32 The Cognitive and Neural Development of Face Recognition in Humans

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ABSTRACT Conventional wisdom has long held that face recognition develops very slowly throughout infancy, childhood, and adolescence, with perceptual experience as the primary engine of this development. However, striking new findings from just the last few years have overturned much of this traditional view by demonstrating genetic influences on the face recognition system as well as impressive face discrimination abilities that are present in newborns and in monkeys that were reared without ever seeing a face. Nevertheless, experience does play a role, for example, in narrowing the range of facial subtypes for which discrimination is possible and perhaps in increasing discrimination abilities within that range. Here we first describe the cognitive and neural characteristics of the adult system for face recognition, and then we chart the development of this system over infancy and childhood. This review identifies a fascinating new puzzle to be targeted in future research: All qualitative aspects of adult face recognition measured behaviorally are present very early in development (by 4 years of age; all that have been tested are also present in infancy), yet functional magnetic resonance imaging and event-related potential evidence shows very late maturity of face-selective neural responses (with the fusiform face area increasing substantially in volume between age 7 years and adulthood).

Introduction

One of the most impressive skills of the human visual system is our ability to identify a specific individual from a brief glance at their face, thus distinguishing that individual from hundreds of other people we know, despite the wide variations in the appearance of each face as it changes in viewpoint, lighting, emotional expression, and hairstyle. Though many mysteries remain, important insights have been gleaned over the last two decades about the cognitive and neural mechanisms that enable humans to recognize faces. Here, we address an even more difficult and fundamental question: How does the machinery of face recognition get wired up during development in the first place?

Our review of the available evidence supports a view of the development of face recognition that is dramatically different from the one suggested by the first studies in the field. Twenty years ago, the standard theory was that core aspects of the ability to discriminate faces were not present until 10 years of age, and their emergence and eventual maturity were determined primarily by experience (Carey & Diamond, 1977; Carey, Diamond, & Woods, 1980). This position has been overturned by recent findings that demonstrate striking abilities even in neonates and by mounting evidence of genetic contributions.

We organize our review by age group. Throughout, we ask how the available data address the following fundamental theoretical questions:

1. What are the inherited genetic contributions to the specification of the adult system for processing facial identity information?
2. What is derived from experience?
3. How exactly do genes and/or experience work separately or together across the course of development to produce the adult system?

The perception of face identity in adulthood

We begin with a characterization of the end state of development: the cognitive and neural basis of the perception of facial identity in adults. Note that this is a major topic in its own right, with much internal theoretical debate. However, to facilitate our present interest in the *developmental* course of face recognition, we focus on empirical phenomena, especially those that are well established in adults and have subsequently been tested in development.

CORE BEHAVIORAL PROPERTIES OF FACE IDENTITY PERCEPTION IN ADULT HUMANS Basic properties of face identification in adults are as follows. Identification is more accurate when faces are upright than when they are inverted (i.e., upside

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down) on both memory and perceptual tasks, and the inversion decrement is substantially larger for faces than for nonface objects (the *disproportionate inversion effect*; Yin, 1969; see also Robbins & McKone, 2007). Generalization from a single image of a novel face in one viewpoint to an image in another is relatively poor, albeit better from the three-quarter view to front or profile views than between the more distinct profile and front views (the *three-quarter view advantage*; Logie, Baddeley, & Woodhead, 1987). For familiar faces, performance on memory tasks relies more strongly on inner face regions than on external regions that include hair; for unfamiliar faces, the pattern is reversed (*inner versus outer features effects*; Ellis, Sheperd, & Davies, 1979). Finally, identification of own-race faces is better than identification of other-race faces (the *other-race effect*; Meissner & Brigham, 2001). Note that the first two properties (i.e., the disproportionate inversion effect and the three-quarter view advantage) derive directly from perceptual processing, but the last two are known to derive at least partly from deliberate task strategies (e.g., reliance on hair for novel faces if distinctive hair is present; Duchaine & Weidenfeld, 2003) or social and attentional factors (other-race effect; Bernstein, Young, & Hugenberg, 2007).

Additional experimental findings can be grouped under the heading of phenomena that have motivated the concept of *holistic/configural* processing. Holistic/configural processing is defined (e.g., Tanaka & Farah, 1993; Maurer, Lewis, & Mondloch, 2005) as (1) a strong integration at the perceptual level of information from all regions of the face (so that altering one region leads to changes in the percept of other regions), which (2) codes the exact spacing between face features (and, more controversially, exact feature shape as well; Yovel & Duchaine, 2006), and (3) is strongly sensitive to face inversion. Relevant phenomena are as follows. Subjects find it harder to identify one half of a combination face (e.g., the top half of George Bush's face with the bottom half of Tony Blair's face) if the inconsistent other half-face is aligned with the target half rather than misaligned (the *composite effect*; Young, Hellawell, & Hay, 1987). Subjects are also better able to distinguish which of two face parts (e.g., two noses) appeared in a previously shown face when these are presented in the context of the whole face than when they are presented in isolation (the *part-whole effect*; Tanaka & Farah, 1993). Part choice is also better in the original whole than in a version of the whole face with an alteration in spacing between nontarget features (the *part-in-spacing-altered-whole effect*; Tanaka & Sengco, 1997), a finding that is consistent with other evidence of strong *sensitivity to spacing changes* (e.g., distance between eyes) in upright faces (e.g., Rhodes, Brake, & Atkinson, 1993; McKone, Aitkin, & Edwards, 2005). When an upright and an inverted version of a face are superimposed in transparency, the upright face is perceived more strongly (*perceptual bias to upright*; Martini,

