

Chapter 20

The neural architecture and developmental course of face processing

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20.1 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). Faces also convey information about internal states; 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 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. In this chapter, we argue 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 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.

20.2 Face processing in adults

Despite the chronological organization of the majority of this chapter, we begin with a discussion of face processing in adults. 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.

20.2.1 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 life span. Moreover, face recognition is surprisingly robust. For example, recognition performance is relatively invariant 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). One of the reasons behind the robustness of face recognition is that, once detected, faces are processed using dedicated, face-specific strategies (Tsao and Livingstone, 2008). Namely, faces are not identified by focusing on specific features in isolation; rather, human observers rely on both specific facial features and the relations among them and perform what has been termed “holistic processing” (Tanaka and Farah, 1993; Young et al., 1987). Several authors have proposed to distinguish between three different types of holistic processing that can be experimentally dissociated (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 spatial 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. The sensitivity to facelike configurations is such that adults excel at detecting the presence of faces even in highly degraded situations such as in extremely blurred images or 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, participants 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, participants 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.

20.2.2 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. To understand fully the nuances of face processing, it is worth discussing in brief theoretical models that have been proposed in the literature. An influential model of face perception by Bruce and Young (dual-route model; 1986) provides 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), whereas 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, whereas 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. Independent processing of identity and expression *after successful structural encoding* is a main prediction of the Bruce and Young model (1986). In practice, the independence of expression and invariant (e.g., identity) face information processing is incomplete (e.g., [Baudouin et al., 2000a,b](#); [Brenna et al., 2012](#); [Calder and Young, 2005](#); [Turati et al., 2011](#)). However, the ideas of view-invariant and structural encoding, of a *relative* functional divide between view-invariant and expression processing, are supported by much empirical evidence (e.g., [Richoz et al., 2015](#); [Vuilleumier et al., 2003](#)). Recent computational models have further established how view-invariant face identity recognition may be achieved mathematically through face-specific internal models of viewpoint transformations ([Anselmi et al., 2016](#); [Leibo et al., 2015](#)). These models provide an important theoretical link between the empirical observations of view invariance and domain specificity in human face identity recognition and give computational flesh to the idea of structural encoding.

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](#)). The concept of “face space” is quite agnostic to what the dimensions of such space specifically represent. In line with other existing empirical data in both species, at least some of the earlier studies in rhesus macaques have tended to emphasize the role of particular facial features in isolation or combination ([Freiwald, Tsao and Livingstone, 2009](#)), whereas studies in humans have additionally emphasized the role of second-order relations ([Burton et al., 1993](#)) and configural encoding ([Renzi et al., 2013](#)). Alternative accounts have proposed that face space dimensions may consist in unsupervised representations akin to principal component analysis (PCA) or multidimensional scaling ([Calder and Young, 2005](#); [Cowen et al., 2014](#); [Gao and Wilson, 2013](#)), implicitly providing a mechanism for developing a face space from mere exposure. Interestingly, a recent study in rhesus macaques used a combination of facial features PCA that dissociated shape and position information from facial appearance information to generate face space dimensions that could account for single unit neural responses to unfamiliar faces in a manner that outperforms other candidate models and generalize to unseen exemplars ([Chang and Tsao, 2017](#)). The dissociation between shape or position information and facial appearance information additionally confers some degree of view invariance to the model and is empirically reflected in the observed differential selectivities of face patches ([Chang and Tsao, 2017](#)). From a developmental perspective, these important results raise the question of how such an internal model of face shape and features may emerge in infancy and childhood, presumably facilitated by an ability to detect facelike patterns from birth ([Tsao and Livingstone, 2008](#)).

An additional debate concerns whether, in the face space, a given face is coded with regard to its own properties (exemplar-based) or its properties relative to the prototype face (norm-based). Both implementations make very similar predictions, although overall norm-based coding appears to better account for empirical data than exemplar-based coding (Chang and Tsao, 2017; Leopold et al., 2001; 2006; Loffler et al., 2005; Rhodes and Jeffery, 2006; but see Ross et al., 2014). Norm-based coding may also, under some assumptions, provide an efficient solution to the view-invariant problem where view invariance would only need to be learned with respect to the prototype (or norm), whereas other faces would be coded with respect to such invariant norm. This means that there is no need to learn how all faces look from all possible angles, etc. Thus, face space models can be reconciled with the original Bruce & Young model (1986) because they provide a potential mechanism for structural encoding—that is, the multidimensional representation of faces with respect to a norm or prototype may form the basis of invariant face identity recognition.

20.2.3 Neural substrates of face processing

The neural substrates of adult face processing have been extensively studied over the past two decades (Grill-Spector et al., 2017). 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 with most common objects; this functional area has been termed the fusiform face area or FFA (Fig. 20.1; Kanwisher et al., 1997), which is sometimes separated into two separate compartments laying on the mid- and posterior fusiform gyrus, respectively, and is distinct in their cytoarchitectonic properties (Weiner et al., 2017).

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 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 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 earlier are directed to either the superior temporal sulcus (STS) (changeable features) or 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 (Hein and Knight, 2008; Said et al., 2011; Yovel and O'Toole, 2016), whereas the fusiform gyrus has been consistently found to be activated when participants are asked to judge facial identity, but less so when they are asked to detect eye gaze direction. From the STS, which itself displays some degree of functional organization that teases apart different social, language, emotion, or biological motion information (Deen et al., 2015; Hein and Knight, 2008; Liebenenthal et al., 2014; Peelen et al., 2010;

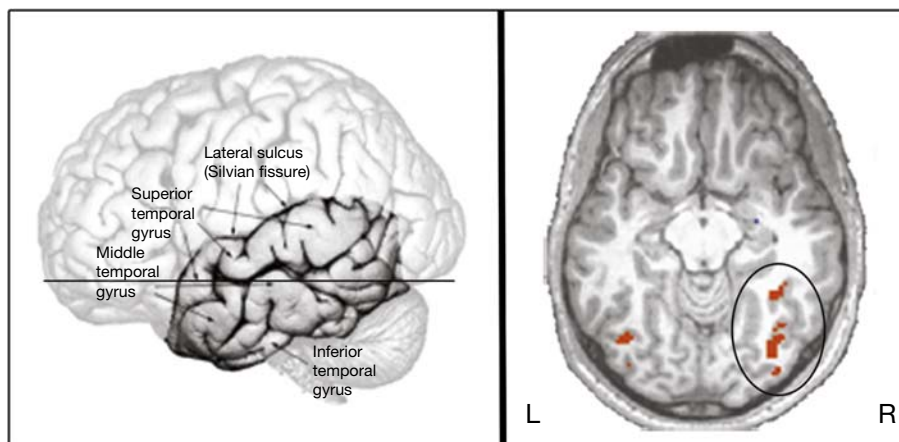


FIGURE 20.1 The fusiform face area in adult participants.

