

## Chapter 2

# Developmental Neurobiology of Face Processing

*Lisa S. Scott, B.S.*

*Charles A. Nelson, Ph.D.*

---

Several lines of research suggest that face processing is a “special” perceptual ability that is subserved by a distinct neural system (Haxby et al. 2001; Kanwisher et al. 1997). Furthermore, face perception has been cited as the most developed visual-perceptual skill in humans (Haxby et al. 2000). Indeed, several researchers have claimed that adult face processing can be characterized as a uniquely expert system in humans (Gauthier and Tarr 1997). The extant literature on the basic organization and neural underpinnings of adult face processing is riddled with controversy and may be better informed by an understanding of the processes involved in the development of this system. The fundamental question of how a perceptual system *becomes* functionally and structurally specialized has great potential to inform us about the basic characteristics of that perceptual system and how it came into being.

Many investigators who study face processing in adults view faces as a “special” class of perceptual stimuli. This view is gener-

---

Support for the writing of this chapter was provided to Dr. Nelson by the National Institutes of Health (NS329976) and by the John D. and Catherine T. MacArthur Foundation through their support of a research network on *Early Experience and Brain Development* and to Lisa Scott from a training grant provided by the National Institute of Child Health and Human Development to the Center for Cognitive Sciences at the University of Minnesota (5T32 HD07151).

---

ally taken to mean that the mechanisms underlying face processing differ from those underlying the processing of nonface objects. Indeed, behavioral, neuropsychological, and neuroimaging data from patient populations support the existence of a “face module.” The special nature of face processing compared with other types of visual processing, such as object processing, originates from reports of patients who are unable to recognize familiar faces but who maintain the ability to recognize and identify objects (Damasio et al. 1982; De Renzi 1986) and from single-cell recordings from nonhuman primates that suggest that cells within the inferior temporal cortex fire preferentially to faces (Gross et al. 1969, 1972; Perrett et al. 1982, 1987).

Although it is beyond the scope of this chapter to provide a comprehensive review of the adult face-processing literature, we refer the interested reader to several relevant articles (Gauthier et al. 1998, 1999a, 2000; Haxby et al. 2000, 2001; Kanwisher et al. 1997). In this chapter, we focus on studies that have investigated the neural and behavioral development of the face-processing system, including studies that have investigated face perception in children with disorders such as autism. Finally, we conclude with a discussion of current models of the development of face processing and how these models inform the study of face processing as a whole.

## **Neural Correlates of Face Processing in Developmental Populations**

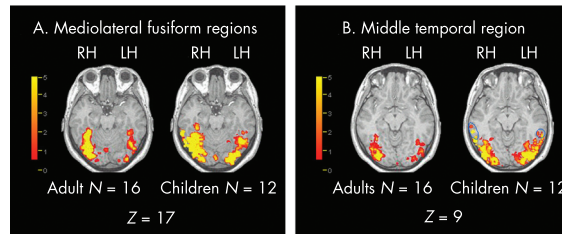
Although our understanding of developmental science has greatly benefited from studies investigating the behavioral correlates of development, relatively few studies have investigated the neural systems that underlie changes in behavior across time. The merging of the fields of neuroscience and psychology has recently begun to provide researchers with the ability to examine brain-behavior relations from multiple levels of analysis (for elaboration, see Nelson and Bloom 1997; Nelson et al. 2002). Particularly noteworthy have been advances in noninvasive functional imaging of the developing brain. Functional magnetic resonance imaging (fMRI) and event-related potentials (ERPs) are the most commonly

used techniques with normative developmental populations. fMRI provides an index of changes in blood oxygenation levels in the brain, and ERPs provide an index of the electric potential directly generated by neuronal activity. fMRI provides excellent spatial resolution of brain metabolism in response to specific stimuli or cognitive tasks. ERPs, on the other hand, have better temporal resolution and are able to record the response of electrical activity (on the order of milliseconds) to different stimuli from the scalp. (For an extensive review of these techniques in the context of development, see M. de Haan and Thomas 2002; DeBoer et al., in press.)

When studying face processing, one needs to take into account several factors that may influence the processing of certain kinds of faces and how this processing is different from other perceptual processing. For example, we should examine the distinction between face and object processing; the role of familiarity; how different species, genders, races, and ages are processed; the difference between configural and featural face processing; and how emotional expressions are processed. The following review of the developmental literature is limited to research that investigated the neural correlates of these different aspects of face processing with both fMRI and ERP, as well as studies of patient populations and children with developmental disorders.

### *Faces Versus Objects*

A fundamental finding in the study of visual processes is the distinction between the visual pathway that analyzes objects and faces (the ventral “what” pathway) and the visual pathway that analyzes spatial information (the dorsal “where” pathway). Although few investigations have examined the development of these pathways, children (ages 10–12 years) have been found to have a more diffuse and distributed area of activation in both the “what” and the “where” pathways compared with adults (Passarotti et al. 2003). More specifically, children, similar to adults, showed more right compared with left fusiform activation in response to faces, but activation in both hemispheres was more distributed across the temporal cortex in children compared with adults (Figure 2–1).



**Figure 2-1.** Face-matching task.

**A:** Significant clusters of functional activation in mediolateral fusiform regions for the face-matching task in 16 adults (*left side*) and 12 children (*right side*). **B:** Significant clusters of functional activation in the middle temporal gyrus in 16 adults (*left side*) and 12 children (*right side*). Note that according to radiological convention, the left side of the brain represents the right hemisphere, and the right side of the brain represents the left hemisphere. *Source.* Adapted from Passarotti AM, Paul BM, Bussiere JR, et al.: "The Development of Face and Location Processing: An fMRI Study." *Developmental Science* 6:100–117, 2003. Used with permission from Blackwell Publishing.

As with adults, both infants and children show apparent neural dissociations between face and object processing (e.g., Carver et al. 2003; M. de Haan and Nelson 1997, 1999). For example, electrophysiological evidence suggests that certain ERP components differentiate faces and objects. ERPs can be defined as transient changes in the brain's electrical activity that occur in response to a discrete (time-locked) stimulus or an event such as a presentation of a face (M. de Haan and Nelson 1997). ERP components represent negative (denoted by N) and positive (denoted by P) deflections in voltage over time. These components can be either described by the latency of the negative or positive deflection (e.g., N170 is a negative component occurring 170 milliseconds after stimulus onset) or denoted by the number of the positive or negative peak (e.g., a P3 refers to the third positive peak). These deflections are thought to represent different aspects of cognitive and perceptual processing. Several studies with adults have found a negatively peaked component, called the N170, which appears to be highly specific to face processing (for example, Carmel and Bentin 2002). In infants, the P400 component discriminates faces and objects, as evidenced by an earlier latency to peak response to faces in 6-month-olds (M. de Haan and Nelson 1999). This difference is most prominent over posterior and temporal electrode locations, suggesting, similar to findings with adults, a temporal advantage

for processing faces. The negative component (Nc), a component associated with attention and recognition memory, is more specific to familiar face stimuli (confined to the midline and right anterior temporal regions) than to familiar object stimuli (distributed across all temporal regions; M. de Haan and Nelson 1999). Furthermore, the Nc is greater in response to familiar objects (e.g., a favorite toy from home), compared with unfamiliar or novel objects. These results suggest differential electrophysiological signatures for objects and faces in 6-month-old infants, which may be related to different levels of experience with specific kinds of object categories (faces vs. objects).

### *Familiar Versus Unfamiliar Faces*

Behavioral studies that used looking time and habituation techniques with newborns reported that infants discriminate between familiar and unfamiliar faces (Pascalis and de Schonen 1994; Pascalis et al. 1995). However, the direction of infants' preference depends on the task used. For example, in a simple visual preference task, infants prefer to look at familiar faces (Pascalis and de Schonen 1994), whereas in studies in which the habituation procedure is used, infants tend to prefer to look at the novel face (Pascalis et al. 1995). Further evidence from electrophysiological investigations indicates that by age 6 months, infants show differential brain activity to familiar (mother's face) and unfamiliar faces (M. de Haan and Nelson 1997, 1999). The Nc has been found to be larger in response to the mother's face than to a stranger's face. This differential activation is influenced by how similar the unfamiliar faces were to the mother's face. This finding, as well as the finding stated earlier with object processing, contrasts with previous research showing a greater Nc to unfamiliar stimuli compared with briefly, or newly, familiarized stimuli (Nelson and Collins 1991). A later positive slow-wave component, maximal over frontal scalp locations and often associated with memory processes (Nelson 1994; Nelson and Monk 2001), was found to discriminate the mother's face from a stranger's face as indexed by a greater response to the stranger's face (M. de Haan and Nelson 1999).

Further research suggests that there may be developmental

changes in the relative importance of viewing different kinds of faces (such as the mother's face vs. strangers' faces). Indeed, children (ages 18–54 months) who were presented with both highly familiar and unfamiliar faces and toys while ERPs were recorded showed changes in only the brain response to faces, and not toys, as a function of age (Carver et al. 2003). More specifically, all age groups showed larger Nc and P400 components to unfamiliar compared with familiar objects, but only children between ages 18 and 24 months showed a greater ERP response to the mother's face than to a stranger's face. Children between ages 45 and 54 months showed a larger response to the stranger's face, and children between ages 24 and 45 months did not show a differential response to either stimulus at the Nc. These findings suggest that the neural correlates of face processing may change across development and may be related to the emotional salience or significance of the face.