McKone, & Nakayama, 2006). All these holistic effects are specific to upright faces; they are not found for inverted or scrambled faces (Young et al., 1987; Tanaka & Sengco, 1997; Robbins & McKone, 2003; Martini et al., 2006) and are weak or absent for objects, including objects of expertise (for reviews, see McKone, Kanwisher, & Duchaine, 2007; Robbins & McKone, 2007).

Finally, other behavioral phenomena have been taken to indicate coding within a perceptual "face-space," defined as a multidimensional space in which each individual face is coded as a point by its value on underlying dimensions describing different aspects of facial structure and for which the "average" face lies at the center of the space (Valentine, 1991). These phenomena include *distinctiveness effects*, in which performance is better for distinctive faces than for typical faces on old-new recognition tasks but the pattern is reversed on face versus nonface classification tasks (Valentine & Bruce, 1986), and *adaptation aftereffects*, in which, for example, adaptation to expanded faces make a physically normal face appear contracted (Webster & MacLin, 1999) and adaptation to "anti-Bill" (the physical opposite of Bill in face space) makes the average face appear like Bill (Leopold, O'Toole, Vetter, & Blanz, 2001).

NEUROPHYSIOLOGY AND FUNCTIONAL MAGNETIC RESONANCE IMAGING IN ADULT MONKEYS   Adult monkeys show cortical mechanisms specialized for face perception. Strongly face-selective responses from single neurons ("face cells") are well established in the temporal lobes of macaques (Desimone, Albright, Gross, & Bruce, 1984; Foldiak, Xiao, Keysers, Edwards, & Perrett, 2004), and face-selective cortical regions have been reported in macaques using functional magnetic resonance imaging (fMRI) (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003; Pinsk, DeSimone, Moore, Gross, & Kastner, 2005). Tsao, Freiwald, Tootell, and Livingstone (2006) demonstrated direct correspondence between face-selective fMRI patches and face selectivity of single cells within those patches. Note that the role of "face cells" in supporting the behavioral phenomena described in the previous section is mostly unexplored, with the exceptions that a preponderance of face-selective cells are tuned to upright (Perrett et al., 1988) and that their tuning to facial distortions from the "average face" is consistent with a face space coding of facial identity (Leopold, Bondar, & Giese, 2006). In development, only basic face selectivity has been studied.

FUNCTIONAL MAGNETIC RESONANCE IMAGING: CORTICAL LOCI OF FACE IDENTITY PROCESSING IN ADULT HUMANS   Brain imaging in humans reveals three face-selective cortical regions (figure 32.1), of which the fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997), is the main one that is investigated in children. This region, which can be
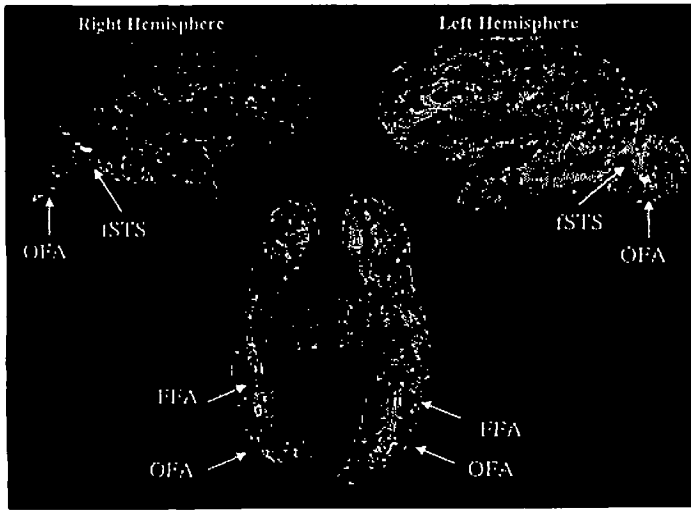
FIGURE 32.1 Face-selective activation (faces > objects, $p < 0.0001$) on an inflated brain of one adult subject, shown from lateral and ventral views of the right and left hemispheres. Three face-selective regions are shown: the FFA in the fusiform gyrus along the ventral part of the brain, the OFA in the lateral occipital area, and the fSTS in the posterior region of the superior temporal sulcus. For studies of face identification (rather than expression, etc.), the FFA and OFA are of greatest interest. (See color plate 46.)