Said et al., 2010; Schobert et al., 2018), 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 participant'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 further processed in areas implicated in emotion processing, such as the medial prefrontal cortex (Peelen et al., 2010). Lip movements are the face-specific component of the multimodal speech signal and as such are processed in 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 correlates of face processing using methods such as event-related potentials (ERPs) or magnetoencephalography (MEG) to shed light on the time course of different aspects of face processing. A review of the findings using ERPs is particularly 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 young children. Studies using ERPs 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, in adults, 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 with 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).

20.2.4 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.

20.3 Face processing in the first year of life

20.3.1 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 (Fig. 20.2).

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 with other visual objects (Fantz, 1961; 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, and perhaps beginning prenatally (Reid et al., 2017), there is a subcortical brain system, possibly including the superior colliculus and the pulvinar (Simion et al., 1998), that causes infants to orient toward facelike patterns (Johnson, 2005; Johnson et al., 2015). This mechanism is supposed to be replaced at around 2 months of age by a cortical mechanism (Conlearn) that is



FIGURE 20.2 Development of the infant visual system within the first year of life.

already somewhat specialized for faces (Johnson, 2005; Johnson et al., 2015). More recently, a small-scale EEG study of newborns has demonstrated that upright facelike patterns may preferentially engage cortical networks at birth that closely align with cortical areas preferentially engaged by face processing in adults (Buiatti et al., 2019); thus, if subcortical mechanisms are responsible for the detection of facelike patterns at birth, then they must be functionally connected to these cortical networks. 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). For example, eye-tracking studies reveal that it is not until approximately 4-month-old of age that infants begin to preferentially fixate toward the eye, nose, and mouth regions of upright but not inverted faces, as adults do (Gallay et al., 2006; Maurer and Salapatek, 1976; Turati et al., 2005).

Recent studies in infant macaques have also shown that robustly face-specific neural domains are not present from birth but emerge during the first months of life as a preceding, weak protoselectivity for faces strengthens (Livingstone et al., 2017). Studies of the early visual environment of infants during the very first few months of life have demonstrated that most of the faces encountered by infants in their first months tend to be upright, in front view, at a close distance, and with both eyes visible (Jayaraman et al., 2015; Sugden et al., 2014; Sugden and Moulson, 2017)—thus, an orienting bias toward facelike patterns, whatever its mechanism or domain specificity, could provide a powerful tool to immediately levy such initial exposure during the very first few months of life, which studies of adults who had congenital cataracts removed in infancy have revealed to be essential to develop typical face-processing abilities (Le Grand et al., 2003; Maurer et al., 2005). Studies of infants' early visual environment additionally reveal that infants are primarily exposed to adult female faces of their own race and that most of the faces that infants experience belong to their caregivers (Sugden et al., 2014; Sugden and Moulson, 2018); this observation is intriguing because it suggests that, during this period, face-specific cortical regions receive critical input that is abundant but mostly limited to a small set of different identities. Work with infant macaques clearly demonstrates that the development of face-specific cortical regions is indeed dependent on visual exposure to faces after birth, at least in macaques and thus presumably in humans as well; face-deprived infant monkeys do not exhibit robust face-selective patches despite preserved retinotopic maps throughout the visual cortex (Arcaro et al., 2017). Because infant monkeys who are raised with exposure to faces exhibit strong looking preferences for faces earlier than the age at which robust face patches emerge (Arcaro et al., 2017; Livingstone et al., 2017), it is tempting to conclude that an early bias toward looking at faces must be driving cortical face selectivity development. Critically, however, face-deprived infant monkeys exhibit a strong looking preference for hands from the earliest age tested (90 days) and, again, earlier than the age at which robust hand patches emerge (Arcaro et al., 2017). Thus, either face-deprived monkeys did have an earlier, innate tendency to look at facelike patterns that was abolished by early face deprivation and replaced by a looking preference for hands as a result of early experience, which in turn paralleled or drove the emergence of hand-selective patches (a possibility that resembles the earlier proposal of Morton and Johnson, 1991), or infant rhesus macaques do not have an innate early tendency to look toward faces but rather develop a tendency to preferentially look toward faces (or, in their absence, hands) as a result of their overabundance in the early environment, typically at

stereotypic locations in the visual field (which maps onto preexisting retinotopic protoorganization), a broader visual bias toward biological motion or animacy, and the reinforcement of face-looking behavior during social interactions (Arcaro et al., 2017). The former account may be more consistent with previous behavioral findings in monkeys raised without exposure to faces (Sugita, 2008), demonstrating that face-deprived monkeys do exhibit a spontaneous looking preference for faces versus *objects* even during the face deprivation period (i.e., even if not for faces versus *hands*, which in the case of face-deprived monkeys come to acquire a particular social significance). Critically, under both accounts, the formation of face- or hand-selective patches would be more strongly determined by early experiences rather than by an innate tendency to fixate faces or facelike patterns (but see Caldara et al., 2006). In addition, it is interesting to note that, in face-deprived monkeys, hand-preferring areas were found in locations that only partially overlapped with these of face-preferring locations in control monkeys. This brings some weight to the authors' suggestion (Arcaro and Livingstone, 2017; Arcaro et al., 2017; Livingstone et al., 2019) that low-level characteristics of faces or hands (including typical location in the visual field; see also: Gomez et al., 2018), rather than solely their functional relevance (e.g., robustly identifying caregivers and conspecifics by sight), may at least partly drive the specific localization of these cortical patches (but see Powell et al., 2018, for an exactly opposite interpretation of the same data).