### *“Other-Race” and “Other-Species” Effects*

Although not yet studied in infants or very young children, the “other-race” effect, a commonly reported experience in which adults describe more difficulty differentiating between faces from races other than their own (Chance et al. 1982; O'Toole et al. 1994), speaks to the role of experience in the development of face processing. Beginning in the late 1960s and continuing through the 1970s, this phenomenon was attributed to greater exposure to faces of your own race than to others (Brigham and Barkowitz 1978; Brigham and Malpass 1985; Malpass and Kravitz 1969). Fallshore and Scholler (1995) showed that recognition of faces of other races is less affected by inversion than recognition of faces of the same race. Imaging studies of the other-race effect show better recognition memory for same-race faces compared with other-race faces that is paralleled by greater activation of the fusiform area in response to same-race faces compared with faces of another race (Golby et al. 2001). Furthermore, the behavioral memory differences between same- and other-race faces correlates with activation in the fusiform and hippocampal areas. The differences in activation found in the fusiform area have been attributed to different levels of expertise or experience with faces of other races.

As stated earlier in this section, no studies have examined this phenomenon in very young children or infants; however, in contrast to Caucasian adults and older children, Caucasian children as young as 6 years do not show a recognition memory advantage for Caucasian compared with Asian faces (Chance et al. 1982).

The other-race effect also has been modeled with computational face recognition algorithms (Furl et al. 2002). Furl and colleagues tested several face recognition algorithms to determine which was most consistent with behavioral results suggesting better recognition accuracy within races compared with across races. Results were consistent with the “developmental contact” hypothesis. Only experience-based models showed the other-race effect, and this effect was seen only when experience warped the perceptual space to enhance encoding distinctions of same-race faces compared with other-race faces (Furl et al. 2002).

Similar to the “other-race” effect, there have been reports of an “other-species” effect. For example, humans and nonhuman primates are better at recognizing faces of their own species (Pascalis and Bachevalier 1998). More specifically, monkeys tend to look longer at novel monkey faces but not novel human faces, and adult humans look longer at novel human faces but not novel monkey faces. This finding suggests a “species-specific” effect in face recognition. Interestingly, the monkeys in this experiment had more experience with human faces than the humans had with monkey faces. Therefore, Pascalis and Bachevalier asserted that if visual experience were solely responsible for the development and specification of this system, then the nonhuman primates in this study should have shown a novelty preference for both human and monkey faces. A somewhat similar dissociation also has been found in the recognition of inverted faces (Pascalis and Bachevalier 1998). Human adults show an inversion effect for human and monkey faces but not for sheep faces, suggesting that primate faces are being processed in a similar manner compared with sheep faces. Furthermore, children (ages 5–8 years), who have less experience with faces than adults do, show a similar pattern of results (Pascalis et al. 2001). In a forced-choice task, older children are better than younger children at recognizing both upright and inverted faces

regardless of species. Recognition was better for human faces than for monkey faces and better for human and monkey faces compared to sheep faces at all ages tested. In addition, similar to adult findings, only human and monkey faces induced an inversion effect. Pascalis and colleagues suggested that the human face-processing system may be tuned to the characteristics of primate (human and monkey) faces by age 5 years.

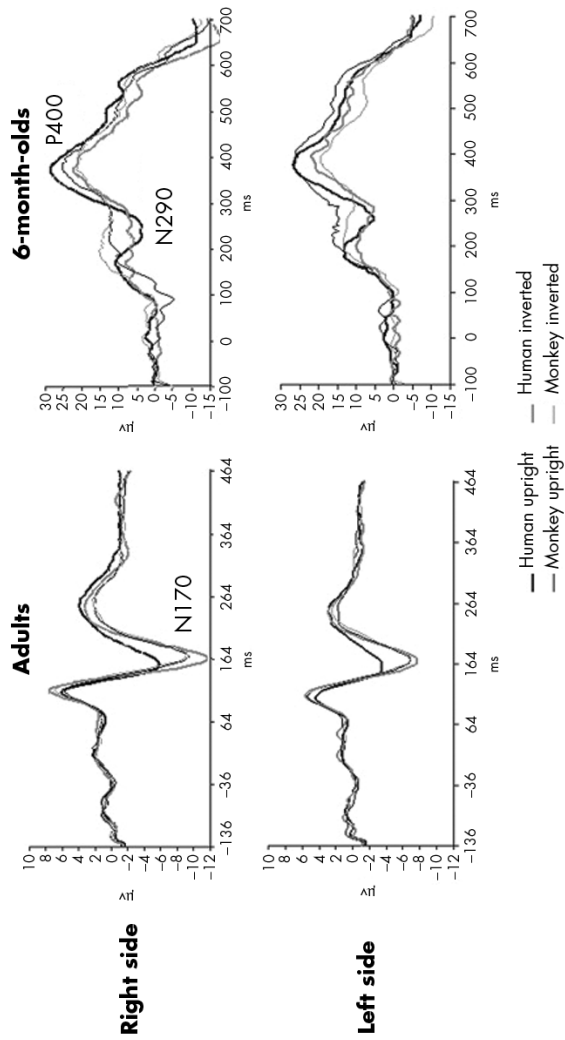
Recently, the visual paired comparison procedure has been used in adults and in infants ages 6–9 months to determine their sensitivity to human versus monkey faces (Pascalis et al. 2002). This study was designed to test directly a model put forth by Nelson (2001, 2003) that hypothesizes a narrowing of perceptual space in face processing and is described later in this chapter, in the section “Developmental Theories of Face Processing.” Pascalis et al. (2002) hypothesized that younger infants would have a more broadly tuned face-processing system and should be better than adults and older infants at discriminating between individual faces within and across different species. Results confirmed this hypothesis, indicating that adults and 9-month-old infants looked longer at novel human faces but looked equally long at novel and familiar monkey faces. In contrast, 6-month-old infants showed novelty preferences in both the human and the monkey conditions.

The findings of the study described in the previous paragraph are supported by the results of an electrophysiological study in which ERPs were recorded from adults and 6-month-old infants while they viewed both upright and inverted monkey and human faces (de Haan et al. 2002b). The purpose of this study was to determine whether adults and infants show the same cortical specificity during face processing. In adults, all stimuli evoked an N170 over temporal and occipital leads. This N170 was larger in amplitude and longer in latency for upright monkey faces compared with upright human faces. Furthermore, inversion effects were apparent in the human but not the monkey conditions (increased amplitude and latency to inverted faces). Results indicated that no component of the infant ERP showed the same specificity as the adult N170 (Figure 2–2). Six-month-old infants showed sensitivity to both inversion and species con-

ditions, but it was distributed across two components. The early Nc (260–336 ms) was greater to human than to monkey faces, and a later positive component (P400) was greater for upright compared with inverted faces. These findings suggest that adultlike patterns of face processing are not mature by age 6 months and may reflect a gradual specialization of cortical face-processing systems.

In a follow-up investigation of this study, 3- and 12-month-old infants were shown upright and inverted monkey and human faces while ERPs were recorded to further elucidate the developmental characteristics of the infant face components (Halit et al. 2003). Results indicated that similar to adults, 12-month-old infants had an Nc (N290) that was larger in amplitude and longer in latency for human than for monkey faces. This component also showed an inversion effect, with a larger amplitude response to inverted compared with upright faces (for humans only). The P400 component also differentiated these conditions, as evidenced by a longer latency response to monkey compared with human faces and a longer latency to inverted compared with upright faces. In contrast, similar to the 6-month data reported earlier in this section, 3-month-old infants did not show the same specificity for human faces that 12-month-olds and adults showed. The results of the previously described studies suggested that the adult N170 may be an emergent product of two developmental components (a negative N290 and a P400) and that the specificity of these components may develop some time between age 6 and 12 months.

Results of the study described in the previous paragraph are somewhat consistent with a study ongoing in our laboratory that uses ERPs with adults and 9-month-old infants to examine discrimination of monkey and human faces in both frontal and profile (as opposed to inverted) orientations (Scott and Nelson 2003). This study was designed to investigate further the neural mechanisms underlying the development of face processing. Adult and 9-month-old participants were familiarized to images of monkey or human faces in the frontal orientation posing neutral expressions (Figure 2–3). After familiarization, participants were tested with novel and familiar monkey or human faces, each in a frontal and profile orientation. Preliminary behavioral analyses



**Figure 2-2.** Adult and infant cortical specificity during face processing. Grand average of adults' (left) and 6-month-olds' (right) event-related potentials to upright human faces (*dark thick line*), inverted human faces (*light thick line*), upright monkey faces (*dark thin line*), and inverted monkey faces (*light thin line*) at the right posterior temporal (T6) and left posterior temporal (T5) electrodes. Adapted from de Haan M, Pascalis O, Johnson MH: "Specialization of Neural Mechanisms Underlying Face Recognition in Human Infants." *Journal of Cognitive Neuroscience* 12:199-209, 2002b. Copyright 2002 by the Massachusetts Institute of Technology. Used with permission.



**Figure 2-3.** Face-processing task.

**A:** Picture of a 9-month-old infant with a 32-channel electrode cap on his head. **B:** Stimuli used in this task. Infants were first habituated to either one human or one monkey face. Then infants passively viewed serial presentations of the familiar and an unfamiliar face in both frontal and profile orientations.

from adults indicated that participants performed significantly better in the human compared with the monkey discrimination task. Furthermore, preliminary adult ERP analyses indicated that the amplitude of the P2 component differentiated monkey and human faces, the P2 latency differentiated orientation, and the N300/400 differentiated familiarity. Interestingly, the 9-month old infants were also processing species, orientation, and familiarity across several components.

