manipulations (Goffaux and Rossion, 2007). Lastly, the bias to produce 'holistic' face representations has been shown using the 'face composite' paradigm (Young et al., 1987). In this paradigm, subjects are presented with a face created by combining tops and bottoms of different individuals, and they are asked to pay attention to only one of the two specific parts; what has been shown is that when the two parts are presented in alignment with one another, subjects make more errors because they get distracted by the irrelevant face part. These experimental effects have been extensively replicated in the adult literature and are considered the hallmarks of expert face processing.

18.2.2 Models of Face Processing

Going beyond face recognition, adults are also very quick at determining many other different types of information from faces, including gender, race, direction of gaze, and emotional expressions. In order to understand fully the nuances of face processing, it is worth discussing in brief theoretical models that have been proposed in the literature. The most influential model of face perception remains Bruce and Young's dual-route model (1986) formulated to provide a theoretical framework that can explain how perceivers extrapolate and process different types of information from faces, such as identity, emotional expression, and facial speech. The core assumption of this model is that independent modules and processing streams support these different tasks and they work in parallel with no cross talk of information between them. Face processing begins with 'structural encoding,' which produces a number of descriptions of a face, some of which are dependent on the specific instance of the face that is presented (view-centered), while others can be more general and contain knowledge about the global structure of that face in a more invariant manner (expression-independent), meaning that they are not related to a specific expression or viewing condition. The segregation of the processing streams takes place after the initial structural encoding phase.

Regardless of whether the face is novel or familiar, expression and facial speech-processing modules receive only the information contained in the view-centered descriptions, while expression-independent descriptions are connected to a processing module that works exclusively for identity recognition. A module separate from the recognition module, which receives both the view-centered and the expression-independent information, processes the physical structure of a novel face. This module is also responsible for extracting information about the physical configurations that can be used to judge gender, race, age, etc. To summarize, after a common initial visual analysis, the information is sent to one or more of the four different modules depending on the objective of the task at hand. In turn, the outputs of each of the modules are sent to a common 'cognitive system.' This system is responsible for directing attention and decision processes, but most importantly it contains memory information about all the semantic knowledge that can be associated with a face. Bruce and Young (1986) divide the stored semantic information on the basis of which processing module provides the physical analysis needed to retrieve it. They suggest four different types of codes: expression codes, facial speech codes, visually derived semantic codes, and identity-derived semantic codes. Expression codes contain the labels for facial expressions. Facial speech codes contain representations for mouth movements connected to speech. Visually derived semantic codes contain the information relative to judgments that can be based on the physical structure alone and are independent of identity, emotional expression, and facial speech, such as gender, race, age, and some social attributions. Identity-derived semantic codes contain all the information one has acquired about a specific person that one knows.

Another class of face-processing models is represented by the prototype-based or face space model (Valentine, 1991, 1999). This type of model has been formulated with the goal of providing a unitary account of various phenomena of face processing including recognition and identification of race and gender. The basic assumption that these models make is that any face can be represented within a multidimensional space. The number of variables needed to discriminate between faces determines the dimensions of the space. The center of the space is assumed to represent the average value of a population on that specific dimension. What makes a face more or less recognizable among other faces is the distance between the target face and neighboring faces in the space. The creation of average faces gives rise to prototypes, which are presumably stored in memory. It has been suggested that observers have prototypes not only for identity but also for gender, race, and possibly even age because despite sharing the basic shape and features, individuals classified in these categories differ on the basis of specific featural and configural information (O'Toole et al., 1997).

18.2.3 Neural Substrates of Face Processing

The neural substrates of adult face processing have been extensively studied over the last decade. The advent of functional magnetic resonance imaging (fMRI) has opened the way to look at the neural networks recruited by face processing. One of the most significant findings of this literature is the identification of a portion of the cortex located within the medial fusiform gyrus that is found to be primarily responsive to faces, compared to most common objects; this functional area has been termed the fusiform face area or FFA (Figure 18.1; Kanwisher et al., 1997).

Subsequent to Kanwisher's important contribution regarding the role of the fusiform gyrus in face processing, other researchers have identified a rich network of areas that are recruited by a variety of face-processing tasks (Haxby et al., 2000; Ishai et al., 2005; Tsao et al., 2008). For example, the findings from a variety of neuroimaging studies have been integrated by Haxby and colleagues (Haxby et al., 2002) into a model of the brain network of face perception. Their proposal is strongly influenced by Bruce and Young's (1986) dual-route model, as they suggest that the recognition of identity

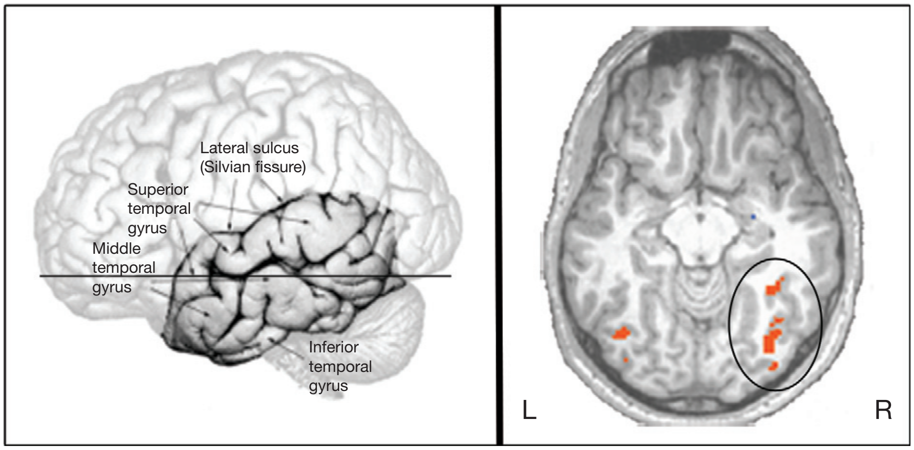

FIGURE 18.1 The fusiform face area in adult subjects.