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, an ability that critically depends on audio–visual cues from exposure to the mother's voice (Sai, 2005) and is not yet robust enough to withstand, for example, the presence of a headscarf (Bushnell et al., 1989; 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). Infants between birth and 3–4 months may recognize newly learned faces despite modest view changes, e.g., from front to $\frac{3}{4}$ pose (Turati et al., 2008), or a short delay (2 min) between learning and test (Pascalis and de Schonen, 1994). However, they are not yet able to do so when the view changes significantly, e.g., from front to side, and cannot yet connect side to full-front views of the same face unless specifically trained to do so (Gliga and Dehaene-Lambertz, 2007; Pascalis and de Schonen, 1994; Turati et al., 2004, 2008). The ability to distinguish between unfamiliar faces as they are presented at varying orientations or with varying expressions in real time doesn't emerge until a few months later, with expression invariance and partial view invariance emerging at 6–8 months (Cohen and Strauss, 1979; Fagan, 1976; Kobayashi et al., 2011, 2012) and profile view invariance emerging between 7 and 12 months (Rose et al., 2002).

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; see also Hugenberg et al., 2010; Kelly et al., 2007; Maurer and Werker, 2014; Pascalis et al., 2014; Sugden and Marquis, 2017). 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 (e.g., own-race, own-species, but also other-race, other-species). However, by 9 months, this flexibility appears lost in most categories, except for the ones with which the infant has the most experience (e.g., own-race, own-species, but not other-race or other-species). 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). Similarly, 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). A study in macaque monkeys with controlled face exposure has demonstrated that perceptual narrowing is triggered by visual experience (Sugita, 2008).

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 seem to show the ability to use configural (as evidenced by the inversion effect) but not holistic (as evidenced by the composite face effect) cues at birth (Turati et al., 2010; Turati et al., 2006), although the ability to use second-order configural cues to identify faces only emerges within the first year of life (Bhatt et al., 2005; Thompson et al., 2001), as do holistic processing (Turati et al., 2010) as well as the processing of identity invariantly of expression (Kobayashi et al., 2014) and view (Kobayashi et al., 2011; Rose et al., 2002); configural and holistic processing may not be reaching adultlike levels until later in development. 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. Similarly, 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).

20.3.2 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, this ability undergoes a series of developmental changes (for a review, see, e.g., Bayet and Nelson, 2019; Leppänen and Nelson, 2009; Nelson, 1987). Starting as early as 36 h after birth, infants show some evidence of being able to discriminate among happy, sad, and surprised faces when presented dynamically by a live model (Field et al., 1982), as well as a visual preference for smiling over neutral or fearful static faces (Farroni et al., 2007; Rigato et al., 2011). Experimental evidence from infants in their first 6 months of life further 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 or 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), whereas 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. A few studies additionally suggest that, in very young infants (i.e., 3–6 but not 9-month-olds), the processing of at least some emotional faces (as measured by behavioral indices such as attentional preference, discrimination, or matching) may be modulated a face's personal familiarity, race, or gender (Bayet et al., 2015; Montague and Walker-Andrews, 2002; Safar et al., 2017; but see Safar and Moulson, 2017).

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 and increased attention allocation toward this expression (Leppänen et al., 2007; Leppänen, 2011; Peltola et al., 2008, 2009, 2011). A low-level sensitivity to fearful faces and eyes (Bayet et al., 2017) or an attention bias to dynamic fearful expressions (Heck et al., 2016) might precede or drive the developmental emergence of the attentional fear bias at 7 months (see also, Hoehl, Wiese and Striano, 2008; Yrttiaho et al., 2014; but see Grossmann and Jessen, 2017). Another important shift that takes place starting at around 7 months is the perception of facial expression in a categorical manner, that is, independently of face identity, which is a signature of emotion processing present in adults. It is around this age that infants demonstrate the ability to generalize their discrimination of facial expressions across multiple exemplars (e.g., Nelson et al., 1979) and to discriminate qualitatively between two facial expressions even though the stimuli used are created using a quantitative morph continuum. The latter effect has been demonstrated 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).

From about the age of 8 months and toward the end of the first year of life, infants further begin to exhibit an increasingly complex understanding of social interactions that is integrated with an understanding of facial emotions as possessing affective (or at least valence) information. While infants at that age will not robustly categorize emotional faces according to valence (Ludemann, 1991), they appear to associate smiling with success in attaining a goal (Skerry and Spelke, 2014) and smiling toward an object with a personal preference toward that object (Phillips et al., 2002). Further evidence of infants' growing understanding of the informative value of facial expressions comes from the classic phenomenon of social referencing, in which infants will actively look for facial cues from a caregiver in an ambiguous situation, which emerges at the same age (Sorce et al., 1985; Walden and Ogan, 1988).

20.3.3 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 challenges, 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, dynamic 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). A larger response was observed in the right hemisphere, suggesting a right hemisphere bias in the processing of faces by 2 months of age. 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 (dynamic dot patterns) was far less attractive and complex compared with faces, and as such it is difficult to determine whether any complex object would have elicited similar patterns of activation. Converging results, however, have been recently obtained in two studies involving slightly older infants (4–6 months). The first of these studies (de Heering and Rossion, 2015) used EEG to uncover the strength and spatial distribution of neural responses to the periodic presentation of face images (1.2 Hz) embedded among a faster periodic presentation of other complex visual stimuli including animals, buildings, and small objects (6 Hz). In 4- to 6-month-old infants, neural responses entrained by faces in this manner were maximal over right occipitotemporal locations at electrode P8, where the adult N170 is typically observed (de Heering and Rossion, 2015). An fMRI study with infants in this age range also found evidence of functional specificity for faces versus scenes in cortical regions including ventral occipitotemporal, STS, and prefrontal areas (Deen et al., 2017). Notably, infants did not exhibit reliable functional specificity for faces versus objects in this study (Deen et al., 2017). Overall, these studies suggest that the infant brain processes faces with some degree of functional specificity by at least 4–6 months, and possibly at least 2 months, of age (see also: Adibpour et al., 2018; Lloyd-Fox et al., 2009; Otsuka et al., 2007). However, such functional specificity remains limited and will be refined over the course of development. Studies in infant macaques, reviewed earlier (Arcaro et al., 2017), lead us to speculate that the burgeoning functional specificity of the infant brain for processing faces, observed here at 4–6 and possibly 2 months of age, may be driven by the abundance, relevance, and stereotypic properties of infants' early experiences with these social stimuli—possibly in conjunction with retinotopic protomaps and other structural organizing biases of the visual cortex (Arcaro et al., 2017).