found in essentially every normal adult in a short "localizer" scan (Saxe, Brett, & Kanwisher, 2006), responds more strongly to faces than to letter strings and textures (Puce, Allison, Asgari, Gore, & McCarthy, 1996), flowers (McCarthy, Luby, Gore, & Goldman-Rakic, 1997), and indeed all other nonface stimuli that have been tested to date, including mixed everyday objects, houses, hands (Kanwisher et al., 1997), and objects of expertise (Kanwisher & Yovel, in press).

fMRI adaptation studies show that neural populations in the FFA can discriminate face identity (Rotshtein, Henson, Treves, Driver, & Dolan, 2005) but not facial expression (Winston, Vuilleumier, & Dolan, 2003). The FFA is involved in individual discrimination of upright but not inverted faces (Yovel & Kanwisher, 2005; Mazard, Schiltz, & Rossion, 2006), and its inversion effect (i.e., higher response to upright than inverted faces) correlates with the behavioral inversion effect (Yovel & Kanwisher, 2005). The FFA also demonstrates holistic processing, specifically a composite effect (Schiltz & Rossion, 2006).

ELECTROPHYSIOLOGICAL SIGNATURES IN HUMAN ADULTS A negative-going event-related potential (ERP) response peaking about 170 ms after stimulus onset over posterior temporal sites (N170) has been widely replicated to be face-selective (Halgren, Raij, Marinkovic, Jousmaki, & Hari, 2000; Liu, Harris, & Kanwisher, 2002). This peak is delayed by 10 ms, and is larger in amplitude for inverted faces than for upright faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996). The N170 also shows identity discrimination (a lower

response for repeated compared to unrepeated faces) when the faces are upright but not inverted (Jacques & Rossion, 2006; Jacques, D'arripe, & Rossion, 2007). An important point that is relevant to the interpretation of developmental studies is that the neural source of the N170 is unknown even in adults, and the sources of suggested equivalent components in children and infants could possibly be different still.

Data from adult subjects relevant to the roles of experience and genetics

Before considering what developmental studies tell us about the roles of experience and genetics in face recognition, we describe several findings from adults that also bear directly upon these issues.

Clearly, *experience in isolation* can influence face perception. Adults continue to learn new faces throughout life, and this improves perceptual discrimination of these faces: Matching the correct face photograph to a degraded security camera video image is more accurate if the face is familiar than if it is unfamiliar (Burton, Wilson, Cowan, & Bruce, 1999; also see Bruce, Henderson, Newson & Burton, 2001). Temporary aftereffects from adaptation to distorted faces (e.g., Webster & MacLin, 1999) also indicate purely experience-based changes in the tuning of perceptual representations of faces. Training effects on the ability to discriminate trained and novel faces have also been demonstrated in an adult prosopagnosic (DeGutis, Bentin, Robertson, & D'Esposito, 2007). Interestingly, however, there is no evidence that experience alone produces any fundamental *qualitative* change in face processing either neurally or cognitively; for example, holistic processing, "face space" effects, and FFA activation all occur strongly for both familiar faces and unfamiliar faces (Young et al., 1987; Kanwisher et al., 1997; Webster & MacLin, 1999; Le Grand, Mondloch, Maurer, & Brent, 2004; Carbon et al., 2007).

Studies of human adults provide two sources of evidence for genetic contributions. Inability to recognize faces in the absence of any known brain injury (developmental prosopagnosia) often runs in families (Duchaine, Germine, & Nakayama, 2007; Grueter et al., 2007; Kennerknecht, Pluempe, & Welling, 2008). Also, in normal adults, fMRI shows greater similarity in the pattern of activation across the ventral visual stream for monozygotic compared to dizygotic twins, but only for stimulus classes for which an evolutionary origin of the observed selective cortical regions could reasonably be proposed: faces and places but not written words or chairs (Polk, Park, Smith, & Park, 2007).

In summary, results from adults tell us that experience can fine-tune face recognition without changing its qualitative properties and that genes explain some of the variation behaviorally and neurally. Importantly, adult studies do not tell us at what developmental stage genes have their

influence. In particular, they do not necessarily demonstrate that a face system is present at birth. Some genetically predetermined processes are present at birth (e.g., the sucking reflex), but others affect maturational processes later in childhood or adolescence (e.g., puberty).

Development: Infancy

In exploring genetic and experience-based contributions to face recognition via infancy studies, several interrelated questions are relevant. First, which abilities, if any, are present at birth? Visual abilities that are present in neonates (or in monkeys that have been deprived of all face input) cannot be derived from experience and therefore provide the only method of revealing genetic influences in isolation from any visual learning. Second, if babies are born with a face representation, is its purpose merely to draw attention to faces (cf. CONSPEC in Morton & Johnson, 1991) or to support individuation? Third, how broadly tuned is any such representation: broad enough to cover any primate face, specific to own-species faces, or perhaps even to own-race faces? Finally, which, if any, of the types of effects of experience in early infancy that are found in other perceptual and cognitive domains occur for faces: Improvements with increasing experience? Perceptual narrowing (i.e., destruction of earlier ability)? Critical periods? Studies of these topics published within the last few years have dramatically altered our understanding of infant face recognition.