and the processing of social information from a face are dependent on different variables that give rise to independent cognitive representations, which in turn produce distinct neural representations (Haxby et al., 2002). In line with Bruce and Young's model (1986), they suggest that while face identification is based on those features that remain invariant over time, other tasks, such as eye gaze perception, expression identification, and lip movement recognition, are derived from the analysis of the changeable features of a face. After an initial visual analysis carried out in the inferior occipital gyri, the two classes of features mentioned above are directed to either the superior temporal sulcus (STS) (changeable features) or to the lateral fusiform gyrus (invariant features). These two areas are in agreement with studies that have reported the STS to be activated by different types of biological movement including those of the eyes and mouth, while the fusiform gyrus has been consistently found to be activated when subjects are asked to judge facial identity, but less so when subjects are asked to detect eye gaze direction. From the STS, information is segregated further such that eye gaze processing is directed to the intraparietal sulcus, lip reading information is directed to auditory cortex, and emotion-related information is directed to the amygdala, insula, and other limbic system structures. The identification of the neural substrates for these three different processes is inspired by considering each process a face-specific instance of a more generic cognitive process. That is, these specific tasks recruit areas that perform the more general operations and become part of this network only when face stimuli are the input of the system. The direction of gaze can be used to direct the subject's attention toward what another individual might be looking at and as such can be considered a special case of attentional mechanisms. Emotional expressions provide information about the emotion that an individual might be experiencing and as such are processed by the same areas that are involved in the experiencing of emotions. Lip movements are the face-specific component of the multimodal speech signal and as such are processed by areas involved in speech perception. The information that reaches the fusiform gyrus is used for judgments of identity and other types of classifications that are independent of dynamic changes in facial structure (possibly gender, race, age, etc.) and as such is suggested to be relayed to areas that contain task-relevant stored knowledge, such as biographical or semantic information. In support of this idea, studies have shown that the recognition of a face is associated with activity in the anterior temporal cortex (Gobbini and Haxby, 2007; Leveroni et al., 2000), suggesting that these areas might contain semantic knowledge that is associated with known faces.

Beyond the individuation of anatomical substrates involved in face processing, many researchers have been interested in identifying functional signatures using methods such as event-related potentials (ERPs) in order to shed light on the time course of different aspects of face processing. A review of the findings using this methodology is also important in the context of development because ERPs are the most widely used technique to study the brain's response to faces in infants, toddlers, and children. Studies using ERP have identified a series of electrical potentials that respond to different aspects of face processing. The most widely studied of these components is the N170, a negative deflection in the ongoing electroencephalography (EEG) that occurs on average around 170 ms after the presentation of a face and is measured over posterior scalp electrodes, which is suggested to reflect the activity of the occipitotemporal face-selective neurons and is specifically responsive to the structural encoding of faces (Bentin et al., 1996; Carmel and Bentin, 2002; Eimer, 2000; Rossion et al., 1999). Moreover, the N170 has also been associated with configural processing as it shows both amplitude and latency modulations in response to inverted faces, when compared to upright faces (Bentin et al., 1999; Jacques and Rossion, 2007). The recognition of facial identity has been suggested to take place later in the processing stream and has been associated with other components such as the N250 (Rossion et al., 1999; Rossion and Gauthier, 2002), the N400, and the P600 (Eimer, 2000).

18.2.4 Conclusions

In summary, with a few exceptions, adults are very good at recognizing and processing the information present in faces. However, it should be evident from the data reviewed in this section that these abilities are dependent on complex processing strategies and rely on the interactions of a rich network of brain regions. Moreover, adult expertise is also dependent on the constant interactions with faces that we all experience in everyday life. The next sections in this chapter will examine how face expertise arises throughout development, with the hope to provide the reader with an understanding on both the behavioral and neural specialization for face processing.

18.3 FACE PROCESSING IN THE FIRST YEAR OF LIFE

18.3.1 How Infants Learn to See Faces

Despite a very immature visual system, infants develop the ability to process facial identities and facial expressions surprisingly quickly over the first year of life (Figure 18.2) (see Chapter 14).

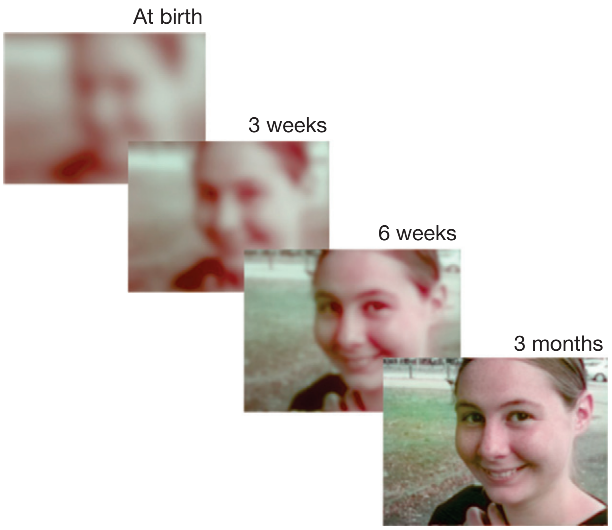

FIGURE 18.2 Development of the infant visual system within the first year of life.

Their experience with faces begins at birth, and one of the most striking findings of the literature looking at face processing in infants is that since birth they show a preference to pay attention to faces and facelike stimuli, compared to other visual objects (Johnson and Morton, 1991; Maurer, 1983; Mondloch, et al., 1999; Valenza et al., 1996). The ontogeny of their face preference is still under debate. On one hand, it has been hypothesized that infants are 'innately' attracted to stimuli that resemble faces (e.g., an oval with three dots in it) and that from birth there is a subcortical brain system, possibly including the superior colliculus and the pulvinar, that causes infants to orient toward facelike patterns (Johnson, 2005). This mechanism is supposed to be replaced at around 2 months of age by a cortical mechanism (Conlearn) that is already somewhat specialized for faces (Johnson, 2005). On the other hand, it has been hypothesized that faces happen to be optimal stimuli for a developing visual system in terms of their physical characteristics (Banks and Salapatek, 1976; Kleiner, 1987). Following this initial orienting toward faces, it is through exposure and active experience that the infant brain starts to develop what become face-sensitive processes and neural structures (Nelson, 2001).

Over the first months of life, infants rapidly learn to perform several types of facial discriminations. Several studies have shown that infants as young as 4 days old show signs of discriminating their mother's face from that of a stranger, although this ability is not yet robust enough to withstand, for example, the presence of a headscarf (Pascalis et al., 1995). However, infants rapidly progress in their ability to recognize their mother's faces such that at 3 months of age, they are able to do so even across variations in viewpoint (Pascalis et al., 1998). It is around 3 months that infants also show the ability to discriminate between male and female faces (Quinn et al., 2002) and also between faces of different races (Bar-Haim et al., 2006; Kelly et al., 2005; Quinn et al., 2008).

Related to the development of the ability to discriminate between faces of different identities, different gender, and different races is a phenomenon called perceptual narrowing (see Nelson, 2001 for discussion). While at 3 months infants seem to be learning to differentiate between different categories of faces, it has been suggested that by 9 months they develop the ability to distinguish between exemplars within a category but only if they have experience with that specific category. Perceptual narrowing refers to the fact that between 3 and 9 months, on average around 6 months, infants are able to discriminate between individual exemplars of many different visual categories. However, by 9 months, this flexibility appears lost in most categories, except for the ones with which the infant has the most experience.

In behavioral studies, it has been shown that 9-month-olds do not successfully differentiate between different individuals of a race other than their own (Kelly et al., 2007). Moreover, by 9 months of age, infants are not discriminating among a pair of monkey faces, something that 6-month-olds are capable of doing, while successfully differentiating between human faces (Pascalis et al., 2002, 2005).