20.3.4 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). Two components 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 12 months of age (De Haan et al., 2003; Halit et al., 2003). The extent and strength of the N290s specificity for faces in infancy remains debated (Halit et al., 2003); however, at least one study of 4.5- to 7.5-month-olds reports larger N290 amplitudes to attended faces versus toys (Guy et al., 2016). The estimated cortical source of the N290 lays in the middle fusiform gyrus and neighboring areas (e.g., temporal pole), suggesting that a progressive refinement of both its face selectivity and spatial specificity gives rise to the adult N170 over the course of early development (Guy et al., 2016; see also Johnson et al., 2005; Xie et al., 2018). The P400 shows an adultlike latency difference between faces and objects in some studies (but see, e.g., Guy et al., 2016), by 3 months also shows an effect of inversion that is not specific to human faces (De Haan et al., 2003; de Haan et al., 2002; Halit et al., 2003), and by 12-months shows an adultlike inversion effect that is specific to human faces (De Haan et al., 2003; Halit et al., 2003). Thus, these two components have been linked to the structural analysis of faces, although the status of the P400 as a face-specific component is debated (Guy et al., 2016). Another component has been linked to the recognition of familiar faces: the negative central (Nc). The Nc, which is typically interpreted as an index of attention allocation (Guy et al., 2016), differentiates 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 (Fig. 20.3; de Haan and Nelson, 1997; see Luyster et al., 2014 for developmental trajectories of the P1, N290, P400, and Nc amplitudes to mother and stranger faces from 6 to 36 months of age).

Emotional expressions modulate these ERP components. The N290, P400, and Nc components appear sensitive to several facial expressions in infants. In one of the first studies using ERPs to examine facial expression processing, Nelson and de Haan (1996) showed that fearful faces elicited an increased Nc amplitude compared with happy faces. Further ERP studies of 6- to 7-month-old infants have confirmed a modulation of the properties of the N290, P400, and/or Nc components by some facial expressions such as angry versus fearful (Hoehl et al., 2008; Kobiella et al., 2008; Xie et al., 2018; but see Nelson and De Haan, 1996), fearful versus happy (Nelson and De Haan, 1996; Peltola et al., 2009a,b; Xie et al., 2018), or angry versus happy (Grossmann et al., 2007; Xie et al., 2018). The specific effects observed (e.g., amplitude or latency difference on a particular ERP component) may vary across studies (e.g., Hoehl et al., 2008 vs. Kobiella et al., 2008), presumably due to methodological differences, relatively small sample sizes (with some exceptions, e.g., Xie et al., 2018), and perhaps modulations by developmental contexts (e.g., parenting style, Taylor-Colls and Pasco Fearon, 2015). In a facial emotion categorization paradigm, Leppänen et al. (2009) additionally found evidence of

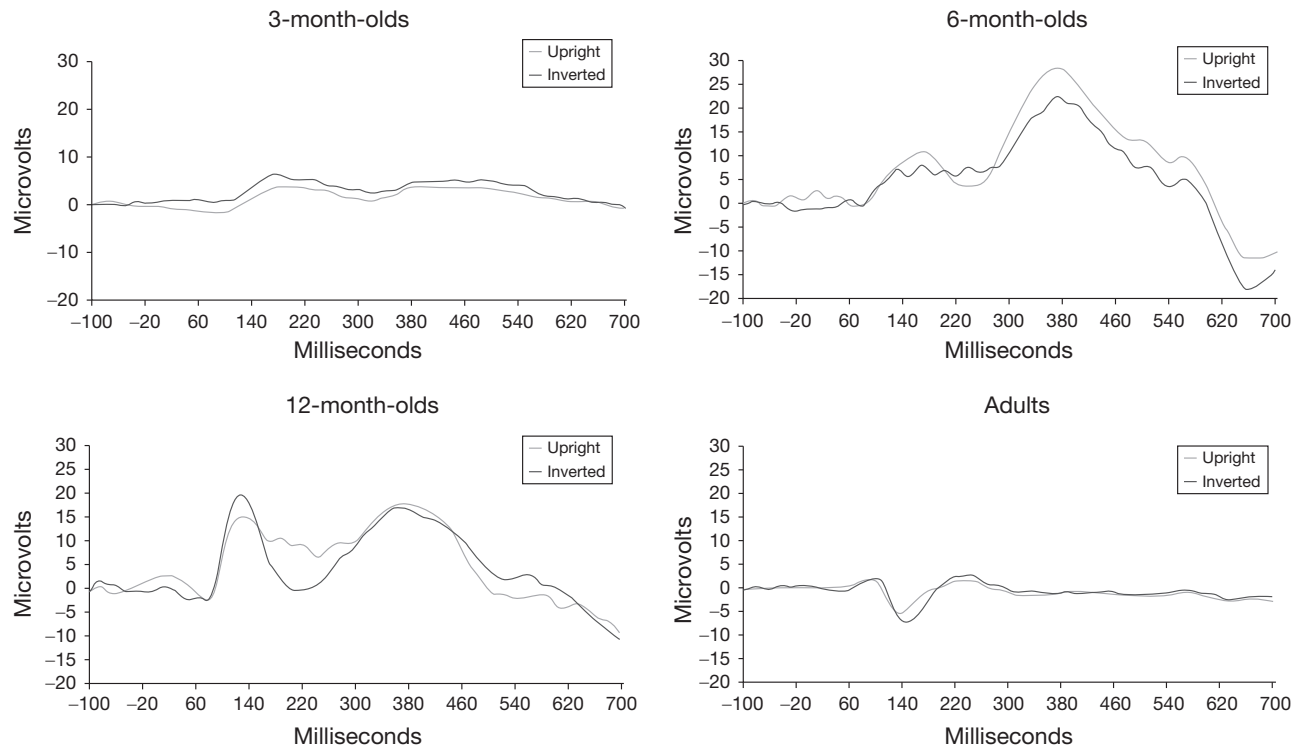


FIGURE 20.3 Functional signatures of face processing as measured using event-related potentials (ERPs) in the first year of life and adulthood.