In summary, it appears that early experience with certain types of faces may influence later processing. Moreover, the kinds of faces (different races, different species) present in one's environment during development may influence the formation and specificity of the face-processing system.

### *Configural Versus Featural Processing*

A distinction exists between featural and configural information contained within a face (Diamond and Carey 1977). *Featural* information refers to individual face elements (such as the eyes or mouth), and *configural* information refers to the spatial layout of these elements within the face (Freire and Lee 2001). These sources of information are not mutually exclusive; changes in features necessitate a change in the configural information and changes in configurations involve a concomitant change in the individual features (Tanaka and Sengco 1997). Humans' reliance on configural information in the recognition and processing of faces is demonstrated when faces are inverted (Yin 1969) and also when features of inverted faces are upright (Thompson 1980). Inversion tends to impair recognition of faces more than objects. This effect was first reported by Yin (1969), who found that inversion disrupts the configural processing of a facial stimulus. Yin further reported that children younger than 10 years discriminate unfamiliar upright faces as accurately as unfamiliar inverted faces, whereas adults and older children are impaired in the unfamiliar inverted condition. Thus, with unfamiliar faces, children seem to be better than adults at processing inverted faces compared with upright faces. Farah et al. (1995) contended that faces are represented as holistic units, whereas objects can be broken down into separable parts. Inverting a face presumably causes a disruption in this configural or holistic processing and thus causes decrements in facial information processing such as impaired recognition and delayed reaction time (Freire et al. 2000).

One way to investigate the development of featural and configural processing is to determine where infants and children fixate on faces, what features they look at more than others (if any), and how this changes with development. Maurer and Salapatek (1976) conducted the only study to date that investigates infants' eye fixations while they view faces. They found that 1-month-old infants fixated away from the face for most of the time but that 2-month-old infants fixated on the faces, looking more at specific features, especially internal features and the eyes.

Developmental changes in the processing of featural and configural face information also have been investigated in 9-year-old

patients with bilateral congenital cataracts removed between age 2 and 6 months (Le Grand et al. 2001). Results of this study indicated that even after 9 years of normal visual processing, configural face processing was disrupted in these patients. In this investigation, experimenters varied featural and configural information in facial stimuli by slightly changing this information (placing eyes further apart vs. replacing individual features, such as eyes). They found that these patients were impaired in detecting changes in configural but not featural information compared with a typically developing control group. The authors concluded that visual experience with faces early in development (within the first 6 months) is necessary for normal development of configural face processing. Consistent with previous research, these findings suggest that configural and featural information may be developmentally dissociable and that a shift may occur from featural to configural processing during a “period of opportunity” sometime during the first 6 months of life. Furthermore, the authors asserted that because typically developing newborns have poor visual acuity, the visual cortex is only exposed to low-spatial-frequency visual information (outer contours and general location of features). Thus, if infants are deprived of low-spatial-frequency visual information during this period, later configural processing may be impaired.

ERPs also have been used to investigate the neural changes associated with face and eye processing in children ages 4–15 years (Taylor et al. 2001). Children were presented with upright and inverted faces and eyes to determine whether they were using featural or configural information while processing faces. The N170 response was much greater in amplitude and shorter in latency to eyes than to faces in children. These data indicate that early processing of eyes may be functional before the processing of whole faces. Furthermore, the cortical areas involved in processing eyes and faces may be somewhat distinct in development.

### ***Facial Expression and Emotion Processing***

It is difficult to study the development of face processing and the mechanisms involved in this development without a discussion of the emotionally salient and highly dynamic information that is

provided in the face. Indeed, human faces contain a preponderance of significant information, necessary for social communication. For example, familiarity, emotion expression, congruent dynamic information (e.g., lip movement synchronized with voice), and direction of gaze can all be gleaned from very brief exposures to static and dynamic images of faces. Some researchers have studied what they call the *still-face effect* and have found that infants attend more and show more positive affect to dynamic displays of faces than to still faces (e.g., D'Entremont and Muir 1997). Furthermore, in a recent series of studies, Bahrack et al. (2002) suggested that early in infancy, socially contingent and dynamic information may be so important that facial identity is ignored during the dynamic phases of face-to-face interactions. Thus, it is important to point out that infants' learning about faces is probably not completely dissociable from learning about emotional expressions or dynamic contingencies. Furthermore, whatever the mechanisms are that are involved in the development of face processing, it is likely that dynamic and emotionally salient information plays a major role in their development.

Evidence that the ability to recognize emotional expressions needs little experience to develop is based on research with visual paired comparison and habituation procedures that showed that newborns (by age 36 hours) are able to discriminate (based on increases in looking time) between different types of facial expressions (Field et al. 1982). Several investigations with older infants found inconsistencies in the types of emotions infants are able to discriminate. For example, 3-month-old infants are able to discriminate (by dishabituating) smiling from frowning faces (Barrera and Maurer 1981) but not sad faces from happy faces or surprised faces (Young-Browne et al. 1977). Furthermore, 7-month-old infants will show a looking preference for fearful faces over happy faces (Nelson and Dolgin 1985) and can discriminate happy from fearful in a habituation test but only if they first habituate to happy faces (Nelson et al. 1979). Therefore, it is apparent that in the first year of life, infants are able to show some discrimination of emotions, but this discrimination has not yet reached adultlike maturity (for review, see M. de Haan and Nelson 1998; Nelson and de Haan 1996).

Investigations of the neural underpinnings of the development of emotion processing suggest that infants as young as 7 months are able to differentiate between static pictures of some emotions (Nelson and de Haan 1996). ERPs were recorded from 7-month-old infants while they viewed pictures of happy and fearful expressions in one experiment and angry and fearful expressions in another. Results indicated electrophysiological differentiation between happy and fearful expressions but not between angry and fearful expressions at age 7 months. As stated earlier, the methods typically used to test discrimination of expressions early in development involve viewing static pictures of faces. The use of a more dynamic and intermodal display of emotional expressions indicated that 7-month-old infants were able to discriminate happy and angry expressions by just motion information alone, suggesting that actually viewing the face may not be a necessary component in this type of perception (Soken and Pick 1992). This study illustrates the inextricably tied nature of face and emotion recognition but leaves us wondering whether face recognition, in general, is mediated by mechanisms different from those involved in emotion recognition—or whether emotion recognition is simply an extension of the face recognition system. This question is related to Haxby and colleagues' (2000) notion that emotion information is part of an extended face-processing system (subserved by the amygdala), suggesting that emotion information may indeed be processed separately from the early perception of faces.

Although evidence is limited regarding the neurobiology of the development of emotion expression processing (especially with infants), several adult investigations have studied the timing and underlying neural substrates of such processing (Eimer and Holmes 2002; Pizzagalli et al. 2002). Data from ERP studies suggest that information about the face may be processed separately from information about emotion or affective judgment (Eimer and Holmes 2002; Pizzagalli et al. 2002). Early perceptual ERP components have been found to process affect information before identity information (Pizzagalli et al. 2002). These data suggest that affect processing may play an important role in the structural encoding and identification of faces. It will be important to study the development of the mor-

phology of these early affective-based responses because it may shed light on the mechanisms involved in face and emotion processing. For example, if infants and children are processing emotion information before they process identity, the emotional information in the face may be a big contributor to the developing specificity of face processing.

The amygdala is thought to be involved in the evaluation of emotionally significant stimuli (LeDoux 1996). Emotion face processing has been investigated with fMRI in both typically developing and non-typically developing populations (Baird et al. 1999; Thomas et al. 2001). In adults, the presentation of fearful faces increases activation in the left amygdala compared with the presentation of neutral faces (Thomas et al. 2001). Children (11 years old), in contrast, show greater amygdala activation to neutral compared with fearful faces (Thomas et al. 2001). The authors suggested that this effect may be due to the increased ambiguity (leading to increased vigilance) that a neutral face elicits. Furthermore, the authors asserted that neutral faces may not yet indicate neutrality, and children may therefore be trying to interpret the meaning of the neutral faces, thus increasing vigilance. In contrast to the previous findings, Baird et al. (1999) found that the pattern of response in adolescents and adults was similar—the amygdala had greater activation to fearful compared with neutral faces. Further investigations are needed to replicate these data. Indeed, further research investigating the developmental neurobiology of emotion processing is needed to elucidate the behavioral and neural correlates of this socially relevant system.

## **Face Processing in Atypically Developing Populations**

The study of typical development often can be informed by the study of children who deviate from a normal trajectory. Such is the case with face processing, in which studying children with known impairments in this ability may shed light on how face processing operates in typically developing children. In this section, we focus on both adult and developmental investigations of individuals with prosopagnosia and individuals with autism.

## *Prosopagnosia*

As mentioned earlier, the special nature of face processing compared with other types of visual processing originates from reports of patients who are reportedly unable to recognize familiar faces while maintaining the ability to recognize and identify objects. Patients with this deficit have a syndrome called *prosopagnosia* (De Renzi 1986). This impairment is often accompanied by focal bilateral (usually) damage to the ventral occipitotemporal and temporal cortices (Damasio et al. 1982). For example, patient LH (reviewed by Farah 1996) had damage to an area within the occipitotemporal cortex and experienced impaired recognition of faces in the absence of impaired object recognition. Interestingly, patients with prosopagnosia have been described as processing faces similar to the way in which they process objects. Whereas adults without prosopagnosia process faces in a holistic manner and thus have impairments recognizing inverted faces, almost no performance decrement is seen when prosopagnosic patients are shown inverted faces compared with upright faces (Farah 1995; Yin 1969). Some individuals with prosopagnosia have been reported to have performance advantages over control subjects without prosopagnosia on inverted face processing (Farah 1995). These patients also have been shown to have an abnormal pattern of activation in the fusiform gyrus (Marotta et al. 2001). These authors report left hemisphere posterior fusiform activation suggesting that these patients are processing stimuli in a more feature-based compared with holistic manner (similar to how objects are processed).