During the first year of life, infants also experience changes in the strategies they use when they process faces. One of the hallmarks of face processing in adults is their reliance on the configural properties of a face, which is at the root of their expertise with faces. Infants do not seem to show the ability to use configural cues at birth, but some investigators have suggested that this ability emerges within the first year of life, even though it may not be reaching adultlike levels until later in development. Recent studies have shown that by 7 months of age, infants are sensitive to prototypical face configurations (Thompson et al., 2001), such that they can discriminate between faces that contain atypical distances between their features and more prototypical exemplars. A recent study has suggested that infants as young as 5 months are able to discriminate between faces that differ only in spacing between the eyes and spacing between the nose and mouth while maintaining identical features (Bhatt et al., 2005).

18.3.2 How Infants Process Facial Expressions

Within the first year of life, infants are also able to discriminate some facial expressions (Barrera and Maurer, 1981; de Haan et al., 1998; Nelson and Dolgin, 1985; Nelson and Salapatek, 1986; Nelson et al., 1979; Young-Browne et al., 1977), and within their first 12 months, they undergo a series of developmental changes. Starting as early as 36 h after birth, infants show evidence of being able to discriminate among happy, sad, and surprised faces (Field et al., 1982). Experimental evidence from infants in their first 6 months of life shows that they continue to be able to discriminate at least some facial expressions from one another, with some variability depending on the intensity of the exemplars used on their specific characteristics. Overall, it seems that happy faces are successfully differentiated from other expressions and neutral faces (Farroni et al., 2007; LaBarbera et al., 1976; Young-Browne et al., 1977), while negative expressions are more difficult to differentiate for young infants (LaBarbera et al., 1976; Nelson and Dolgin, 1985; Young-Browne et al., 1977). It has been hypothesized that during the first few months of life, infants may learn to discriminate the expressions that they are most often exposed to, which are usually positive, and are not yet capable of discriminating among ones that they do not see often. It is between 7 and 12 months that, perhaps, emotion processing experiences the most dramatic changes and infants start showing the ability to discriminate expression with which they do not have much experience. For example, it is around 7 months that infants first show the ability to consistently discriminate fearful faces (Nelson and Dolgin, 1985) and start showing longer fixations toward this expression (Leppänen et al., 2007; Peltola et al., 2009). Another important shift that takes place starting at around 7 months is the perception of facial expression in a categorical manner, which is a signature of emotion processing present in adults. Thus, it is around this age that infants demonstrate the ability to (a) generalize their discrimination of facial expressions across multiple exemplars (e.g., Nelson et al., 1979) and (b) discriminate qualitatively between two facial expressions even though the stimuli used are created using a quantitative morph continuum. This effect has been using faces that are morphed in a continuous way between happiness to sadness (Leppänen et al., 2009) and fear and happiness (Kotsoni et al., 2001).

18.3.3 Neural Substrates of Face Processing in Infants

The study of the neural substrates of face processing in infants has received much attention in recent years. One of the questions that is still debated is whether faces are processed by specialized neural structures since birth (Johnson, 2005; Johnson and Morton, 1991) or whether the neural structures that are found to be face-selective in the adult brain become specialized for face processing through active experience over the course of development (Gauthier and Nelson, 2001; Nelson, 2001). Because of obvious methodological difficulties, there are very few studies that have used functional brain imaging methods to test whether infants show face-selective brain activations. To our knowledge, the only investigation of this type used PET scanning in six 2-month-old infants, who at birth had experienced hypoxic–ischemic encephalopathy (Tzourio-Mazoyer et al., 2002). In this study, infants were presented with faces of adult females and schematic dot patterns. The infants' brain showed a surprisingly rich network of clusters of activation in response to faces akin to what is found in the adult brain in the inferior occipital cortex, but it also showed activation for faces in parietal and frontal regions (Tzourio-Mazoyer et al., 2002). These results are important as they confirm the presence of a neural system sensitive to faces as early as 2 months of age. However, there are two issues to consider with this study. First of all, the infants tested were not neurologically normal. Second, the comparison stimulus used was far less attractive and complex compared to faces, and as such it is difficult to determine whether any complex object would have elicited similar patterns of activation.

18.3.4 Neural Signatures of Face Processing in Infants

The most widely used method to assess infants' brain responses to faces is ERPs, and the adaptability of this methodology to infant studies has given rise to an extensive literature that has investigated the functional signatures of face processing in infants. ERP components that are sensitive to faces have been shown to emerge as early as 3 months of age (Halit et al., 2004). There are two components that are considered to be the antecedents of the adult N170: the N290 and the P400. The N290 shows an adultlike effect of inversion starting around 6 months of age (Halit et al., 2004), but as pointed out by de Haan and colleagues (de Haan et al., 2003), the selectivity for faces of this component has yet to be tested in infants. The P400 shows an adultlike latency difference between faces and objects and by 12 months also shows an effect of inversion (Halit et al., 2004). Similar to the adult literature, these two components have been linked to the structural analysis of faces, while another set of components has been linked to the recognition of familiar faces: the Nc and the positive slow wave. The Nc appears to show a difference between the mother's face and a stranger's face starting at 6 months of age as long as the two faces are different enough from one another (Figure 18.3; de Haan and Nelson, 1997).

ERP components elicited in response to faces have also been shown to be modulated by the presence of emotional expressions. Among face-sensitive components, the Nc component appears to be sensitive to several facial expressions in infants. In one of the first studies using ERP to look at facial expression processing, Nelson and de Haan (1996) showed that fearful faces elicited an increased amplitude of the Nc component, compared to happy faces. Leppänen and colleagues (Leppänen et al., 2009) also found differential sensitivity to happy and sad faces in the Nc component in 7-month-olds, but no differences were found in the N290 and P400. Grossman and colleagues found amplitude modulations in this component in response to angry and happy faces in 7-month-olds (Grossmann et al., 2007). Interestingly, it is only around 12 months that infants start showing modulations of emotional expressions on more posterior components (Grossmann et al., 2007).