categorical differentiation of happy versus sad faces in the Nc component in 7-month-olds (i.e., larger response to a novel expression in the between-category but not within-category condition), but no such effect found in the N290 and P400. These studies demonstrate that, by approximately 7 months of age, the infant brain possesses some degree of sensitivity to several facial expressions, some of which may lead to differential responses as early as about 290 ms postonset. Yet, there remains some degree of uncertainty regarding the neural structures involved in processing facial emotions in infants. Existing studies, using functional near-infrared spectroscopy (fNIRS), have demonstrated an involvement of temporal cortices (possibly, the STS) in differentiating angry versus happy faces at 6.5 months (Nakato et al., 2011). Future studies using fNIRS or fMRI will shed light on the potential involvement of broader areas, possibly including areas of the pre-frontal cortex.

20.3.5 Conclusions

During the first year of life, face processing undergoes rapid development as evident in both behavioral and neural responses. In the first 12 months of life, infants start to show many of the face-processing skills that will strengthen throughout development and reach full maturity in adolescence and adulthood. Neural responses to faces also start to show signs of face specialization in infancy, although it is apparent that much anatomical and functional maturation will take place before such neural signatures of face processing become adultlike. 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 plays a critical role in laying the groundwork to develop expert face processing.

20.4 Face processing in toddlers and preschoolers

20.4.1 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 1. As discussed in the following, 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.

Few studies have quantified the behavioral performance of toddlers and preschoolers in facial recognition and facial expression recognition. [Bruce et al. \(2000\)](#) carried out an extensive behavioral investigation of how children as young as 4 and 5 years 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 difficulty 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 that they 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" (e.g., presented with a hat) between the original presentation and the subsequent ones, suggesting that perhaps they are not encoding faces using their configural properties (e.g., [Mondloch and Thomson, 2008](#)) 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 to demonstrate that even very young children rely on face-specific, holistic strategies to process faces. These investigators have found positive evidence of a difference in performance between upright and inverted faces in children as young as 3 years ([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 low compared with older children and adults.

Even though these two hypotheses point to diverging developmental trajectories, their findings may be reconciled. 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. Interestingly, and in contrast with the protracted development of face recognition, the effects of social stereotypes on face perception emerge as early as the preschool period, such as the effect of racial stereotyping on face race categorization ([Dunham et al., 2013](#)) or the influence of facial features on social judgments of character ([Cogsdill et al., 2014](#)).

In summary, performance in face processing tasks generally increases during early and later childhood, but it remains unclear whether these improvements in performance reflect qualitative, as opposed to quantitative, changes and whether they are supported by improvements in face specific, as opposed to domain-general abilities ([Lee et al., 2013](#); [McKone et al., 2012](#); [Weigelt et al., 2014](#)). The question remains delicate to address, as issues surrounding task difficulty make it difficult to assess effect sizes across age groups ([Crookes and McKone, 2009](#)). Results from electrophysiological and neuroimaging investigations, which do not require overt behavioral responses and are discussed later in this section, may shed more light on this question ([Box 20.1](#)).

20.4.2 How young children process facial expressions

The ability to recognize facial expression has not reached adultlike levels of performance in toddlers and preschoolers. Interestingly, the recognition of different facial expressions appears to follow different developmental trajectories, happiness being the most readily recognized expression followed by sadness, anger, and fear (for a review, see [Bayet and Nelson, 2019](#); [Gross and Ballif, 1991](#); [Herba and Phillips, 2004](#)). It has also been shown that preschoolers need more

BOX 20.1 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 (ERPs) and functional magnetic resonance imaging (fMRI). Traditionally, ERP has been used to study face processing in developmental populations, sometimes alongside with functional near-infrared spectroscopy (fNIRS), whereas both techniques have been used with adults. However, in recent years, fMRI has been used successfully in visual face processing paradigms with children as young as 4–5 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, 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 participants with faces and other types of objects and then measure the BOLD response to the different stimuli across the entire brain, to understand whether there are specific regions that modulate their response on the basis of the stimuli that they see.

intense expressions to successfully recognize emotions, compared with older children (Bayet et al., 2018; Gao and Maurer, 2009, 2010), although differences in intensity threshold were not found to underlie the large observed accuracy differences between emotions in preschoolers (Bayet et al., 2018). 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) because such different tasks may be measuring different abilities. As the neural substrates supporting emotion recognition are far from fully mature at these ages, it is of course not surprising that young children show behavioral differences in emotion processing compared with older children and adults.

20.4.3 Functional signatures of face processing in young children

As is true with infants, toddlers and preschoolers also present challenges in evaluating face processing; not surprisingly, there are relatively few studies investigating how the brain of young children responds to faces, and for the most part, these studies employed ERPs. Overall, one would not expect major developmental changes in the types of components elicited by faces, such as the P1 and the N170. The nature of developmental changes is expected to primarily concern the 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 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 social or emotional significance with age. For example, 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- to 3-year-olds and 4- to 5-year-olds with the younger children showing increased amplitude to the mother's face and the older children showing the opposite pattern. A similar result was found in approximately the same age range in a different sample (Moulson et al., 2009). Overall, while the morphology and topography of face-sensitive ERP components is maturing, their development is far from over within this age group (Taylor et al., 1999, 2004); even though young children show some evidence of adultlike face processing, face processing continues to mature during and beyond early childhood as evident both behaviorally and neurally.