In a classic result, newborns (median age: 9 minutes) track an upright "paddle face" (figure 32.2A) further than versions in which the position of the internal blobs is scrambled or inverted (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991). Although it has been suggested that this preference could arise from general visual biases (e.g., for stimuli with more elements in the upper visual field; Simion, Macchi Cassia, Turati, & Valenza, 2003), preference only for the normal contrast polarity of a (Caucasian) face (Farroni et al., 2005) argues for a level of specificity to facelike structure. Thus humans are born with some type of innate preference that, at the very least, attracts infants' attention to faces. Note that the innate representation supporting face preference could be different from that supporting face individuation in adults (Johnson, 2005); indeed, a finding that neonates track faces in the temporal but not nasal visual field (Simion, Valenza, Umlita, & Dalla Barba, 1998) suggests a subcortical rather than cortical origin.

Our concern in this chapter is primarily with the development of face individuation ability. This can be measured in infants by looking time measures that assess preference and dishabituation-to-perceived-novelty. A classic finding is that neonates less than 4 days old can discriminate their mother from similar-looking women (Pascalis, de Schonen, Morton, Deruelle, & Fabre-Grenet, 1995; Bushnell, 2001), although
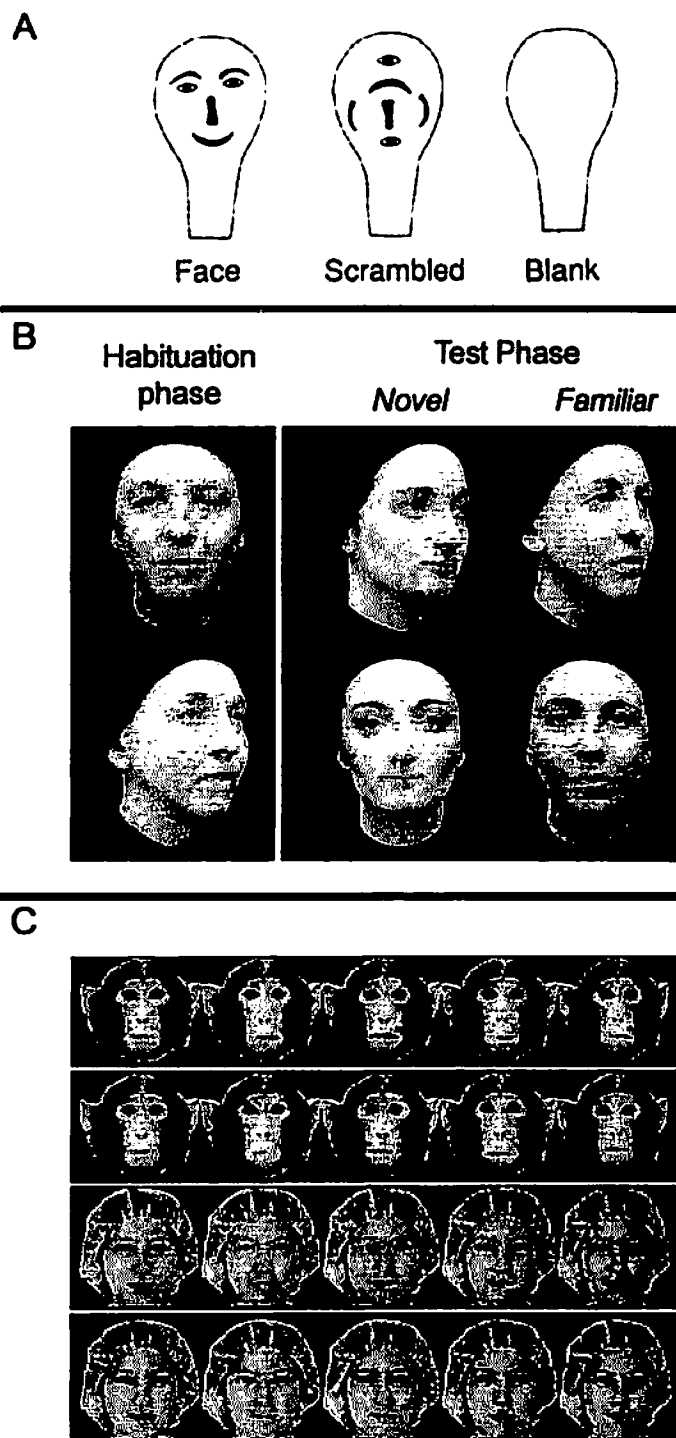