18.3.5 Conclusions

During the first year of life, face processing undergoes rapid development both behaviorally and neurally. In the first 12 months of life, infants start to show many of the face-processing skills that will gain strength throughout development and will reach full maturity in adolescence and adulthood. Moreover, their neural responses to faces also start to show signs of face specialization, although it is apparent that much anatomical and functional maturation will take place with

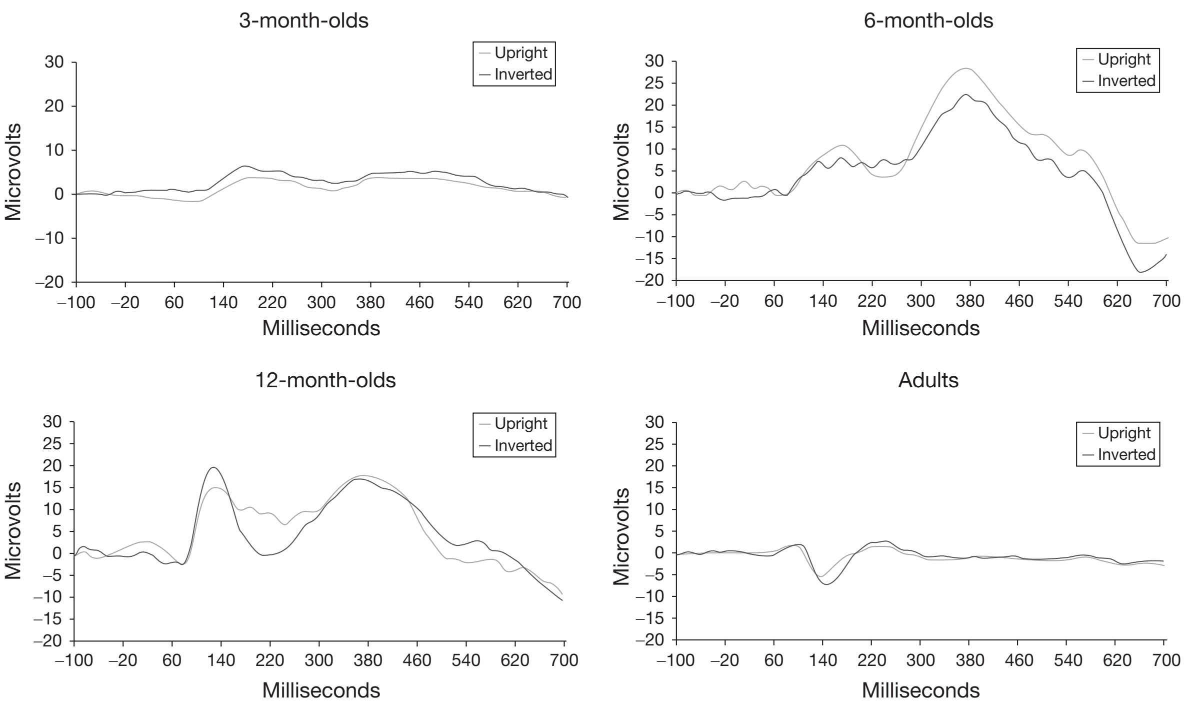

FIGURE 18.3 Functional signatures of face processing as measured using ERPs in the first year of life and adulthood.

development in order to reach adultlike neural signatures of face processing. Even though issues regarding the ontogeny of face processing have yet to be resolved in the literature, it is clear that experience with faces since birth is very important for infants in order to lay the groundwork to develop expert face processing.

18.4 FACE PROCESSING IN TODDLERS AND PRESCHOOLERS

18.4.1 How Young Children Process Faces

Even though infants make incredible strides in the first year of life, their face-processing abilities are far from fully developed by the time they turn one. As discussed below, a great deal of development takes place after a child's first birthday. However, while infants' face-processing abilities are studied extensively, there are fewer investigations available of toddlers and preschoolers, with very few studies documenting the performance of 2- and 3-year-olds and relatively more data available for 4- and 5-year-olds.

There are few studies that have quantified the behavioral performance of toddlers and preschoolers in facial recognition and facial expression recognition. Bruce and colleagues (Bruce et al., 2000) have carried out an extensive behavioral investigation of how children as young as 4 and 5 perform on a variety of measures of face processing including the processing of facial identity, the processing of direction of gaze, and the processing of facial expressions. In this investigation, young children's performance was above chance across all tasks but still significantly below the proficiency attained by adults. Preschoolers also had trouble matching facial expression and direction of gaze with a specific target face, while they were easily able to discriminate along these dimensions (Bruce et al., 2000).

The results of Bruce and colleagues' investigation of face processing in young children suggest that they have yet to reach adultlike face-processing proficiency. There are two main hypotheses as to how these children differ from adults. On one hand, these differences have been hypothesized to be due to the fact that toddlers and preschoolers have yet to develop the face-specific processing strategies found in adults, namely, configural and holistic processing, and rely more heavily on feature-based strategies (see Mondloch et al., 2003a,b for a review). This hypothesis has been supported by studies showing that preschoolers experience difficulty in recognition when faces are 'disguised' (i.e., presented with a hat) between the original presentation and the subsequent ones, suggesting that perhaps they are not encoding faces using their configural properties but rather rely on specific isolated features (Carey and Diamond, 1977; Freire and Lee, 2001). Further support for this hypothesis has come from studies using artificial face sets that are created such that different faces can vary exclusively either in terms of individual facial features, in terms of the spacing between facial features, or in terms of the facial contours (Mondloch et al., 2002). These studies have shown that toddlers and preschoolers fail to discriminate different identities when they have to rely exclusively on configural information but perform above chance when they can use featural and contour information (Mondloch et al., 2002, 2003a,b, 2006).

Alternatively, some researchers have proposed that the differences found in performance between young children, older children, and adults are produced by the protracted development of generic cognitive functions that can support the employment of more complex processing strategies (i.e., configural and holistic processing) more effectively (see McKone and Boyer, 2006 for a review). That is, it has been suggested that toddlers and preschoolers show a quantitative shift in their processing strategies and not a qualitative one. In support of this hypothesis, several researchers have used tasks such as the classic inversion effect task (Yin, 1969) and the composite effect task (Young et al., 1987) and measured young children's performance using faces and nonface objects such as cars or shoes. These investigators have found positive evidence of a difference in performance between upright and inverted faces in children as young as 3 (Macchi Cassia et al., 2006; Picozzi et al., 2009; Sangrigoli and de Schonen, 2004) and of holistic processing in children as young as 3½ years of age (de Heering et al., 2007; Macchi Cassia et al., 2009; Pellicano and Rhodes, 2003), even though across all these studies, overall performance in young children was usually worse compared to older children and adults.

Even though these two hypotheses point to diverging developmental trajectories, it may also be the case that their findings are not diametrically opposed. First of all, there are marked methodological differences among these studies, and different types of stimulus manipulations are used to measure configural and holistic processing, which could in part lead to diverging behavioral effects. Moreover, the tasks used vary in the relative difficulty of the different manipulations, and as such it is difficult to compare their findings objectively. Perhaps, results from electrophysiological investigations, which will be discussed below in this section, may shed more light on this controversy (Box 18.1).

18.4.2 How Young Children Process Facial Expressions

The ability to recognize facial expression has also not reached adultlike levels of performance in toddlers and preschoolers. Interestingly, there appear to be different developmental trajectories for different facial expressions

BOX 18.1

Electrophysiological and neuroimaging methods used in face processing

There are two primary techniques that are most widely used in the study of face perception: related potentials (ERP) and functional magnetic resonance imaging (fMRI). Traditionally, ERP has been used to study face processing in developmental populations, while both techniques have been used with adults. However, in recent years, fMRI has been used successfully with children as young as 7 years of age.