A small number of developmental prosopagnosic cases have been reported. The vast majority of these cases have occurred in individuals who have more general visual processing deficits in addition to difficulties recognizing faces (E.H. de Haan and Campbell 1991; Young and Ellis 1989). However, there is a report of a boy who sustained brain damage at age 1 day, now in late adolescence, who has structural damage to occipitotemporal pathways and impairments similar to those typically reported in adults with prosopagnosia (Farah et al. 2000). These authors suggested that this report may be evidence for an innately specified

face-processing system; that is, a system that does not require perceptual experience to develop.

### *Autism*

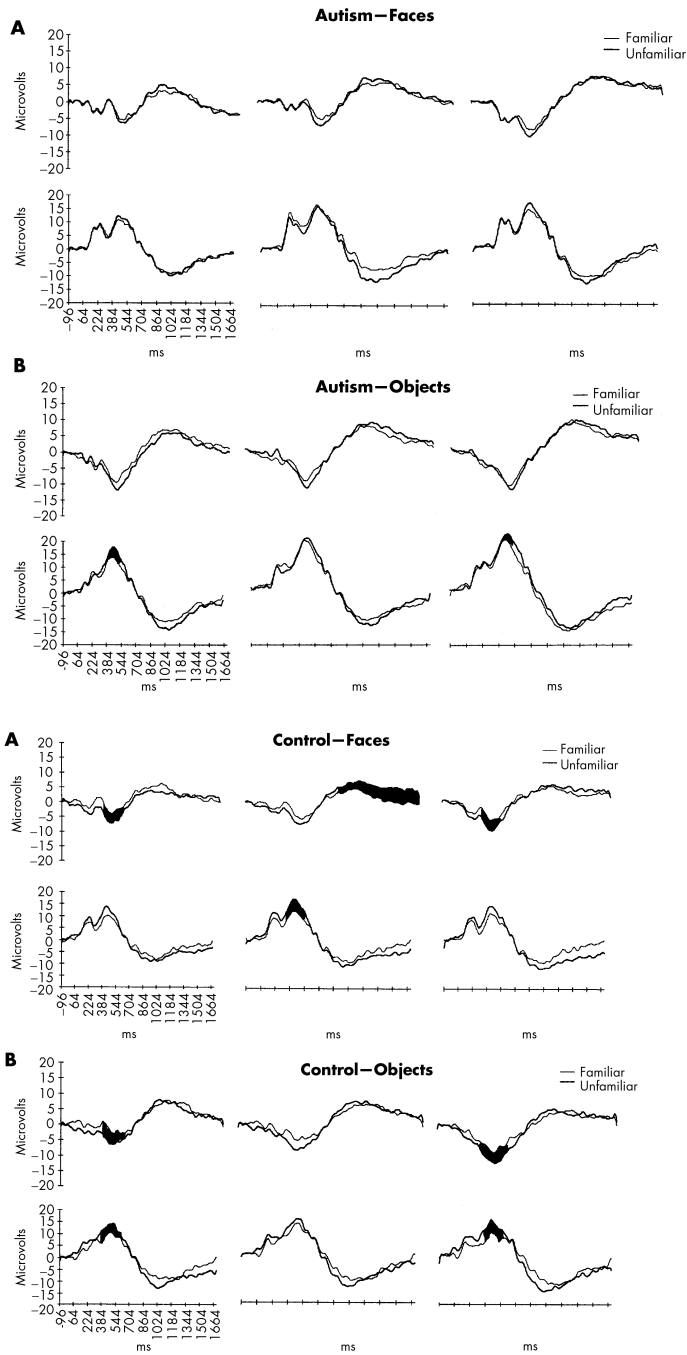
Children with autism are often reported to have deficits in face-processing abilities (Hobson et al. 1988; Kanner 1942; Langdell 1978; Marcus and Nelson 2001). Although a deficit in face processing is not a defining feature of autism, the kinds of impairments these children experience early in development may be a helpful indicator of future social or emotional impairments (Marcus and Nelson 2001). Indeed, children with autism are not proficient at using faces to determine identity. Individuals with autism tend to make little eye contact and have been described as treating people as if they were objects (Kanner 1942). Langdell (1978) first reported a lack of the typical inversion effect in processing of faces in autistic children. Langdell found that older autistic children performed better than control subjects on an inverted face task. This finding has since been replicated; Hobson and colleagues (1988) found that individuals with autism were better than a control group at an emotion-face picture sorting task when the faces were inverted. Trepagnier (1998) asserted that autism may be caused by a failure to develop orientation to facial cues, which then disrupts perceptual and social information processing. Furthermore, other studies of face processing have found aberrant processing of familiar face matching (Boucher et al. 1998) and memory for faces (Hauck et al. 1999) in individuals with autism.

The findings in the previous paragraph suggest that individuals with autism do not appear to process faces in the same specialized manner as do adults and typically developing children. Recent neuroimaging evidence augments this conclusion. Schultz and colleagues (2000) found decreased activation in the fusiform region in a group with autism and Asperger's disorder and increased activation in the inferior temporal gyrus compared with control subjects. Similar to previous behavioral research, the authors suggested that the group with autism and Asperger's disorder may process faces similar to how they process objects and thus do not have a specialized face-processing system. How-

ever, it is indeed plausible that this deficit may be secondary to the disorder, and these individuals may have less exposure to faces because they simply orient less to faces compared with typically developing individuals.

In an earlier study, Osterling and Dawson (1994) reported that impairments in social cognition in children with autism might be due to early impairments in face-processing abilities. In this study, home videotapes of infants' 1-year birthdays were retrospectively analyzed. Results of these analyses indicated that failure to attend to other people's faces was the best discriminator between children with and without autism. Dawson and colleagues (2002) further investigated this apparent face-processing deficit by recorded ERPs in a population of 3- and 4-year-old children with autism. Relative to a typically developing group of children and a group of children with developmental delays, children with autism failed to show electrophysiological differentiation of familiar and unfamiliar faces (mother's face vs. a stranger's face) for the Nc and the P400 and positive slow wave components. However, children with autism did show differentiation between familiar and unfamiliar toys for the Nc and P400 (greater amplitude to unfamiliar objects at both components) (Figure 2–4). These results suggest that children with autism may have face-processing deficits at the cortical level and that these deficits occur in the absence of impairments in object processing. In a second ERP study, McPartland et al. (2001a, 2001b) recorded ERPs from adolescents with high-functioning autism. The results of this study also indicated face-processing impairments relative to an IQ-matched control group. More specifically, the latency to peak response of the N170 component was longer in latency and did not show the typical differences between upright and inverted faces. Furthermore, this component was also right lateralized in control subjects but not in individuals with autism.

Recently, Marcus and Nelson (2001) suggested three possible pathways to deficits seen in face processing in individuals with autism. These possible pathways also can be applied to the development of face-processing deficits in Williams syndrome and Turner's syndrome. They suggested that this face-processing system develops in an experience-expectant manner. First, these def-



---

**Figure 2–4.** Averaged event-related potential waveforms (*opposite page*) at the anterior (top) and posterior (bottom), right hemisphere, midline, and left hemisphere scalp locations for familiar and unfamiliar **A) faces** and **B) objects** for children with autism spectrum disorders (**top panels**) and children with typical development (**bottom panels**).

Areas in which significant differences were found for familiar versus unfamiliar stimuli are shaded in black.

*Source.* Adapted from Dawson G, Carver L, Meltzoff A, et al.: “Neural Correlates of Face and Object Recognition in Young Children With Autism Spectrum Disorder, Developmental Delay and Typical Development.” *Child Development* 73:700–717, 2002. Used with permission.

icits could be accounted for by a lack of the “expected” visual stimuli (faces), which would subsequently influence synaptic pruning (the assumption being that “correct” information in the environment leads to a stabilization of synaptic circuits and a concomitant pruning of unconfirmed and, thus, irrelevant synapses). Second, they suggested that this system may not be receiving normal input; thus, facial stimuli may be present in the environment, but deficits in processing this information, such as social gaze (or failure to recognize important aspects of the stimuli), may fail to sustain normal development of this system. Finally, similar to the second mechanism, they suggested that exposure to a stimulus may not be tantamount to the experience required for that system to develop. For example, children with autism may treat faces as objects, so the development of one specialized system for both objects and faces seems appropriate.

The following question remains: Why are faces and objects being treated similarly in autism? Intuitively, the main difference between objects and faces is the affective or emotional and dynamic information that is portrayed in the face compared with objects. Thus, aberrant interpretation of affective or dynamic stimuli may later influence the development of specialized systems. Indeed, Grelotti and colleagues (2002) suggested that because individuals with autism have reduced social interest, they may fail to develop an expert face-processing system. Grelotti and colleagues reported that adults with autism process faces via more inferior occipitotemporal areas (typically object-processing areas) rather than the expected fusiform area, even in the absence of any structural abnormalities. They further suggested that the damage to the amygdala may influ-

ence the apparent lack of social interest because it is likely involved in identifying emotionally salient information. A closer look at the development of facial expression and emotion processing as it relates to the development of general face-processing abilities may be necessary to understand the deficits previously described in the neurodevelopmental disorders as well as the normal development of face processing.