A Face Scrambled Blank

B

| Habituation phase | Test Phase | |
| | *Novel* | *Familiar* |

C

FIGURE 32.2 Face perception without experience. (A) Newborn humans (<1 hour old) track the "paddle face" on the left further than the scrambled version (Morton & Johnson, 1991). (B) Newborn humans (<3 days) look longer at the novel than habituated face, indicating recognition of face identity even across view change (Turati et al., 2008). (C) Japanese macaques raised with no exposure to faces can, on first testing, discriminate very subtle differences between individual monkey faces (including differences both in shape and in spacing of internal features) and can also do this for human faces (Sugita, 2008).

mother recognition in the first 24 hours may be partially dependent on prenatal familiarity with her voice (Sai, 2005). More recent data demonstrate even more striking abilities. Three-month-olds can recognize the identity of *novel* individuals, with *similar-looking* faces (same sex, age, race), *without hair*, and *across view changes* (Pascalis, De Haan, Nelson, & de Schonen, 1998; Kelly et al., 2007). Indeed, it has very recently been discovered that newborns (<3 days) can perform this task (Turati, Bulf, & Simion, 2008; see figure 32.2B). Moreover, the newborns discriminated only front to three-quarter view changes and not three-quarter to profile, in a pattern somewhat (although not precisely) similar to the three-quarter view advantage that is seen in adults. Finally, newborns demonstrate an inversion effect on discrimination, with babies 1–3 days old discriminating same-view faces without hair upright but not inverted (Turati, Macchi Cassia, Simion, & Leo, 2006).

The newborn discrimination findings strongly suggest that a face representation, tuned to upright and able to support individual-level representation, is present at birth. It seems unlikely that 3 "days" of experience with faces—in fact, a maximum of perhaps 12 hours of visual experience of any kind (newborns sleep 16 hours per day and have their eyes shut during breastfeeding and crying)—would be sufficient for a purely learning-based system to support the level of fine discrimination ability that is observed.

Even more compelling, however, is a recent behavioral study in monkeys (Sugita, 2008). Japanese macaques were raised by human caregivers wearing masks, giving the monkeys no exposure to faces but otherwise normal visual experience in a complex environment. On their *very first* experience with faces (aged 6–24 months), the monkeys showed a preference to look at static photographs of faces over photographs of objects that were equally novel in their visual environment (e.g., cars, houses) and discriminated very subtle differences between individual faces (figure 32.2C) in a habituation paradigm.

A variety of other infant findings also either directly argue that a representational capacity for differentiating individual face structures is present at birth or at least do not reject this conclusion. Newborns (<1 week) prefer faces rated by adults as attractive over unattractive faces when the faces are upright but not inverted (Slater, Quinn, Hayes, & Brown, 2000). Regarding holistic processing, Sugita's (2008) monkeys discriminated spacing changes (figure 32.2C) with almost no prior experience of faces (they had been exposed to faces only during the short face preference task), and five-month-old humans discriminate spacing changes small enough to fall within the normal physical range, upright but not inverted (Hayden, Bhatt, Reed, Corbly, & Joseph, 2007); also babies 6–8 months old show a composite-like effect in which the combination of the inner features of one old face with the outer features of another old face is treated as a new

individual, upright but not inverted (Cohen & Cashon, 2001). At 3 months (although not at 1 month), human infants falsely recognize the average of four studied faces as "old," a phenomenon that is also shown by adults (de Haan, Johnson, Maurer, & Perrett, 2001). Importantly, there are no major behavioral properties of face recognition present in adults that are known *not* to be present in infants; where we have not mentioned properties (e.g., adaptation aftereffects), this is because no relevant data exist, not because infants have been tested and failed to show effects.

Findings of *perceptual narrowing* indicate that (1) a representational capacity for faces that is present at birth can initially be applied to a wide range of faces but that (2) this range gets restricted during the first several months of life to include only the kinds of faces (i.e., species or race) that have been seen in this period. Perceptual narrowing is best known from the domain of language (e.g., Kuhl, Tsao, & Liu, 2003). Infants are born with the ability to discriminate phoneme boundaries from all possible languages in the world (e.g., English and Japanese), but over the first 6–12 months of life, they lose the ability to discriminate phonemes from nonexperienced languages (e.g., Japanese for a child from a monolingual English-speaking family), and even extensive exposure as an adult is usually insufficient to regain native-speaker levels of discrimination and reproduction. For faces, five studies have reported and explored properties of perceptual narrowing. In humans, Pascalis, de Haan, and Nelson (2002) showed that 6-month-old infants could discriminate both human and monkey faces, while 9-month-olds and adults could discriminate only human faces. Kelly and colleagues (2007) reported that Caucasian babies from the north of England, with high exposure to Caucasians but essentially no exposure to African or Asian faces, could recognize individuals (across view change) from all three races at 3 months of age. At 6 months, Caucasian babies could no longer individuate African faces; at 9 months, they had additionally lost the ability to individuate Asians. The Sugita (2008) study described earlier reported that on first exposure to faces, the monkeys not only could discriminate individual monkey faces (other macaques), but also could make extremely fine discriminations among human faces (figure 32.2C). Following 1 month of exposure to a single face type (either human or monkey, involving live interaction for least 2 hours per day), Sugita's monkeys lost the ability to discriminate individuals of the nonexperienced species. Relearning was also difficult; monkeys that were initially exposed only to humans failed to discriminate monkey faces even after subsequently sharing a cage with 10 other monkeys for 11 months. (Note, however, that there is some evidence of flexibility in humans into middle childhood: Korean children adopted to Caucasian Francophone countries at age 3–9 years showed, as adults, better recognition memory for Caucasian faces than for Korean faces; Sangrigoli, Pallier,