Event-related potentials measure the synchronous activity of large populations of neurons in response to a specific event. In a typical ERP experiment, stimuli of various types will be repeated many times, in order to be able to compute an average response by collapsing across repeated presentations of the same stimulus or category of stimuli. ERPs are collected using arrays of electrodes. In recent years, the number of recording electrodes has grown from 32 to 64, 128, and even 256, available in caps or nets that can be used with infants, children, and adults. Researchers use several characteristics of the ERP signal in a diagnostic manner: latency of a specific waveform, amplitude of a specific waveform, and the location of potentials across the scalp at specific time points (scalp topography).

fMRI measures the hemodynamic response in the brain related to the presentation of specific experimental stimuli. It has been shown that when nerve cells are active, they increase their oxygen consumption. In response to the increased need for oxygen, there is an increase in blood flow in local capillaries. As a consequence, there will be an imbalance in the relative concentration of oxyhemoglobin and deoxyhemoglobin. Because the magnetic properties of blood vary depending on the level of oxygenation, pulse sequences can be used to detect these imbalances and measure the blood oxygen level-dependent (BOLD) contrast. In turn, the BOLD response can be used as an indirect measure of localized brain activity. Studies of face processing using fMRI will present subjects with faces and other types of objects and then measure the BOLD response to the different stimuli across the entire brain, in order to understand whether there are specific regions that modulate their response on the basis of the stimuli that they see.

with happiness being the most readily recognized expression followed by sadness, anger, and fear (see Herba and Phillips, 2004 for a review). Moreover, it has also been shown that preschoolers need more intense expressions in order to successfully recognize emotions, compared to older children (Gao and Maurer, 2009). These findings may initially seem at odds with those described in the previous section suggesting that infants are already capable of discriminating basic facial expression. However, it is important to point out that the nature of the tasks used between infants and toddlers can be very different and, as such, it is difficult to compare directly the results across age groups (McClure, 2000), and as a consequence researchers have wondered whether the different tasks are measuring similar processing abilities. Moreover, given that the neural substrates supporting emotion recognition are far from fully mature at these ages, it is not surprising that young children show behavioral differences in emotion processing compared to older children and adults.

18.4.3 Functional Signatures of Face Processing in Young Children

If infants present a challenge for the study of the neural underpinnings of face processing, toddlers and preschoolers may be even more difficult to test. Thus, there are relatively few studies investigating how the brain of young children responds to faces, and for the most part, these studies employed ERPs. Nevertheless, these investigations can be particularly informative to help us understand the ability of young children to discriminate among different faces and different facial expressions, as the behavioral investigations alone have produced somewhat conflicting evidence. Overall, one would not expect major changes in the types of components elicited by faces, such as the P1 and the N170, and the nature of the changes is expected to be primarily in terms of latency (i.e., decreased latencies), morphology (i.e., more defined waveforms), and topography (i.e., hemispheric specialization) of these components, as toddlers' and preschoolers' brains undergo structural changes such as increased myelination, increased functional specialization, and changes in the underlying neural generators (de Haan et al., 2003; Gauthier and Nelson, 2001). There are, however, other changes that are taking place in these components that are more specific to the stimuli used, as the specific faces used acquire different significance with age. For example, Carver and colleagues (Carver et al., 2003) found that relative amplitude differences in the Nc and P400 components in the mother's face and a stranger's face switched between 2–3-year-olds and 4–5-year-olds with the younger children showing increased amplitude to the mother's face and the older children showing the opposite pattern.

Overall, while the morphology and topography of face-sensitive ERP components is changing toward adultlike brain signatures, their development is far from over within this age group (Taylor et al., 1999, 2004), possibly suggesting that even though young children show some evidence of adultlike face processing, they are still undergoing maturational changes both behaviorally and neurally.

Components reflecting differences in responding to emotional faces also show developmental changes, and these studies can further the understanding of how young children perceive facial expressions. Despite the fact that from a behavioral perspective, toddlers and preschoolers have difficulty recognizing fear in a face, Dawson and colleagues have shown that fearful faces elicit faster and larger P200 and N300 components, compared to neutral faces (Dawson et al., 2004). Batty and Taylor (2006) found that facial expressions also affected early components such as the P1. Toddlers and preschoolers had faster P1 latencies across all six emotions compared to neutral faces and more specifically showed the fastest latencies for positive emotions and, in particular, for happiness (Batty and Taylor 2006).

18.4.4 Conclusions

Taken together, the results of behavioral investigations and ERP studies looking at various aspects of face processing and face-processing strategies have led the majority of investigators to believe that toddlers and preschoolers are still on a developmental trajectory toward adultlike face processing. Nevertheless, it is important to point out that in very few years of life, young children demonstrate an uncanny proficiency in extracting information from faces.

18.5 FACE PROCESSING IN SCHOOL-AGE CHILDREN AND ADOLESCENTS

18.5.1 How Children and Adolescents Process Faces

The behavioral performance of school-age children and adolescents is relatively well documented, compared to that of toddlers and preschoolers. The majority of studies performed with these age groups have used experimental paradigms that are commonly used with adults (i.e., recognition memory paradigms, inversion face task, composite face task, etc.) in order to examine when and how children achieve adultlike levels of performance in face recognition and also when they show evidence of using configural and holistic processing strategies.

It is primarily within this age group that the scientific debate over children experiencing quantitative or qualitative changes in face-processing strategies is contested. This debate ensues because experimental results are heterogeneous. On the one hand, there are several studies pointing to the fact that school-age children, and in some cases even adolescents, differ in the type of information they use within a face (see Mondloch et al., 2003a,b for a review). For example, it has been demonstrated that children up to the age of 15 are not yet able to rely on the internal facial features of a face without contour information in order to successfully identify unfamiliar faces but rather perform better when they are provided only with the external contour information, compared to the internal features alone (Campbell and Tuck, 1995; Campbell et al., 1999; Want et al., 2003), which is opposite to the pattern that is observed in adults. Using a set of faces created in the laboratory that can differ only in terms of the external contour, or internal features, or the spacing among the internal features, Mondloch and colleagues found that, unlike adults, 6-, 8-, and 10-year-olds produced the most errors when discriminating faces differing in feature spacing (Mondloch et al., 2002). Moreover, Mondloch and colleagues have shown that 6-, 8-, and 10-year-olds failed to show an increased cost of face inversion in the feature-spacing set, compared to the other two stimuli manipulations, which is also different from how adult subjects perform (Mondloch et al., 2002).