We now turn to a review of current models of the neural bases of the development of face processing, including models based on studies of typically and atypically developing populations.

## **Developmental Theories of Face Processing**

Often, the special nature of face processing is predicated on research reporting that newborns prefer viewing facial stimuli compared with a variety of other complex visual stimuli at birth (Morton and Johnson 1991; Valenza et al. 1996). Some researchers suggest that this initial propensity of newborns to preferentially fixate on facelike stimuli is evidence of an innate or a genetically determined face-processing system (Johnson and Morton 1991; Morton and Johnson 1991). Morton and Johnson proposed a system that they termed *CONSPEC*, which is operational from birth and functions to bias newborns to orient toward stimuli that contain the same basic structure as faces (see recent reviews by M. de Haan et al. 2002a; Nelson 2003). *CONSPEC* is part of a two-process model proposed to account for the development of face processing (Morton and Johnson 1991). According to this model, *CONSPEC* is a primitive “kick-start” mechanism that is expressed only when infants first view faces. *CONSPEC* serves as a guide or foundation to subsequent learning about faces. In this theory, *CONSPEC* responds exclusively to faces moving in the periphery. The *CONSPEC* mechanism appears to be functional at birth and thus has been hypothesized to be an innate mechanism that facilitates attention to faces. Moreover, Johnson and colleagues argued that the pulvinar may control the *CONSPEC* mechanism because of its strong inputs from the superior colliculus, its sensitivity to visual form information, and its highly salient stimuli (Grieve et al. 2000). This orienting response, in effect, biases infants to direct their gaze

toward faces. An infant's attention to faces is then held by a more diffuse network of connections that are either strengthened or pruned, based on experience. Thus, CONSPEC does not mediate the fixation of attention; it merely directs the infant's gaze. At approximately age 2 months, CONSPEC is replaced with or "set" by CONLERN, an experientially based face-processing mechanism. At this point, face processing becomes more dependent on the learning of faces in the environment surrounding the infant.

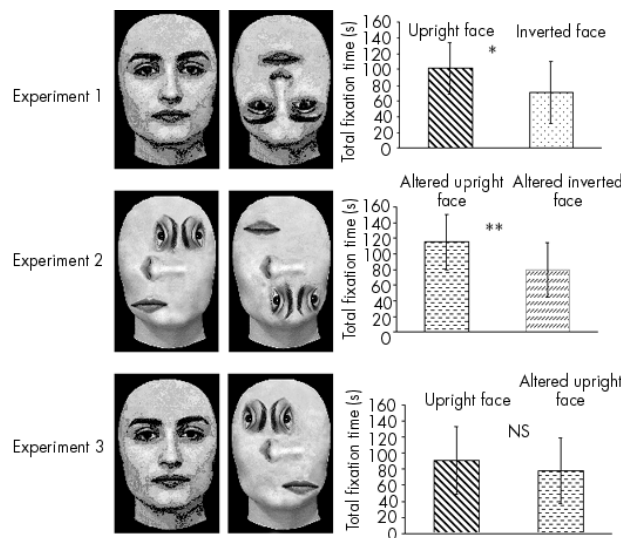
Recently, Johnson (2000) updated this two-process model of development and proposed an "interactive specialization" theory to explain why an area of the occipitotemporal cortex called the *fusiform face area* is selectively involved in face processing. This theory suggests that there are developmental changes in the tuning properties and cortical localization of this system that result in specialized activation. Johnson suggested that changes in behavioral specialization will result in changes in cortical localization and that the more finely specified or tuned an area of the cortex becomes, the less likely it will be activated for other types of stimuli. However, the mechanisms responsible for this resultant localization and why this localization occurs preferentially in the occipitotemporal cortex remain unclear. This model suggests that early in development, infants have diffuse cortical activation in response to faces that then becomes more specific with environmental exposure to faces. Subsequently, during the first few months of life, infant face perception is an emergent product of the interaction of early orienting tendencies and the overabundance of facial stimuli in the environment. These early orienting abilities are not the result of an innate cortical face module but instead reflect more primitive innate neural circuitry, involving subcortical areas of the brain. With experience, the diffuse neuronal activation becomes more specific, and the face-processing system thus becomes more specialized.

Developmental experiments investigating early visual preferences in newborns have found that newborns not only have a preference for looking at faces but also have a tendency to prefer looking at patterned stimuli arranged in the configuration of a face but without the details of the face (Simion et al. 2001). Simion and colleagues (2001) suggested an alternative to Morton and Johnson's (1991)

CONSPEC mechanism. They conducted a series of experiments to determine whether newborn preferential orientation to faces compared with other stimuli is because faces are “special” or qualitatively different from nonface stimuli or whether a more general process could account for this preference. The first possibility, the *structural hypothesis*, suggests that an innate face-detecting mechanism exists (CONSPEC). Evidence supporting this hypothesis comes from a study that used visual paired comparison and found that infants prefer to look at a facelike pattern, even when presented together with a stimulus of greater physical salience (e.g., Valenza et al. 1996). Additionally, newborns will preferentially track a moving schematic face over several other nonface patterned stimuli or face-like stimuli with the features scrambled (Johnson et al. 1991; Maurer and Young 1983).

An alternative view to the previously described theories, the *sensory hypothesis*, suggests that faces may not be any different from any other stimuli. According to this hypothesis, faces are subject to filtering by the visual system, and a preference for faces may be due to low-level processes that determine the visibility of the pattern. Easterbrook et al. (1999) reported a study that supports the sensory hypothesis. They found that infants tracked both a schematic face and patterned stimuli containing different arrangements of the same features equally. Based on the evidence for both the structural and the sensory hypotheses, Simion and colleagues (2001) suggested that these two hypotheses may not be mutually exclusive. To examine this further, Simion et al. (2002) reported a series of studies that found that infants prefer to look at stimuli that have a greater number of elements in the upper rather than the lower part of the configuration. This result is supported by research that suggests that the upper part of the visual field is less sensitive than the lower part (in adults) (Previc 1990; Rubin et al. 1996; Sheng et al. 1996); this preference disappears when the outer and inner components of the schematic are congruent. For example, infants look equally at both an upside-down triangle with two squares at the top and one square at the bottom (facelike) and a right-side-up triangle with two squares at the bottom and one square at the top (nonfacelike). Newborns seem to consistently prefer the stimulus in which both faceness

(more components in the upper part of the configuration) and congruency are present compared with stimuli in which only one of the above is present. They suggested that both faceness and the congruence of the inner and outer features combine to create a preference for facelike stimuli. Furthermore, they suggested that infants' preferences for faces at birth are a result of their spontaneous preference (constrained by the visual system) for the structural properties that are embedded in faces. Macchi Cassia et al. (2004) further examined newborns' preferences for faces by using images of natural and scrambled (features rotated but kept in the same general layout and asymmetrical) upright and inverted (inversion was isolated to inner features only) neutral faces while recording fixation time. Results indicated that newborns preferred to look at faces with more features in the upper part of the face regardless of whether they were scrambled (Figure 2–5).



**Figure 2–5.** Three pairs of stimuli presented in the three experiments and the total fixation times toward each stimulus in the pairs.

Note. NS=not significant; \* $P < 0.05$ ; \*\* $P < 0.001$ .

Source. Adapted from Macchi Cassia V, Turati C, Simion F: "Can a Nonspecific Bias Toward Top-Heavy Patterns Explain Newborns' Face Preference?" *Psychological Science* (in press). Used with permission from Blackwell Publishing.

This latter account provides an alternative to CONSPEC: newborn preferences for faces may be a result of the match between structural properties of facelike stimuli and the constraints of the newborn's sensory systems as opposed to an innate subcortical mechanism responsible for directing infants' attention to faces (Simion et al. 2001). Both Morton and Johnson's and Simion and colleagues' accounts explain newborns' initial propensity to fixate on and track faces. Johnson and colleagues (1991) went one step further and proposed an additional mechanism, CONLERN, that guides specialization of face processing. This account does not, however, explain the apparent increasing specificity of the face-processing system or how newborns go on to become "experts" in face processing.

Johnson and Morton's CONLERN mechanism is involved in the maintenance of attention to faces or facelike stimuli. This mechanism takes over for CONSPEC at around age 2 months and is influenced by stimuli in the environment. CONLERN tunes the fusiform face area to become preferentially activated to facial stimuli (M. de Haan et al. 2002a). M. de Haan and colleagues (2002a) argued that this increased specificity of the fusiform face area occurs because of its anatomical location on the ventral visual pathway and high interconnectivity to the hippocampus.

Consistent with adult visual field studies (Ellis and Shepard 1975), lesion sites in adults with prosopagnosia (De Renzi et al. 1994), and adult neuroimaging studies (Gauthier et al. 1999b; Kanwisher et al. 1997), de Schonen and Mathivet (1989, 1990) proposed a model that emphasizes the role of the right hemisphere in the development of face recognition. They found a right hemisphere advantage in face-processing tasks with 4- to 9-month-old infants (de Schonen and Mathivet 1990). They hypothesized that the right hemisphere advantage is a result of the enhanced ability of the right hemisphere to process configural information in early infancy compared with the left hemisphere. Additionally, the right hemisphere is more sensitive to low spatial frequencies (a dominant feature of faces). Because of the competitive nature of the visual system, they hypothesized that experience with faces drives the development of the right hemisphere, which then results in cortical specialization. de Schonen

and Mathivet (1989) also pointed out that the left hemisphere does benefit from configural facial information and with time also responds to facial stimuli. Although the difference between configural and featural processing of stimuli during development is compelling, the anatomical basis for a right hemisphere advantage for faces over other low spatial frequency stimuli is unclear. Indeed, most other aspects of the visual system seem to develop in a symmetrical fashion. Furthermore, this theory does not account for why faces drive the development of this specialized visual system over other complex stimuli.