Argenti, Ventureyra, & de Schonen, 2005). During human infancy, perceptual narrowing can be avoided by deliberate exposure to face types that the infant would not naturally see; regular exposure to monkey faces beginning at 6 months leads to retained ability to discriminate monkey faces at 9 months (Pascalis et al., 2005). Perceptual narrowing for faces also has an interesting possible link with narrowing for language. Lewkowicz and Ghazanfar (2006) reported that human infants could make cross-modality matches of a monkey vocalization to a picture of a monkey face making that particular sound at 4 and 6 months but that this ability was lost at 8 and 10 months.

Importantly, the perceptual narrowing effects for faces described above indicate only a destructive effect of experience across infancy (i.e., loss of initial ability with other species and other races). In the domain of language, loss of phonetic discrimination ability within nonexperienced languages has been shown to co-occur with an improvement of phonetic discriminability within the experienced language (Kuhl et al., 2006). Thus perceptual narrowing for faces might similarly include enhanced ability to discriminate experienced face subtypes; that is, discrimination for own-species own-race faces might start crude and *improve* with practice. Potentially consistent with this prediction, Humphreys and Johnson (2007) showed that the physical difference between faces that was required to produce novelty preference was smaller in 7-month-olds than in 4-month-olds, indicating that the older babies could either make finer perceptual discriminations or keep these in memory longer across the 1–5 item test delay. Neural systems that are present at birth are often associated with a *critical* (or *sensitive*) *period* (Sengpiel, 2007), requiring environmental input of the appropriate stimulus type within a specified period after birth to avoid being taken over for other purposes. In a classic example, cats are born with cells tuned to all line orientations, but if raised in an environment containing only vertical lines, they lose horizontal-responsive cells and demonstrate a corresponding lack of behavioral sensitivity to horizontal lines. For faces, Le Grand and colleagues report evidence consistent with a critical period for one important aspect of face perception: holistic processing. Congenital cataract patients, specifically people born with dense cataracts disrupting all pattern vision who had the cataracts removed at 2–28 months of age, were tested at ages ranging between 9 years and adulthood. Despite their many years of postcataract exposure to faces, patients who had had early bilateral cataracts showed no composite effect for faces (Le Grand et al., 2004). Also, patients who had had right-eye-only or bilateral cataracts, which produce a deficit of input to the right hemisphere due to the wiring of the infant visual system, showed a later deficit in processing spacing information in faces, while patients who had had left-

eye-only cataracts did not (Le Grand, Mondloch, Maurer, & Brent, 2003), a pattern that is consistent with the normal role of the right hemisphere in holistic processing (Rossion et al., 2000). Interestingly, there does not appear to be a critical period for the ability to discriminate faces per se. Anecdotally, the Canadian cataract patients are not functionally prosopagnosic (Daphne Maurer, personal communication); for example, they report even being able to recognize other-race students when teaching English in Korea (Rachel Robbins, personal communication). Formal testing shows good ability to match novel faces (without view change) both in these patients (Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002) and in an Indian woman whose congenital cataracts were not removed until 12 years of age (Ostrovsky, Andalman, & Sinha, 2006). Also, lack of visual experience with faces for the first 6–24 months in Sugita's (2008) monkeys did not destroy discrimination ability. The reason why a requirement for early visual input exists for holistic processing but not face discrimination remains to be resolved. One possibly relevant observation is that holistic processing could perhaps have a particular role in cross-view recognition (McKone, 2008), and the Canadian cataract patients have a specific problem with recognition of once-seen faces across view changes (Geldart et al., 2002). (Note that the Indian patient and Sugita's monkeys were tested on same-view faces only.)

The behavioral findings reviewed above, demonstrating abilities present at birth, perceptual narrowing and critical periods, are all consistent with a genetically determined "innate" contribution to infant face recognition. In particular, they argue for an innate contribution to face individuation.