Although these studies and others (Freire and Lee, 2001; Mondloch et al., 2006) suggest that children are less sensitive than adults to configural information, other researchers have produced results providing support for the hypothesis that children apply adultlike processing strategies from a young age. Children as young as 4 have demonstrated evidence of holistic processing as demonstrated using the composite face task (Mondloch et al., 2007; Pellicano and Rhodes, 2003), and Tanaka and colleagues (Tanaka et al., 1998) have found an adultlike whole-part advantage in 6-year-olds. Moreover, children as young as 6 have performed in a manner similar to that of adults on an inversion effect task, producing comparable differences between performance on upright and inverted faces (Mondloch et al., 2002).

In order to examine the controversy mentioned in the previous paragraphs regarding the nature of the development of face-processing strategies, there are some methodological considerations to be made. First, one possible explanation for the divergent results is the methodological differences employed across studies. For example, in some cases, memory-encoding paradigms are used, which require children to learn a specific set of faces prior to the testing phase, while in other cases the children are presented with simultaneous matching paradigms, in which there is very little memory load. Second, depending on the specific nuances of each study, the children are sometimes compared to the adults in terms of their quantitative performance, while in other cases their behavioral trends are compared to those found in adults. Thus, this makes it difficult to examine directly all these results and draw unified conclusions. In order to aid the resolution of this debate, it may be useful to consider it in the context of neurophysiological findings, which will be discussed below in this section.

Identity recognition, however, appears to be a process that does not reach full maturation until adolescence. In an extensive study looking at performance both on face and emotion recognition, Bruce and colleagues (Bruce et al., 2000) showed that performance on face recognition and emotion recognition increased steadily from 5 years of age until about 11 years of age. Moreover, they showed that when the experimental faces used were highly dissimilar, 11-years-olds performed as well as adolescents, but this was not the case when more similar faces were used, suggesting that more challenging face recognition follows a slow progression. Similarly, using a recognition memory paradigm, Golarai and colleagues have shown that adultlike levels of recognition memory performance for faces are not reached until at least 14 years of age (Golarai et al., 2007), while these authors did not find any age effects in the recognition memory performance for common objects. Moreover, school-age children tend to make more errors than adults when asked to recognize faces across viewpoints, lighting conditions, and changes in facial expression (Bruce et al., 2000; Mondloch et al., 2002, 2003a,b). While in the majority of studies it has been found that children perform worse than adolescents in recognition memory tasks, it is important to acknowledge that this may not be specific to faces, but it may be an issue of task difficulty. Why this issue is not easily solved is because, to our knowledge, there are no extensive studies comparing face processing to the processing of other complex visual objects.

18.5.2 How Children and Adolescents Process Facial Expressions

The recognition of emotional facial expression is also still undergoing development from childhood through adolescence, and the specific pattern of improvement appears dependent on the types of emotional faces used, on the intensity of the facial expression, and on the specific expression itself (Durand et al., 2007; Gao and Maurer, 2009; Herba et al., 2006; Kolb et al., 1992; Thomas et al., 2007; Vicari et al., 2000). Overall, behavioral studies of emotion recognition with children and adolescents show that children as young as 5 recognize happy faces accurately (Gao and Maurer, 2009; Vicari et al., 2000) but also show that sad and fearful faces remain more difficult to recognize especially if the face stimuli used depict less intense emotion (Gao and Maurer, 2009; Thomas et al., 2007; Vicari et al., 2000). The speed of processing of facial expression also undergoes a maturation change between the ages of 7 and 10 (De Sonneville et al., 2002). There are nevertheless some differences in studies, in terms of the specific age ranges and their performance, and these differences are likely due to the different methodologies employed and the types of stimuli used. However, a protracted pattern of development for the recognition of facial expression makes sense even in the context of the development of the neural regions recruited when children and adolescents look at emotional faces.

The behavioral studies of development provide somewhat heterogeneous evidence, but by and large, they suggest that by 10–11 years of age, children perform in a manner comparable to adults across a variety of tasks that involve facial recognition, the use of face-specific processing strategies (i.e., configural processing, holistic processing), and recognition of emotional expressions. Given the heterogeneity of behavioral findings, it is particularly important to study the neural substrates of face processing in different age groups in order to understand whether by the time performance has reached adultlike levels, the underlying neural substrates and processes have also stabilized to what is found in adults or whether brain and behavior follow two different trajectories.

18.5.3 Neural Substrates of Processing in Children and Adolescents

In contrast to the relatively few studies examining the neural bases of face processing in toddlers and preschoolers, this topic has been more heavily addressed in older children. Of particular interest are recent investigations using fMRI to look not only at the functional signatures of face processing but also at the specificity of the neural substrates recruited. The question of interest in this literature is whether neural selectivity for faces has emerged by the time children are of school-age, that is, whether there are already measurable clusters of neurons that respond more strongly to faces than to most other objects. Several recent studies have been particularly focused on whether category selectivity for faces is present in the brains of children as young as 7 years of age (Aylward et al., 2005; Golarai et al., 2007, 2010; Passarotti et al., 2003; Scherf et al., 2007). Overall, these studies suggest that category selectivity in the right fusiform gyrus emerges around 7 years of age. More specifically, Golarai et al. (2007) have shown that the volume of these regions in the adult brain is larger compared to that in both children and adolescents and that it gets progressively larger between children and adolescents. More evidence of slow maturation is provided also by a recent study comparing the neural activations in response to upright and inverted faces in fMRI. Pasarrotti and colleagues (Passarotti et al., 2007) found that children ages 8–11 did not show showed increased activation for inverted faces, compared to upright faces, while older children ages 13–15 showed a trend in the opposite direction, which is what is commonly reported in adult studies.

Further evidence of protracted neural face selectivity is also provided by studies using ERP. Investigations using this technique have demonstrated that in children and adolescents, there are still differences in the latency and topography of face-selective neural signatures, compared to adult data. Adultlike characteristics of the latency of N170, for example, are not reached until adolescence (Taylor et al., 1999). Moreover, children do not show an adultlike latency difference between upright and inverted faces in the N170 until about 11 years of age (Itier and Taylor, 2004; Taylor et al., 2004), and the differences in amplitude with the inverted faces eliciting larger amplitudes, compared to upright faces, are observed only in adolescents (Taylor et al., 2004). Moreover, adultlike topography with higher amplitudes in the right hemisphere compared to the left for the N170 does not appear to emerge until adolescence (Taylor et al., 1999).

Although the neural responses to emotional faces are not widely studied within this age group, the few studies available on the topic have shown differences between adults and school-age children, and adolescents have also been reported in the context of emotional face processing. Passarotti and colleagues (Passarotti et al., 2009) tested adolescents with happy and sad faces in fMRI and found that while there were no differences in the areas that were recruited when adolescents and adults looked at emotional faces, there were differences that emerged in the relative activations in different brain regions, such that the adolescents activated paralimbic regions more strongly than the adults, but the adults activated prefrontal regions more strongly than the adolescent subjects. Similarly, Guyer and colleagues found more activation of the amygdala in response to fearful faces in adolescents, compared to adults, who in turn showed stronger functional connectivity between the amygdala and the hippocampus.