In a recent review, Elgar and Campbell (2001) suggested that investigating the impairments of children with autism, Williams syndrome, and Turner's syndrome will better inform our understanding of normal face processing. Elgar and Campbell suggested that children with autism have face-processing deficits because of aberrant affective and social "drivers." Children with Williams syndrome tend to be highly sociable but have deficits in visual-spatial abilities. Children with Turner's syndrome have mild impairments in social functioning and relatively poor visual-spatial and perceptual-organizational abilities. Elgar and Campbell proposed a model that asserts that two "drivers" are involved in face processing—an affective/social driver and a visual-spatial driver. They suggested that these drivers are interactive and multiplicative in modulating the development of face expertise. They also argued that deficits in the visual-spatial driver may be a result of damage to magnocellular visual projections from the lateral geniculate nucleus to the occipital cortex and then up through the dorsal stream. Compared with the ventral visual pathway, the dorsal visual pathway receives most of the information from magnocellular projections. The ventral visual pathway receives information from both magno- and parvocellular projections. They suggested that the function of the magnocellular cells (sensitive to high temporal and low spatial frequency and highly responsive to movement) further supports this idea. Elgar and Campbell also suggested that because the superior temporal sulcus receives information from both the ventral and the dorsal streams, the superior temporal sulcus may be preferentially involved in processing dynamic facial information. They suggested that the affective/so-

cial driver is mediated by the ventromedial parts of the inferior frontal cortex, which plays a key role in moderating activity flowing to the cortex from the amygdala and thalamus, among other subcortical structures.

Nelson (1993, 2001, 2003) proposed a model of the development of face perception that accounts for how humans become experts at perceiving and processing facial information. This model suggests that infants mold their face-processing system based on the visual experiences they encounter. Nelson's model of the development of face perception draws an analogy to speech perception, in that, similar to speech perception, there appears to be a potential for cortical specialization that is dependent on experience (for review, see Kuhl 1993, 1997). Among other investigators, Kuhl and colleagues have reported that before age 6–8 months, infants are able to discriminate between a wide range of phonemes, or basic sound units. This ability tends to narrow with repeated experience to phonemes in one's native language and a lack of experience with phonemes outside one's own language (Cheour et al. 1998; Kuhl et al. 1997). Nelson (2001, 2003) suggested that this type of "perceptual narrowing" also may occur in face perception. Moreover, he asserted that early in development, humans may have the ability to discriminate between a wide range of faces and facial features and that based on environmental stimulation, or the types of faces infants are exposed to, this system becomes more specific. Thus, with development, the ability to discriminate between faces that one has not had exposure to is not as good as the ability to discriminate between faces one has had experience differentiating. This model of the development of face processing contrasts some of the previously discussed models by proposing a solely experience-expectant and activity-dependent developmental progression (Nelson 2001, 2003). Support for Nelson's (2001, 2003) perceptual narrowing model comes from several adult and developmental investigations, including research on the other-race and other-species effects, the formation of a prototypical face, and the perceptual expertise effect. For example, although further research is needed, it is plausible that the other-race and other-species effects are due to the amount of differential expe-

rience infants have with different types of faces while forming an expert face-processing system.

Consistent with this idea, some researchers have suggested that faces are represented as a comparison to a prototype that has been formed through experience. This prototype roughly represents an average of the kinds of faces or features one has seen. Indeed, Rhodes et al. (1993) argued that the coding of faces occurs by making a comparison between the perceived face and a prototype. Thus, the decrement in performance that is seen while processing inverted faces may be due to the difficulties that occur when comparing rotated faces with the prototype. Many models of face recognition (both developmental and adult theories) agree that the brain must store some sort of representation of faces (at many different levels), but they differ as to the form of this representation and how it is compared with other faces already encoded in memory. Support for the development of a “prototype” comes from studies suggesting that infants consistently prefer to view attractive faces when paired with unattractive faces (Langlois et al. 1987; Slater et al. 1998). Attractive faces are seen as more facelike because they more closely match the facial representation or prototype that infants either acquire from their experience of seeing faces or are born with. Johnson and de Haan (2001) assessed infants’ ability to extract a prototype from a series of individual faces. They observed that in 3-month-old infants but not 1-month-old infants, the prototypical stimulus was more familiar than the familiar trained face. They suggested that the ability to extract invariances from a set of input faces develops between ages 1 and 3 months.

Gauthier and colleagues suggested that visual areas selective for recognition of faces can be recruited through expertise for nonface objects, such as greebles (or facelike objects), birds, or cars (Gauthier and Tarr 1997; Gauthier et al. 2000). Therefore, without expertise, face perception would be similar to any other kind of object processing (Gauthier and Nelson 2001). The idea of perceptual expertise emphasizes the importance of early and continued visual experience with faces in order for adultlike (expert) face processing to develop. Further research on perceptual expertise supports Nelson’s perceptual narrowing theory, but it

does not describe the mechanisms involved in the development of this expert system.

### *Analytical Summary of Theories*

Each of these models and interpretations is intriguing; however, there are several unanswered questions, as well as several unfounded assumptions, for which new models of face processing development need to account. None of the above views appears sufficient to explain 1) why this apparent progression from a general to a more specific face-processing system occurs and 2) why specific areas of the cortex are targeted to preferentially process faces. Johnson's interactive perspective attempts to account for some of the above, but the neural and behavioral mechanisms involved in the developmental progression from a genetically or subcortically controlled system to an experience-based system are not well specified. For example, it is unclear why CONSPEC is specific to faces and not to more general complex visual patterns (particularly moving patterns). It is also not clear why both systems are not functional at birth or how CONLERN "takes over" for CONSPEC. Additionally, the development of a specialized cortical area devoted to processing only facial stimuli is puzzling. Is there any evidence, as de Schonen and colleagues asserted, that the neural tissue in the right hemisphere or, more specifically, in the right fusiform area is more appropriate for processing faces compared with objects? If so, how does CONLERN, or whatever mechanisms are responsible for translating this information during development, know which cortical area(s) should become specialized for faces? Johnson postulated an initial genetic mechanism, but it is still unclear why this mechanism is necessary. For example, given that newborns are inundated with facial information from the moment they are born, it is not clear why a genetic mechanism needs to be postulated to account for early facial preferences. Moreover, it is unclear whether CONLERN is influenced by changes in cortical specialization that result in changes in behavior or whether changes in behavior result in cortical specialization.

Nelson's model (2001, 2003) has support from fields spanning developmental and cognitive science, but the mechanisms

involved in this increasing specialization are not yet well understood. For example, it is unclear what narrows, what parts of the brain are involved in controlling this narrowing, and whether such narrowing is specific to faces (and speech). Also, several questions remain unanswered regarding the evidence that supports this model. For example, the specificity and malleability of the formation of a prototype are not well specified. It is plausible to imagine a system that forms a prototype through experience with different types of features and faces and the simultaneous development of configural processing, but further investigations are needed to verify this hypothesis and determine the underlying neurobiology of configural and featural processing as well as prototype formation. The effects of the formation of a prototype may result in the other-race and other-species biases reported earlier in this chapter. Another interesting question is whether the other-race effect is apparent in infants and/or young children. Or, based on Nelson's model, do infants and/or young children have an enhanced ability, compared with adults, to perceive and differentiate novel types of features and faces? Furthermore, it may be interesting to examine age effects. For example, do 7-year-old children have a 7-year-old prototype that allows them to process 7-year-old faces more rapidly than faces of other ages?

Notably, only one of the previously described models accounts for the role of the highly dynamic and emotionally salient information provided in faces that newborns encounter just a few seconds after birth and for the rest of their lives. Elgar and Campbell give a provocative account of the development of face processing, based on research with individuals who have developmental disorders, and suggest a role for the influence of socioemotional information. Although rather intriguing, further research needs to be conducted to validate the proposed neuroanatomical pathways and behavioral correlates to these pathways. Additionally, Elgar and Campbell's model does not account for the development of expertise or the increasingly specific processing of faces across development and why their proposed drivers only pick up the dynamics of face information.

## Conclusion

In summary, the study of the developmental neurobiology of face processing is still in its infancy. Despite the relatively large body of literature on adult face processing as well as the behavioral correlates of the development of face processing, relatively little is known about the neural correlates that mediate the development of this system. The evidence presented in this chapter largely suggests that the development of face processing can be characterized as an experience-expectant process, influenced by many different factors. Moreover, the development of this perceptual ability may occur during a “period of opportunity” when visual face information present in the environment molds the specificity of this system. Although it is unclear what kind of visual information is necessary to shape this system, it is likely a combination of many factors, including preferences or limitations of the newborn visual system, basic perceptual information about faces (symmetry; more features in the upper half), social and dynamic information, familiarity, and simply because we see so many faces every day (possibly leading to expertise).

As summarized earlier, neuroimaging techniques have recently begun to be used to study the development of face processing. Studies that use these techniques have not only begun to elucidate the neural machinery involved in the development of this system but also have begun to shed light on the neural mechanisms involved in mature face processing. Future advances in imaging technologies that allow for noninvasive investigations in both developmental and disordered populations will greatly benefit the study of face processing. Moreover, collaborative efforts that focus on the acquisition and development of face processing across the life span, using both behavioral and neuroscientific methods, may provide more informative models and theories related to this perceptual ability. More specifically, a complete theory of face processing must characterize face processing from start to finish and must account for the mechanisms that influence the behavioral and cortical specificity in the formation of this system.