Neurally, face individuation in adults is associated with cortical rather than subcortical function. What is the evidence regarding cortical face-processing function in infants? There are few available studies and none in neonates. Results do, however, demonstrate face selectivity and inversion effects. In infant macaques, Rodman, Scalaidhe, and Gross (1993) found that the response magnitude of single units in inferotemporal cortex was lower overall than in adults, but selectivity for form, including face selectivity, was present at the youngest ages that were tested, within 2 months of birth. In humans, a PET study of 2.5-month-olds is somewhat suggestive of face-selective activation in the fusiform gyrus (and other cortical regions), although the infants were not neurologically normal, the statistical threshold was extremely lenient ($p < 0.05$ uncorrected), and the contrast (faces versus blinking diodes) confounds selectivity for faces with responses to visual shape information (Tzourio-Mazoyer et al., 2002). With the use of ERPs, human 3-month-olds exhibit an "N290" component that has larger amplitude for human faces than for monkey faces in the right hemisphere only

(Halit, de Haan, & Johnson, 2003), although adult N170 shows the opposite pattern. At 12 months of age, this N290 was higher in amplitude for inverted faces than for upright faces only for human faces, not monkey faces (like the adult N170). Although the same study reported that this sensitivity to inversion was not found in 3-month-olds, another analysis of the same data using a different method (Johnson et al., 2005) did claim to find such inversion sensitivity. Further, other ERP components (the P400 and the P1) do show inversion effects at 3 months, the youngest age tested (Halit et al., 2003). Similarly, near-infrared spectroscopy (NIRs) responses in 5- to 8-month-old infants are stronger for upright faces than for inverted faces over the right hemisphere only (Otsuka et al., 2007; note the cortical source of this effect was most likely the STS). Overall, the available neural evidence from infants is consistent with the existence of cortical machinery for processing faces within a few months after birth, and there is no evidence to suggest that this is not present earlier.

Taking all findings together, we conclude that infants are born with a rich capacity to represent the structure of upright faces that supports face discrimination rather than merely drawing attention to faces. Results further show that this representation interacts with experience during infancy in particular ways. A probable critical period suggests that holistic processing is "experience-expectant" (i.e., early environmental input is required for its maintenance). Perceptual narrowing shows that early experience restricts the range of faces that can be accommodated; that is, an initial representation of faces is sufficiently broadly tuned to support individuation of all face types including those of other primates, and experience with one subtype of face (own-species, own-race) removes this initial ability with other face types (other-species, other-races) at the same time that it possibly improves perceptual tuning for faces of the experienced subtype. Regarding neural origin of face discrimination in infants, there is evidence of relevant cortical representation by midinfancy, but no data are available regarding whether the discrimination ability that is present at birth is supported by cortical as opposed to subcortical representations.

Development: Four-year-olds to adults

In understanding the interaction of genetic inheritance and learning, investigation of the developmental trajectory of face processing in childhood through adulthood can be informative. When no change is found in a given behavioral or neural measure of face perception in this period, that argues against extended maturation or learning as being necessary for the construction of the adult system. If instead protracted development is observed, this could reflect learning (as often assumed), though crucially it could also reflect

biological maturation (Carey et al., 1980) or an interaction of genetic and experiential factors.

BEHAVIORAL MEASURES OF FACE IDENTITY PERCEPTION   For children 4–5 years and older, it is possible, with care, to adapt adult behavioral paradigms directly and thus to compare child performance with adult performance on exactly the same tasks. For each phenomenon that is established in adults, two empirical questions are of interest. First, is there some age below which children simply do not show that phenomenon at all (i.e., is there *qualitative* change with age)? Second, regarding any phenomena that are observed, when are full maturity levels reached (i.e., is there *quantitative* change with age)?

We consider qualitative change first. Early behavioral research appeared to suggest that core perceptual processes involved in face identification did not emerge at all until quite late in development (e.g., 10 years for holistic processing; Carey & Diamond, 1977; Carey et al., 1980). Unfortunately, researchers in the face neuroscience literature (e.g., Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Aylward et al., 2005; Golarai et al., 2007; Scherf, Behrmann, Humphrey, & Luna, 2007) commonly emphasize only these few early findings, which give an inaccurate representation of the current state of knowledge. In fact, research in the last 15 years has clearly established that all standard adult face recognition effects are present in young children. (Indeed, we showed earlier in the chapter that all phenomena that were tested, including inversion effects, were present in infancy.)