Differences in facial expression processing across children, adolescents, and adults are also observed using ERPs. Batty and Taylor (2006) have shown that from the age of 5 to the age of 15, there are changes in the sensitivity of the P1 and the N170 to facial expressions. More specifically, while children show latency modulations in the P1, older children show latency modulations only in the N170. Amplitude changes also vary across components within this age group, showing the same patterns as the latencies. Overall, what does not seem to be changing across development is the fact that positive emotions are processed with shorter latencies compared to negative emotions (Batty and Taylor, 2003, 2006).

18.5.4 Conclusions

Taken together, both the majority of behavioral findings and the results of neurophysiological investigations seem to suggest that face processing is still undergoing maturational changes through childhood and adolescence. Thus, even though children and adolescents already show some of the hallmarks of adultlike face processing, experimental evidence points to the fact that throughout childhood and adolescence, there are quantitative changes that take place in how these observers process faces.

18.6 IMPAIRMENTS IN FACE PROCESSING

While most of us rarely forget a face we have seen before, or have trouble identifying facial expressions, there is a subset of children and adults that experience great difficulties with these seemingly effortless operations. Dysfunctions in different aspects of face processing can arise from structural abnormalities within the brain and visual organs such as brain lesions and cataracts. Difficulties in processing faces can also be found in populations with neurological disorders such as autism spectrum disorder (see Chapter 34) and Williams syndrome (WS).

18.6.1 Prosopagnosia

In the literature, the majority of cases describing face-processing impairments are linked to brain injury to the occipital and temporal cortices, occurring either in the right hemisphere or bilaterally. The impairment that results from this kind of injury and produces primarily a deficit in recognizing familiar people has been termed prosopagnosia (Bodamer, 1947). Prosopagnosics not only show great difficulty in recognizing and learning new faces but also display atypical face-processing strategies (Barton, 2003). More specifically, they appear to be overly dependent on specific facial features, to be insensitive to the configural properties of faces, and to be unable to use holistic processing as reliably as healthy controls (Barton, 2003; Bukach et al., 2006, 2008; Wilkinson et al., 2009). However, prosopagnosics do not typically show difficulty identifying facial expressions (Young, 1992).

While prosopagnosia usually occurs in adults, there are documented cases of prosopagnosia in children following brain injury (Dutton, 2003; Dutton et al., 2006; Young and Ellis, 1989). Similarly to the adults, these children have great difficulty in recognizing individuals by their face, and they also show differences with configural/holistic processing compared to age-matched controls. However, as brain injury in children is rarely localized to the occipitotemporal cortex, these patients manifest neurological and perceptual problems beyond face perception (Dutton et al., 2006). Moreover, in contrast with adult prosopagnosics, children with this type of brain damage also tend to have difficulty recognizing facial expressions (Dutton, 2003).

Prosopagnosia can be also diagnosed in people who have not suffered any brain trauma (Behrmann et al., 2005a; Duchaine and Nakayama, 2006; Kress and Daum, 2003). Recent case studies documenting this type of prosopagnosia have termed it 'congenital,' to distinguish it from the form that follows brain injury ('acquired' prosopagnosia). Congenital prosopagnosics self-report difficulties in recognizing familiar faces that date to childhood and usually have learned to rely on cues other than facial information to recognize people; thus, they appear less impaired than acquired prosopagnosics. In recent years, this population has received much attention, and several studies have been aimed to categorize the nature of these patients' deficits. These patients can reliably detect a face among nonface objects and perform judgments of gender and age on faces successfully. However, they have difficulty in both matching and recognition tasks when they are under time pressure and/or the stimuli used are impoverished (i.e., face ovals with no hair; Behrmann et al., 2005b). Similar to acquired prosopagnosia, congenital prosopagnosics show a different manner of processing of face stimuli, demonstrating a heavier reliance on featural strategy in place of configural and holistic processing (Behrmann et al., 2005b). So far in the literature, this syndrome has primarily been studied in adults. However, a few cases of this syndrome have also been reported in children, and even the adult studies suggest an early onset of these problems (Ariel and Sadeh, 1996; Grueter et al., 2007).

The neural bases of congenital prosopagnosia are yet to be fully understood. Studies using ERPs have shown a reduced brain response to faces in congenital prosopagnosics as measured by the amplitude of face-sensitive components (Bentin et al., 1999). Studies using fMRI have produced discordant results, such that in few instances congenital prosopagnosics did not show brain activation in the right fusiform gyrus in response to faces (Hadjikhani and de Gelder, 2002), while others report typical right fusiform gyrus activation in response to faces (Avidan et al., 2005; Hasson et al., 2003). Brain activations alone have not been a diagnostic measure with these patients, as the relationship between these neural responses and their impairment is not clear. Thus, it has been suggested that congenital prosopagnosia could be caused by anatomical abnormalities in the temporal lobes, the same structures that when damaged produce acquired prosopagnosia. For example, Behrmann and colleagues have measured a reduction in the volume of the anterior fusiform gyrus in congenital prosopagnosics, compared to control subjects (Behrmann et al., 2007). Recent data using diffusion tensor imaging (DTI) have suggested that the recognition impairments may be due to the thinning of white matter fiber tracts connecting the ventral temporal cortex to the anterior temporal and prefrontal cortices (Thomas et al., 2009).

18.6.2 Congenital Cataract Patients

Given how rapidly face processing develops in the first year of life, researchers have wondered whether congenital visual impairments such as cataracts, which are present at birth but are usually surgically repaired within the first 2–6 months of life, have an impact on the ability to process faces later in life. Le Grand and colleagues have conducted a series of studies with children and young adults, aged 9–29, who were congenitally blind at birth because of bilateral cataracts but gained vision between 2 and 6 months of age following corrective surgery. These studies have shown that, despite the extensive experience with faces that these subjects have acquired since their cataracts were removed, they are not able to achieve the same level of performance as age-matched controls on tasks that tap complex face-processing strategies. More specifically, these patients had difficulty recognizing different faces that varied in terms of the distance between internal features (Le Grand et al., 2001), and they also failed to show the traditional 'composite effect' (Le Grand et al., 2004), which is used as an indirect measure of holistic processing (Maurer et al., 2002). Moreover, they experience particular difficulty with recognition when faces change orientation or facial expression across multiple presentations (Geldart et al., 2002). However, these patients are able to recognize faces fairly well in the real world, which is likely due to the fact that they can identify specific faces using the distinctive shape of the internal features and contour information (Mondloch et al., 2003a,b). No studies to date have looked at the functional responses that these patients' brains show when they are viewing faces. However, the dissociation found in this population between featural and configural/holistic processing abilities suggests that their neural network supporting face processing may have developed differently compared to healthy adults (Mondloch et al., 2003a,b).