Components reflecting differences in responding to emotional faces also show developmental changes during early childhood. Despite the fact that from a behavioral perspective, toddlers and preschoolers have difficulty explicitly recognizing fearful faces (Bayet et al., 2018; Székely, 2013), Dawson et al. (2004) have shown that fearful faces elicit faster and larger P200 and N300 components in 3- to 4-year-old children, compared with neutral faces. 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 with neutral faces and more specifically showed the fastest latencies for positive emotions and, in particular, for happiness (Batty and Taylor, 2006).

20.4.4 Conclusions

Taken together, the results of behavioral and neurophysiological investigations strongly suggest that various aspects of face processing and face-processing strategies in toddlers' and preschoolers' remain far from adultlike. 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.

20.5 Face processing in school-age children and adolescents

20.5.1 How children and adolescents process faces

The behavioral performance of school-age children and adolescents is relatively well documented, compared with 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.) 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 from adults in the type of information they use within a face for recognition (see Mondloch et al., 2003a,b for a review). For example, it has been demonstrated that children up to the age of 15 years are not yet able to rely on the internal facial features of a face without contour information to successfully identify unfamiliar faces but rather perform better when they are provided only with the external contour information, compared with 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 et al. (2002) found that, unlike adults, 6-, 8-, and 10-year-olds produced the most errors when discriminating faces differing in feature spacing. Moreover, Mondloch et al. (2002) have shown that 6-, 8-, and 10-year-olds failed to show an increased cost of face inversion in the feature-spacing set, compared with the other two stimuli manipulations, which is also different from how adult participants perform.

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 years have demonstrated evidence of holistic processing as demonstrated using the composite face task (Mondloch et al., 2007; Pellicano and Rhodes, 2003), and Tanaka et al. (1998) have found an adultlike whole-part advantage in 6-year-olds. Moreover, children as young as 6 years have performed in a manner similar to that of adults on an inversion effect task, exhibiting comparable differences between performance on upright and inverted faces (Mondloch et al., 2002).

Again, methodological considerations may partly explain this relative heterogeneity of findings. 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, whereas 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 with the adults in terms of their quantitative performance, whereas in other cases their behavioral trends are compared with those found in adults. Thus, this makes it difficult to examine directly all these results and draw unified conclusions. Again, to aid the resolution of this debate, it may be useful to consider it in the context of neurophysiological findings, which will be discussed in this section.

Face identity recognition, however, does not appear to reach full maturation until adolescence. In an extensive study looking at performance on both face identity and emotion recognition, [Bruce et al. \(2000\)](#) showed that performance on face identity 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-year-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 et al. \(2007\)](#) have shown that adultlike levels of identity recognition memory performance for faces are not reached until at least 14 years of age, whereas 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](#)). Finally, adolescence appears to reorient face recognition abilities toward the recognition of peers of similar pubertal status, reflecting a more general shift in social functioning from caregivers to peers ([Picci and Scherf, 2016](#)). 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 may reflect task difficulty more generally. This issue is not easily solved because, to our knowledge, there are no extensive developmental studies in this age group comparing face processing with the processing of other complex visual objects.

20.5.2 How children and adolescents process facial expressions

The recognition of emotional facial expressions 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, 2010](#); [Herba et al., 2006](#); [Herba and Phillips, 2004](#); [Kolb et al., 1992](#); [Rodger et al., 2015](#); [Thomas et al. 2007](#); [Vicari et al., 2000](#)). Overall, behavioral studies of emotion recognition with children and adolescents not only show that children as young as 5 years recognize happy faces with adultlike accuracy ([Gao and Maurer, 2009, 2010](#); [Vicari et al., 2000](#)) but also show that sad and fearful faces remain more difficult to recognize in this age range especially if the face stimuli used depict less intense emotion ([Gao and Maurer, 2009, 2010](#); [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 years ([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, again, 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. Finally, an emerging body of work suggests that more subtle aspects of facial emotion processing, such as an increased ability to decode complex facial expressions, emerge in adolescence, are driven by pubertal changes, and reflect the increasing importance of peer relations in the social life of adolescents ([Garcia and Scherf, 2015](#); [Lawrence et al., 2015](#); [Motta-Mena and Scherf, 2017](#); [Scherf et al., 2012](#)).

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 with 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 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.

20.5.3 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 and adolescents. It should be noted here that, not unlike behavioral paradigms, neuroimaging paradigms that compare children, adolescents, and adults face the methodological difficulty in separating face-specific from other developmental trends, including age-related trends in interparticipant variability, artifacts (e.g., movement-related), and head size ([Kuefner et al., 2010](#)). To our knowledge, most developmental studies of face processing in these age groups are cross-sectional rather than longitudinal, further limiting the developmental conclusions that may be drawn. Despite these difficulties, a number of robust findings have emerged of the past decade. Of particular interest are investigations, using fMRI and related methods, which investigated not only the functional signatures of face processing but also the spatial 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, to which extent there are