## References

- Bahrnick LE, Gogate LJ, Ruiz I: Attention and memory for faces and actions in infancy: the salience of actions over faces in dynamic events. *Child Dev* 6:1629–1643, 2002
- Baird AA, Gruber SA, Fein DA, et al: Functional magnetic resonance imaging and facial affect recognition in children and adolescents. *J Am Acad Child Adolesc Psychiatry* 38:195–199, 1999
- Barrera ME, Maurer D: The perception of facial expressions by the three-month old. *Child Dev* 52:203–206, 1981
- Boucher J, Lewis V, Collis G: Familiar face and voice matching and recognition in children with autism. *J Child Psychol Psychiatry* 39:171–181, 1998
- Brigham J, Barkowitz P: Do “they all look alike?” The effect of race, sex, experience and attitudes on the ability to recognize faces. *J Appl Soc Psychol* 8:306–318, 1978
- Brigham J, Malpass R: The role of experience and contact in the recognition of own- and other-race persons. *J Soc Issues* 41:139–155, 1985
- Carmel D, Bentin S: Domain specificity versus expertise: factors influencing distinct processing of faces. *Cognition* 83:1–29, 2002
- Carver LJ, Dawson G, Panagiotides H, et al: Age-related differences in neural correlates of face recognition during the toddler and preschool years. *Dev Psychobiol* 42:148–159, 2003
- Chance JE, Turner AL, Goldstein AG: Development of differential recognition for own- and other-race faces. *J Psychol* 112:29–37, 1982
- Cheour M, Ceponiene R, Lehtokoski A, et al: Development of language-specific phoneme representations in the infant brain. *Nat Neurosci* 1:351–353, 1998
- D’Entremont B, Muir DW: Five-month-olds’ attention and affective responses to still faced emotional expressions. *Infant Behavior and Development* 20:563–568, 1997
- Damasio AR, Damasio HC, Van Hoesen GW: Prosopagnosia: anatomic basis and behavioral mechanisms. *Neurology* 4:1–15, 1982
- Dawson G, Carver L, Meltzoff A, et al: Neural correlates of face and object recognition in young children with autism spectrum disorder, developmental delay and typical development. *Child Dev* 73:700–717, 2002
- DeBoer T, Scott LS, Nelson CA: Event-related potentials in developmental populations, in *Event-Related Potentials: A Methods Handbook*. Edited by Handy TC. MA, MIT Press (in press)

- de Haan EH, Campbell R: A fifteen year follow-up case of developmental prosopagnosia. *Cortex* 27:489–509, 1991
- de Haan M, Nelson CA: Recognition of the mother's face by 6-month-old infants: a neurobehavioral study. *Child Dev* 68:187–210, 1997
- de Haan M, Nelson CA: Discrimination and categorization of facial expressions of emotion during infancy, in *Perceptual Development: Visual, Auditory, and Language Perception in Infancy*. Edited by Slater AM. London, University College London Press, 1998, pp 287–309
- de Haan M, Nelson CA: Electrocortical correlates of face and object recognition by 6-month-old infants. *Dev Psychol* 35:187–210, 1999
- de Haan M, Thomas KM: Application of ERP and fMRI techniques to developmental science. *Developmental Science* 5:335–343, 2002
- de Haan M, Humphreys K, Johnson MH: Developing a brain specialized for face perception: a converging methods approach. *Dev Psychobiol* 40:200–212, 2002a
- de Haan M, Pascalis O, Johnson MH: Specialization of neural mechanisms underlying face recognition in human infants. *J Cogn Neurosci* 12:199–209, 2002b
- De Renzi E: Current issues in prosopagnosia, in *Aspects of Face Processing*. Edited by Ellis HD, Jeeves MD, Newcombe F, et al. Dordrecht, The Netherlands, Nijhoff, 1986, pp 243–252
- De Renzi E, Perani D, Carlesimo GA, et al: Prosopagnosia can be associated with damage confined to the right hemisphere—an MRI and PET study and review of the literature. *Neuropsychologia* 32:893–902, 1994
- de Schonen S, Mathivet E: First come, first served: a scenario about the development of hemispheric specialization in face recognition during infancy. *European Bulletin of Cognitive Psychology* 9:3–44, 1989
- de Schonen S, Mathivet E: Hemispheric asymmetry in a face discrimination task in infants. *Child Dev* 61:1192–1205, 1990
- Diamond R, Carey S: Developmental changes in the representation of faces. *J Exp Child Psychol* 86:55–87, 1977
- Easterbrook MA, Kisilevsky BS, Hains SMJ, et al: Faceness or complexity: evidence from newborn visual tracking of facelike stimuli. *Infant Behavior and Development* 22:17–35, 1999
- Eimer M, Holmes A: An ERP study on the time course of emotional face processing. *Neuroreport* 13:427–431, 2002
- Elgar R, Campbell R: The development of face-identification skills: what lies behind the face module? *Infant and Child Development* 10:25–30, 2001

- Ellis HD, Shepard JW: Recognition of upright and inverted faces presented in the left and right visual fields. *Cortex* 11:3–7, 1975
- Fallshore M, Scholler JW: Verbal vulnerability of perceptual expertise. *J Exp Psychol Learn Mem Cogn* 21:1608–1623, 1995
- Farah MJ: Face perception and within-category discrimination in prosopagnosia. *Neuropsychologia* 33:661–674, 1995
- Farah MJ: Is face recognition ‘special’? Evidence from neuropsychology. *Behav Brain Res* 76:181–189, 1996
- Farah MJ, Wilson KD, Drain M, et al: The inverted face inversion effect in prosopagnosia: evidence for mandatory, face-specific perceptual mechanisms. *Vision Res* 35:2089–2093, 1995
- Farah MJ, Rabinowitz C, Quinn GE, et al: Early commitment of neural substrates for face recognition. *Cognitive Neuropsychology* 17:117–123, 2000
- Field TM, Woodson RW, Greenberg R, et al: Discrimination and imitation of facial expressions by neonates. *Science* 218:179–181, 1982
- Freire A, Lee K, Symons LA: The face-inversion effect as a deficit in the encoding of configural information: direct evidence. *Perception* 29:159–170, 2000
- Freire A, Lee K: Face recognition in 4- to 7-year-olds: processing of configural, featural, and paraphernalia information. *J Exp Child Psychol* 80:347–371, 2001
- Furl N, Phillips JP, O’Toole AJ: Face recognition algorithms and the other-race effect: computational mechanisms for a developmental contact hypothesis. *Cognitive Science* 96:1–19, 2002
- Gauthier I, Nelson CA: The development of face expertise. *Curr Opin Neurobiol* 11:219–224, 2001
- Gauthier I, Tarr MJ: Becoming a “Greeble” expert: exploring mechanisms for face recognition. *Vision Res* 37:1673–1682, 1997
- Gauthier I, Williams P, Tarr MJ, et al: Training ‘greeble’ experts: a framework for studying expert object recognition processes. *Vision Res* 38:2401–2428, 1998
- Gauthier I, Behrmann M, Tarr MJ: Can face recognition really be dissociated from object recognition? *J Cogn Neurosci* 11:349–370, 1999a
- Gauthier I, Tarr MJ, Anderson AW, et al: Activation of the middle fusiform ‘face area’ increases with expertise in recognizing novel objects. *Nat Neurosci* 2:568–573, 1999b
- Gauthier I, Skudlarski P, Gore JC, et al: Expertise for cars and birds recruits brain areas involved in face recognition. *Nat Neurosci* 3:191–197, 2000

- Golby AJ, Gabrieli JDE, Chiao JY, et al: Differential responses in the fusiform region to same-race and other-race faces. *Nat Neurosci* 4:845–850, 2001
- Grelotti DJ, Gauthier I, Schultz RT: Social interest and the development of cortical face specialization: what autism teaches us about face processing. *Dev Psychobiol* 40:213–225, 2002
- Grieve KL, Acuna C, Cudeiro J: The primate pulvinar nuclei: vision and action. *Trends Neurosci* 23:35–39, 2000
- Gross CG, Bender DB, Rocha-Miranda CE: Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science* 166:1303–1306, 1969
- Gross CG, Rocha-Miranda CE, Bender DB: Visual properties of neurons in inferotemporal cortex of the macaque. *J Neurophysiol* 35:96–111, 1972
- Halit H, de Haan M, Johnson MH: Cortical specialization for face processing: face-sensitive event-related potential components in 3- and 12-month-old infants. *Neuroimage* 19:1180–1193, 2003
- Hauck M, Fein D, Maltby N, et al: Memory for faces in children with autism. *Child Neuropsychology* 4:187–198, 1999
- Haxby JV, Hoffman EA, Gobbini MI: The distributed human neural system for face perception. *Trends Neurosci* 4:223–233, 2000
- Haxby JV, Gobbini MI, Furey ML, et al: Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293:2425–2430, 2001
- Hobson RP, Ouston J, Lee A: What's in a face? The case of autism. *Br J Psychol* 79:441–453, 1988
- Johnson MH: Functional brain development in infants: elements of an interactive specialization framework. *Child Dev* 71:74–81, 2000
- Johnson MH, de Haan M: Developing cortical specialization for visual-cognitive function: the case of face recognition, in *Mechanisms of Cognitive Development: Behavioral and Neural Perspectives*. Edited by McClelland JL, Siegler RS. Mahwah, NJ, Lawrence Erlbaum, 2001, pp 253–270
- Johnson MH, Morton J: *Biology and Cognitive Development: The Case of Face Recognition*. Oxford, England, Blackwell, 1991
- Johnson MH, Dziurawiec S, Ellis H, et al: Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 40:1–19, 1991
- Kanner L: Autistic disturbances of affective contact. *Nerv Child* 2:217–250, 1942