18.6.3 Autism and WS

18.6.3.1 How Subjects with Autism Process Faces

Atypical face processing has also been reported in certain populations of individuals diagnosed with autism spectrum disorder (ASD) and WS. ASD is a neurological disorder that is diagnosed early in childhood, usually around the age of 3, and characterized by impairments in social interactions and language development; it is usually accompanied by repetitive behaviors and restricted interests (DSM-IV). In recent years, great interest has been devoted to understanding the nature of face-processing difficulties experienced by children and adults diagnosed with ASD because face-processing deficits are suggested to be strongly related to the social impairments experienced by these individuals. Moreover, some investigators have suggested that face-processing deficits may be one of the earliest indicators for the presence of autism (Dawson et al., 2005; Schultz, 2005; Schultz et al., 2000). The impairments found in ASD individuals since childhood span many different face-processing tasks with studies reporting deficits in recognizing facial identity (Boucher and Lewis, 1992; Boucher et al., 1998; Klin et al., 1999), less reliance on holistic and configurational processing (Behrmann et al., 2006; Gauthier et al., 2009; Joseph and Tanaka, 2003; Schultz et al., 2000; Teunisse and de Gelder, 2003) and reduced visual attention to internal facial features (Chawarska and Shic, 2009; Klin et al., 2002).

18.6.3.2 How Subjects with ASD Process Facial Expressions

Because of the social nature of ASD impairments, much attention has also been devoted to studying whether these patients have difficulties recognizing facial expressions. Overall, the majority of studies conducted on this topic would argue that ASD individuals have difficulty, beginning in childhood, recognizing, identifying, and classifying facial expressions (Braverman et al., 1989; Celani et al., 1999; Gross, 2004; Hobson, 1986). In several studies, it has been reported that these patients experience particular difficulties in recognizing negative emotions (Humphreys et al., 2007; Pelphrey et al., 2002) possibly because of ineffective use of information from the eye region of a face (Baron-Cohen et al., 1997, 2001; Gross, 2004). Moreover, recent studies using facial morphs that vary parametrically in the strength of visible facial expressions have shown that most ASD individuals have difficulty identifying and categorizing more subtle facial expressions (Rump et al., 2009; Teunisse and de Gelder, 2001).

18.6.3.3 Neural Substrates of Face Processing in ASD

The behavioral differences found between ASD individuals and typically developing controls have been connected to a variety of differences found in brain responses to faces between these two subject groups. Studies using ERPs have shown that both children and adults with ASD show shorter latencies for objects compared to faces for the N170 component (Webb et al., 2006). Moreover, the scalp topography of face-sensitive ERP components is different between these two subject groups, suggesting a smaller degree of hemispheric lateralization for face processing in ASD subjects (Dawson et al., 2005). Atypical ERP responses have also been demonstrated when ASD individuals are shown emotional faces (Dawson et al., 2004). Differences between ASD individuals and healthy controls have also been found using fMRI, with several studies showing hypoactivity not only in brain regions associated with processing of facial identity, such as the right fusiform gyrus (Dawson et al., 2002; Grelotti et al., 2002; Pierce et al., 2001; Schultz et al., 2000), but also in brain regions associated with the processing of facial expressions and gaze, such as the STS (Dalton et al., 2005; Pelphrey et al., 2005) and the amygdala (Adolphs et al., 2001; Hadjikhani et al., 2007; Schultz, 2005).

While the majority of studies of face processing in ASD individuals point to atypical development of this skill, this population shows a great deal of variability both in terms of behavioral patterns and neural responses. This heterogeneity of results has produced several debates in the literature regarding the true origins of these deficits. Nevertheless, atypical face processing, both at the behavioral and neural levels, remains one of the hallmarks of ASD.

18.6.3.4 Face Processing in WS

Another neurological disorder that has received attention in association with face processing is WS. WS is a rare genetic disorder characterized by a series of physical deformities, language and motor delays, and atypical cognitive functions in a variety of domains, including atypical social functioning (see Bellugi et al., 2000 for a review). Unlike ASD individuals, children and adults diagnosed with WS show face recognition abilities comparable to healthy controls (Bellugi et al., 1994; Tager-Flusberg, and Joseph, 2003). However, it has been suggested that they do not process faces configurally and holistically but rather rely more heavily on featural processing (Deruelle et al., 1999); but not all researchers agree on this interpretation (Karmiloff-Smith et al., 2004; Tager-Flusberg et al., 2006). Patients with WS are akin to ASD patients in that they also show deficits in emotion recognition from facial expressions (Tager-Flusberg et al., 2003).

These two subject populations also show divergences and similarities in the context of neural responses to faces, which map the dissociations found at the behavioral level. Studies using fMRI in adults diagnosed with WS have found activation in the right fusiform gyrus in response to faces that is comparable to that of healthy controls (Meyer-Lindenberg et al., 2004; Schultz et al., 2000). However, WS patients show hypoactivation in brain regions recruited when processing facial expressions, specifically the amygdala and the orbitofrontal cortex (Meyer-Lindenberg et al., 2005).

18.7 CONCLUSIONS

The goal of this chapter was to provide the reader with a comprehensive overview of the literature concerning face processing and its development from birth to adulthood.

Faces are very important stimuli for humans, as they convey a multitude of information about the people that we encounter in the world. While some debate remains regarding the initial mechanisms that orient infants toward faces, it is most likely that the development of face processing relies on both experience-independent early specificity and an experience-dependent sensitive period (Sugita, 2008). That is, while the initial orienting toward faces may be driven by a genetically specified primitive architecture (Johnson, 2005), the development of the ability to extract information from a face is heavily dependent on experience, and it is through exposure and interactions with specific types of faces that we learn to become 'face experts,' which is a lengthy process that requires the first 10–15 years of life (Nelson, 2001).

Despite the many things that are known in the face-processing literature, it is the authors' wish to conclude this review with some of the questions that are still unanswered. First of all, while it has been demonstrated that experience with faces is very important for one to become an 'expert,' relatively little is known about the specific nature of this experience. Secondly, it is unclear whether the effect of experience is dependent on a sensitive period. Although the data produced by investigations with cataract patients and congenital prosopagnosics would suggest that any derailment from typical development affects face processing, more work will be necessary to establish the precise nature of a sensitive period and its relations to different aspects of face processing. Lastly, we would like to highlight a real conundrum of face processing, which is its apparent lack of plasticity. It has been demonstrated that once a portion of the face-processing system becomes compromised, the ability to recognize faces appears gone for good. This is a very troublesome observation for this literature because it is difficult to reconcile how an operation of such evolutionary importance that relies on a large network of neural substrates can show so little ability to reorganize itself following an insult, especially given the fact that our brains are overall quite plastic. In our view, this remains an essential issue to resolve in the coming years.

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