already measurable clusters of neurons that respond more strongly to faces than to most other objects, and how face-processing networks may undergo further structural or functional changes in adolescence. Several 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; the spatial extent and functional selectivity of the FFA (functionally defined) continue to increase during childhood and adolescence, although adultlike functional selectivity may be attained earlier than spatial extent (Cantlon et al., 2011; Cohen Kadosh and Johnson, 2007; Golarai et al., 2007, 2010; Grill-Spector et al., 2008; Scherf et al., 2007; Scherf et al., 2011) and the representational properties of the FFA continue to mature between adolescence and young adulthood (Scherf et al., 2011). Age-related increases in the spatial extent of the right FFA appear to track increases in the volume of the inferior longitudinal fasciculus, a major occipitotemporal tract (Scherf et al., 2014). More evidence of slow maturation is also provided by a study comparing the neural activations in response to upright and inverted faces in fMRI. Passarotti et al. (2007) found that children aged 8–11 years did not show increased activation for inverted faces, compared with upright faces, whereas older children aged 13–15 years showed a trend in the opposite direction, which is what is commonly reported in adult studies. Two recent investigations shed light on the structural and behavioral correlates of the developing functional specificity of face-processing areas between childhood and adulthood. First, the amount of tissue (such as myelin, dendrites, and synapses) of the FFA increases between childhood and adulthood, which, when restricted to its right posterior portion, correlate with increases in functional selectivity and behavioral face recognition performance beyond the effect of age (Gomez et al., 2017). In addition to myelination, increases in the amount and extent of dendritic trees may reflect an increasing pooling of information over larger areas (Gomez et al., 2018); indeed, receptive fields in bilateral posterior FFA increase in size between childhood and adulthood (Gomez et al., 2018). Second, the right posterior FFA appears to become more biased toward the fovea, presumably competing for foveal coverage with the posterior portion of the Visual Word Form Area, and this change is paralleled by differences between children's and adult's scanning patterns (Gomez et al., 2018). Further evidence of protracted neural face selectivity is also provided by studies using ERPs. Investigations using this technique have demonstrated differences in the latency and topography of face-selective neural ERPs in children and adolescents compared to adults. 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 with upright faces, are observed only in adolescents (Taylor et al., 2004). Moreover, adultlike topography with higher amplitudes in the right hemisphere compared with 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. Neuroimaging studies of facial emotion processing in children and adolescents show the involvement of the regions including the amygdala (Herba and Phillips, 2004; Hung et al., 2012; Thomas et al., 2001), STS (Lobaugh et al., 2006), and fusiform gyrus (Lobaugh et al., 2006) in processing emotional faces, as expected from studies in adults, although a number of developmental trends emerge. For example, 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 adolescents. Similarly, Guyer et al. (2008) found more activation of the amygdala in response to fearful faces in adolescents, compared with adults, who in turn showed stronger functional connectivity between the amygdala and the hippocampus; pubertal development during early adolescence has been generally linked with widespread increases in neural responses to facial emotions over multiple regions including the extrastriate cortex, thalamus, and amygdala (Moore et al., 2012).

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 years to the age of 15 years, 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 with negative emotions (Batty and Taylor, 2003, 2006).

20.5.4 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, quantitative changes take place in how these observers process faces.

20.6 Impairments and atypical development of 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 (ASD) and Williams syndrome (WS).

20.6.1 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). Individuals with this disorder 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, not all prosopagnosics show difficulty identifying facial expressions (Young, 1992).

While prosopagnosia usually occurs in adults, there are a handful of well-documented cases of prosopagnosia in children following brain injury (Dutton, 2003; Dutton et al., 2006; Young and Ellis, 1989). Similar to the adults, these children have great difficulty in recognizing individuals by their face, and they also show differences with configural/holistic processing compared with age-matched controls. However, as brain injury in children is rarely localized to the occipitotemporal cortex, children with acquired prosopagnosia 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), in which case the disorder tends to run in families (e.g., Lee et al., 2010). Recent case studies documenting this type of prosopagnosia have termed it “developmental” or “congenital,” to distinguish it from the form that follows brain injury (“acquired” prosopagnosia). Individuals with congenital prosopagnosia 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 individuals with acquired prosopagnosia, although the disorder is heterogeneous (Susilo and Duchaine, 2013). In recent years, this population has received much attention, and several studies have been aimed to categorize the nature of their deficits. Some individuals with congenital prosopagnosia 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, individuals with congenital prosopagnosia show a different manner of processing of face stimuli, generally demonstrating a heavier reliance on featural strategy in place of configural and holistic processing (Behrmann et al., 2005; Zhang et al., 2015) although results have sometimes been mixed (Le Grand et al., 2006; Susilo et al., 2010) and deficits of holistic processing may be restricted to the eye regions of the face (DeGutis et al., 2012). 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 (Bentin et al., 1999) or functionally atypical (Towler and Eimer, 2012; Towler et al., 2012) brain response to faces in congenital prosopagnosics as measured by the amplitude of face-sensitive components; however, again the disorder is heterogeneous (Susilo and Duchaine, 2013). Studies using fMRI have produced discordant results, such that in few

instances individuals with congenital prosopagnosia did not show brain activation in the right fusiform gyrus in response to faces (Hadjikhani and de Gelder, 2002) or exhibited decreased selectivity toward faces (vs. objects) in multiple face-selective areas including the FFA and STS, as well as decreased selectivity for other visual categories (scenes, bodies) in their respective preferring areas (Jiahui et al., 2018), whereas 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 in congenital prosopagnosia, as the relationship between neural responses and impairment is not clear. Beyond brain activations to faces, recent investigations have also revealed more subtle profiles of impairments in some individuals with prosopagnosia, such as an impairment in the representation of individual faces or one or more region of the face-processing network despite preserved activations to faces generally (Fox et al., 2013; Schiltz et al., 2006). Impairment in functional connectivity between different regions of the face processing network have also been reported such as between early visual areas and posterior face-selective areas (Lohse et al., 2016) and between these areas and the anterior temporal lobe (Avidan et al., 2014; Rosenthal et al., 2017). 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 et al. (2007) have measured a reduction in the volume of the anterior fusiform gyrus in individuals with congenital prosopagnosia, compared with controls. Recent data using diffusion tensor imaging (DTI) have suggested that the recognition impairments may be due to atypical properties of white matter fiber tracts connecting the ventral temporal cortex to the anterior temporal and prefrontal cortices (Gomez et al., 2015; Thomas et al., 2009). However, while quantitative properties of this tract linearly relate to individual differences of face-processing skills in typical adults, that relationship is absent in individuals with prosopagnosia (Gomez et al., 2015), which suggests differences in the functional properties of this tract in the disorder.