- Kanwisher N, McDermott J, Chun MM: The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci* 17:4302–4311, 1997
- Kuhl PK: Innate predispositions and the effects of experience in speech perception: the native language magnet theory, in *Developmental Neurocognition: Speech and Face Processing in the First Year of Life*. Edited by de Boysson-Bardies B, de Schonen S, Jusczyk P, et al. Hingham, MA, Kluwer Academic Press, 1993, pp 259–274
- Kuhl PK, Andruski JE, Chistovich IA, et al: Cross-language analysis of phonetic units in language addressed to infants. *Science* 277:684–686, 1997
- Langdell T: Recognition of faces: an approach to the study of autism. *British Journal of Child Psychology and Psychiatry* 19:255–268, 1978
- Langlois JH, Roggman LA, Casey RJ, et al: Infant preferences for attractive faces: rudiments of a stereotype? *Dev Psychol* 23:363–369, 1987
- LeDoux JE: *The Emotional Brain*. New York, Simon & Schuster, 1996
- Le Grand R, Mondloch CJ, Maurer D, et al: Neuroperception: early visual experience and face processing (letter). *Nature* 410:890, 2001
- Macchi Cassia V, Turati C, Simion F: Can a non-specific bias toward top-heavy patterns explain newborns' face preference? *Psychol Sci* (in press)
- Malpass RS, Kravitz J: Recognition for faces of own and other race. *J Pers Soc Psychol* 13:330–334, 1969
- Marcus D, Nelson CA: Neural bases and development of face recognition in autism. *CNS Spectr* 6:36–59, 2001
- Marotta JJ, Genovese CR, Behrmann M: A functional MRI study of face recognition in patients with prosopagnosia. *Neuroreport* 12:1581–1587, 2001
- Maurer D, Salapatek P: Developmental changes in the scanning of faces by young children. *Child Dev* 47:523–537, 1976
- Maurer D, Young R: Newborns' following of natural and distorted arrangements of facial features. *Infant Behavior and Development* 6:127–131, 1983
- McPartland J, Dawson G, Carver L, et al: Neural correlates of face perception in autism. Poster presented at the meeting of the Society for Research in Child Development, Minneapolis, MN, April 2001a
- McPartland J, Dawson G, Carver L, et al: Neural correlates of face perception in individuals with autism spectrum disorder. Poster presented at the International Meeting for Autism Research, San Diego, CA, November 2001b

- Morton J, Johnson MH: CONSPEC and CONLERN: a two-process theory of infant face recognition. *Psychological Press* 98:164–181, 1991
- Nelson CA: The recognition of facial expressions in infancy: behavioral and electrophysiological correlates, in *Developmental Neurocognition: Speech and Face Processing in the First Year of Life*. Edited by de Boysson-Bardies B, de Schonen S, Juszyk P, et al. Hingham, MA, Kluwer Academic Press, 1993, pp 187–193
- Nelson CA: Neural correlates of recognition memory in the first postnatal year of life, in *Human Behavior and the Developing Brain*. Edited by Dawson G, Fischer K. New York, Guilford, 1994, pp 269–313
- Nelson CA: The development and neural bases of face recognition. *Infant and Child Development* 10:3–18, 2001
- Nelson CA: The development of face recognition reflects an experience-expectant and activity dependent process, in *The Development of Face Processing in Infancy and Early Childhood: Current Perspectives*. Edited by Pascalis O, Slater A. New York, Nova Science Publishers, 2003, pp 79–97
- Nelson CA, Bloom FE: Child development and neuroscience. *Child Dev* 68:970–987, 1997
- Nelson CA, Collins PF: Event-related potential and looking time analysis of infants' responses to familiar and novel events: implications for visual recognition memory. *Dev Psychol* 27:50–58, 1991
- Nelson CA, de Haan M: A neurobehavioral approach to the recognition of facial expressions in infancy, in *The Psychology of Facial Expression*. Edited by Russell JA. Cambridge, MA, Cambridge University Press, 1996, pp 176–204
- Nelson CA, Dolgin K: The generalized discrimination of facial expressions by 7-month-old infants. *Child Dev* 56:58–61, 1985
- Nelson CA, Monk C: The use of event-related potentials in the study of cognitive development, in *Handbook of Developmental Cognitive Neuroscience*. Edited by Nelson CA, Luciana M. Cambridge, Massachusetts Institute of Technology Press, 2001, pp 125–136
- Nelson CA, Morse PA, Leavitt LA: Recognition of facial expressions by seven-month-old infants. *Child Dev* 50:1239–1242, 1979
- Nelson CA, Bloom FE, Cameron J, et al: An integrative, multidisciplinary approach to the study of brain-behavior relations in the context of typical and atypical development. *Dev Psychopathol* 14:499–520, 2002
- Osterling J, Dawson G: Early recognition of children with autism: a study of first birthday home videotapes. *J Autism Dev Disord* 24:247–257, 1994

- O'Toole AJ, Deffenbacher KA, Valentin D, et al: Structural aspects of face recognition and the other-race effect. *Mem Cognit* 22:208–224, 1994
- Pascalis O, Bachevalier J: Face recognition in primates: a cross-species study. *Behav Processes* 43:87–96, 1998
- Pascalis O, de Schonen S: Recognition memory in 3- to 4-day-old human neonates. *Neuroreport* 5:1721–1724, 1994
- Pascalis O, de Schonen S, Morton J, et al: Mother's face recognition by neonates: a replication and extension. *Infant Behavior and Development* 18:79–95, 1995
- Pascalis O, Demont E, de Haan M, et al: Recognition of faces of different species: a developmental study between 5 and 8 years of age. *Infant and Child Development* 10:39–45, 2001
- Pascalis O, de Haan M, Nelson CA: Is face processing species-specific during the first year of life? *Science* 296:1321–1323, 2002
- Passarotti AM, Paul BM, Bussiere JR, et al: The development of face and location processing: an fMRI study. *Developmental Science* 6:100–117, 2003
- Perrett DI, Rolls ET, Caan W: Visual neurons responsive to faces in the monkey temporal cortex. *Experimental Brain Research* 47:329–342, 1982
- Perrett DI, Mistlin AJ, Chitty AJ: Visual neurons responsive to faces. *Trends Neurosci* 10:358–364, 1987
- Pizzagalli DA, Lehmann D, Hendrick AM, et al: Affective judgments of faces modulate early activity (~160 ms) within the fusiform gyri. *Neuroimage* 16:663–677, 2002
- Previc FH: Functional specialization in the lower and upper visual field in humans: its ecological origins and neurophysiological implications. *Behav Brain Sci* 13:519–575, 1990
- Rhodes G, Brake D, Atkinson AP: What's lost in inverted faces? *Cognition* 47:25–57, 1993
- Rubin N, Nakayama K, Shapley R: Enhanced perception of illusory contours in the lower versus upper visual hemifield. *Science* 271:651–653, 1996
- Schultz RT, Gauthier I, Klin A, et al: Abnormal ventral temporal cortical activity during face discrimination among individuals with autism and Asperger syndrome. *Arch Gen Psychiatry* 57:331–340, 2000
- Scott LS, Nelson CA: Increasing specificity in face processing: a developmental ERP study. Poster presented at Cognitive Neuroscience Society Annual Meeting, New York, NY, March 2003

- Sheng H, Cavanagh P, Intriligator J: Attentional resolution and the locus of visual awareness. *Nature* 383:334–337, 1996
- Simion F, Macchi Cassia V, Turati C, et al: The origins of face perception: specific versus non-specific mechanisms. *Infant and Child Development* 10:59–65, 2001
- Simion F, Valenza E, Macchi Cassia V, et al: Newborns' preference for up-down asymmetrical configurations. *Developmental Science* 5:427–434, 2002
- Slater A, Von der Schulenburg C, Brown E, et al: Newborn infants prefer attractive faces. *Infant Behavior and Development* 21:345–354, 1998
- Soken NH, Pick A: Intermodal perception of happy and angry expressive behaviors by seven-month-old infants. *Child Dev* 63:787–795, 1992
- Tanaka JW, Sengco JA: Features and their configuration in face recognition. *Mem Cognit* 25:583–592, 1997
- Taylor MJ, Edmonds GE, McCarthy G, et al: Eyes first! Eye processing develops before face processing in children. *Neuroreport* 12:1671–1676, 2001
- Thomas K, Drevets WC, Whalen PJ, et al: Amygdala response to facial expressions in children and adults. *Biol Psychiatry* 49:309–316, 2001
- Thompson P: Margaret Thatcher: a new illusion. *Perception* 9:483–484, 1980
- Trepagnier C: Autism etiology: a face-processing perspective. *Brain Cogn* 37:158–160, 1998
- Valenza E, Simion F, Cassia VM, et al: Face preference at birth. *J Exp Psychol Hum Percept Perform* 22:892–903, 1996
- Yin RK: Looking at upside-down faces. *J Exp Psychol Gen* 81:141–145, 1969
- Young AW, Ellis HD: Childhood prosopagnosia. *Brain Cogn* 9:16–47, 1989
- Young-Browne G, Rosenfeld HM, Horowitz FD: Infant discrimination of facial expressions. *Child Dev* 48:555–562, 1977