20.6.2 Congenital cataract

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 years, 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 individuals 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, they 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 individuals 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). 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 with typical adults (Mondloch et al., 2003a,b). A small number of studies to date have looked at the functional responses that these individuals’ brains show when they are viewing faces or other visual objects. In addition to reduced activation and selectivity to faces in the extended face processing network (Grady et al., 2014), these studies reveal atypical low- and midlevel visual processing in these individuals as evidenced by differences in ERPs to visual stimulation (Segalowitz et al., 2017) and atypical recruitment of small regions of the occipital visual cortex during auditory processing (Collignon et al., 2015). Overall, these studies suggest that a period of early postnatal visual deprivation can trigger long-lasting remodeling of early to high-level visual cortices, with clear behavioral effects on face perception.

20.6.3 Autism spectrum disorder and Williams syndrome

20.6.3.1 How individuals with autism process faces

Atypical face processing has also been reported in certain populations of individuals diagnosed with ASD and WS. ASD is a neurological disorder that is diagnosed early in childhood, usually around the age of 3 years, and characterized by impairments in social interactions and social communication accompanied by restricted, repetitive behaviors or interests (DSM-5). 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 related to the social impairments experienced by these individuals (McPartland et al., 2011). 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), reduced social interest and attention to faces (Grelotti et al., 2002; Osterling and Dawson, 1994), eye contact avoidance (Tanaka and Sung, 2016), and reduced visual attention to internal facial features (Chawarska and Shic, 2009; Klin et al., 2002) despite relatively preserved orienting toward faces (Elsabbagh et al., 2013) and facelike patterns (Shah et al., 2013); face processing deficits may be less pronounced in tasks with no memory demand (Weigelt et al., 2012, 2013). These observations have generated much interest in early face-processing behavior in young infants at high risk of developing ASD, as it had been suggested that reduced scanning of faces might constitute an early behavioral marker of ASD (Jones and Klin, 2013). However, investigations of face processing in infants at high familial risk of developing ASD have yielded somewhat paradoxical results, revealing *longer* looking to faces (i.e., more sustained attention) in high-risk compared with low-risk infants (Elsabbagh et al., 2013) or in high-risk infants who are later diagnosed with ASD compared with high-risk infants who are not (Wagner et al., 2018), and a relation between higher attention to faces in infancy and *poorer* language (Wagner et al., 2018) and face-processing (de Klerk et al., 2014) skills in high-risk infants during early childhood. Overall, individual differences in early attention to faces do not consistently predict later diagnosis in high-risk infants and may instead reflect face processing difficulties in this population.

20.6.3.2 *How individuals with autism spectrum disorder process facial expressions*

Because of the social nature of ASD impairments, much attention has also been devoted to studying whether individuals with ASD 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; Lozier et al., 2014; Uljarevic and Hamilton, 2013). In several studies, it has been reported that these individuals 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). Unaffected siblings of children with ASD also tend to exhibit mild impairments in facial emotion perception (Oerlemans et al., 2014). However, an open question in this field concerns whether the observed deficits in facial emotion processing in ASD are specific to the disorder and to facial emotion processing (Nuske et al., 2013) or whether they may be accounted for by common comorbidities, such as alexithymia (Bird and Cook, 2013; Cook et al., 2013; Hill et al., 2004) or by other characteristics of ASD, such as difficulties with theory of mind (Frith, 2001) or emotion awareness (Hill et al., 2004).

20.6.3.3 *Neural substrates of face processing in autism spectrum disorder*

The behavioral differences found between neurotypical and ASD individuals have been connected to a variety of differences found in brain responses to faces between these two groups. Studies using ERPs have shown that both children and adults with ASD show shorter latencies for objects compared with faces for the N170 component (Webb et al., 2006), although infants at high risk of ASD show mostly typical ERPs to familiar and unfamiliar faces (Luyster et al., 2011, 2014). Moreover, the scalp topography of face-sensitive ERP components is different between these two groups, suggesting a smaller degree of hemispheric lateralization for face processing in individuals with ASD (Dawson et al., 2005), which is also found in infants at high risk for developing the disorder (Keehn et al., 2015). Atypical ERP responses have also been demonstrated when ASD individuals are shown emotional faces (Dawson et al., 2004; Luyster et al., 2017; Monteiro et al., 2017). Differences between ASD individuals and neurotypical 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 in terms of both 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, at both the behavioral and neural levels, remains one of the hallmarks of ASD.

20.6.3.4 Face processing in Williams syndrome

Another neurological disorder that has received attention in association with face processing is Williams Syndrome (WS). WS is a rare (prevalence is 1:10–20,000) 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; Plesa Skwerer, 2017; for a review). Unlike ASD individuals, children and adults diagnosed with WS show face recognition abilities comparable with healthy controls (Bellugi et al., 1994; Tager-Flusberg, and Joseph, 2003) and tend to fixate on faces and eyes longer than typically developing individuals (Porter et al., 2010; Riby and Hancock, 2008, 2009; Riby et al., 2011). 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). Individuals with WS are akin to individuals with ASD in that they also show deficits in emotion recognition from facial expressions (Tager-Flusberg et al., 2003). More specifically, individuals with WS have difficulty detecting signals of social threat such as angry faces (Plesa-Skwerer et al., 2006; Santos et al., 2010), a deficit that is congruent with the relative “social fearlessness” that is characteristic of the disorder and contrasts with otherwise high rates of nonsocial anxiety and difficulty in social interactions (Plesa-Skwerer, 2017; Riby et al., 2014). Individuals with WS and ASD 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 with that of healthy controls (Meyer-Lindenberg et al., 2004; Schultz et al., 2000). However, individuals with WS show hypoactivation in brain regions recruited when processing facial expressions, specifically the amygdala and the orbitofrontal cortex (Binelli et al., 2014; Meyer-Lindenberg et al., 2005).

20.7 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, there remain a large number of unanswered questions. First, although 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 in humans. Although the data produced by investigations with individuals with congenital cataract and congenital prosopagnosia 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 facts that our brains are overall quite plastic and that other similarly complex face-processing abilities such as facial emotion processing exhibit relatively high levels of robustness to atypical variations in early visual or psychosocial experience (Gao et al., 2013; Moulson et al., 2015). In our view, this remains an essential issue to resolve in the coming years.

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