In child-age studies using adult tasks, every key adult property of face recognition that has been investigated has been obtained at the youngest age tested. With respect to holistic processing, these results include the inversion effect on short- and long-term recognition memory (3 years old: Sangrigoli & de Schonen, 2004; 4 years old: Carey, 1981; 5–6 years old: Brace et al., 2001; 7 years old: Flin, 1985), the composite effect (4 years old: De Heering, Houthuys, & Rossion, 2007; 6 years old: Carey & Diamond, 1994; 6 years old: Mondloch, Pathman, Maurer, Le Grand, & de Schonen, 2007), the part-whole effect for upright but not inverted faces (4 years old: Pellicano & Rhodes, 2003; 6 years old: Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998), the part-in-spacing-changed-whole effect for upright but not inverted faces (4 years old: Pellicano, Rhodes, & Peters, 2006) sensitivity to exact spacing between facial features (4 years old: McKone & Boyer, 2006; Pellicano et al., 2006), the perceptual bias to upright in superimposed faces (8 years old: Donnelly, Hadwin, Cave, & Stevenage, 2003), and the internal-over-external features advantage for familiar face identification (5–6 years old: Wilson, Blades, & Pascalis, 2007). Regarding face-space coding, results include

distinctiveness effects on perception at 4 years (McKone & Boyer, 2006) and on memory at 6–7 years (Gilchrist & McKone, 2003), an other-race disadvantage on recognition memory at 3 years (Sangrigoli & de Schonen, 2004) and a recent conference report of adaptation aftereffects in 4–5-year-olds (Jeffrey & Rhodes, 2008). Where early studies did not show effects, this has generally been established to have arisen from methodological problems, the most common one being floor effects on the task in young children (e.g., see Carey et al., 1980, versus Carey, 1981; or Johnston & Ellis, 1995, versus Gilchrist & McKone, 2003). Another case of note is the early suggestion that children could not perform face identification at all in the presence of distracting paraphernalia (Carey & Diamond, 1977); this finding was overturned (Lundy, Jackson, & Haaf, 2001) by simply making the faces larger. (Also note that even adults are sometimes strongly distracted by paraphernalia; Simons & Levin, 1998.) In summary, it is clear that there is no qualitative change in face perception beyond 4–5 years of age; quite possibly, there is none beyond infancy.

The question of whether quantitative change occurs is more difficult to answer. Certainly, performance on just about any experimental task involving faces improves very substantially across childhood and well into adolescence (see figures 32.3A and 32.3B). The crucial issue is how much of this development reflects development in face perception (e.g., in holistic processing or in the fine tuning of face-space) and how much reflects development in other general cognitive factors that are known to improve substantially across this age range and would affect task performance whatever the stimuli (e.g., explicit memory ability, ability to concentrate on the task to instruction). A common bias of face researchers is to assume, given data showing increasing memory for faces with age (e.g., figure 32.3A), that it is face perception that is changing, and that the task type—explicit memory—is irrelevant; yet an implicit memory researcher looking at the same set of data would likely conclude that "explicit memory" is developing and presume that the particular stimulus type—faces—is irrelevant.
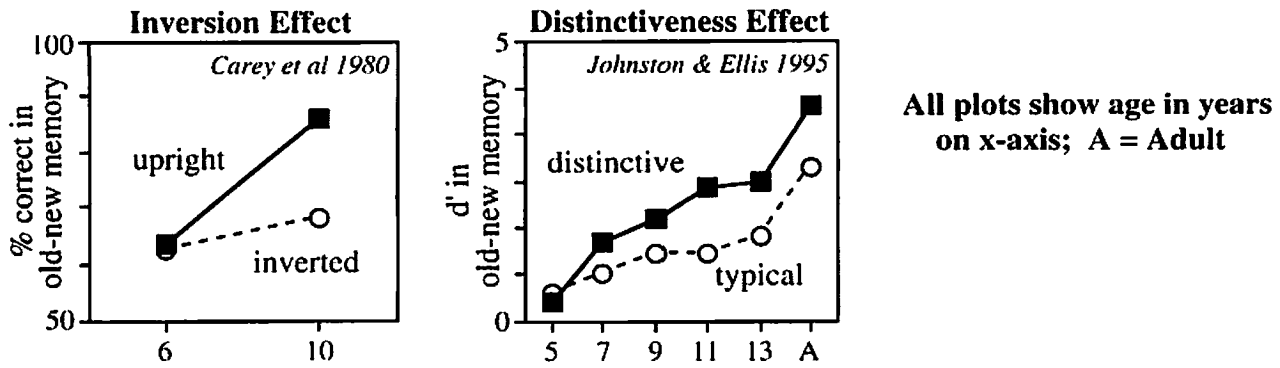
Various attempts have been made to overcome the limitations of simply tracking age-related improvement in raw performance. To our minds, none of these are methodologically satisfactory, and none produce a clear conclusion regarding whether face perception per se does, or does not, improve between early childhood and adulthood. One approach is to compare two conditions across development, for example, asking whether the size of the difference between upright and inverted (or typical and distinctive, etc.) changes with age (e.g., Carey et al., 1980; Johnston & Ellis, 1995). The results of almost all such studies, however, are confounded with overall "baseline" changes across age groups, such that (1) when room to show effects is potentially compressed by approaching floor in young children but is not

restricted (i.e., no ceiling effect) in adults, results seem to suggest quantitative *increases* in the effect of interest with age (figure 32.3A), but (2) when room to show effects is restricted by approaching ceiling in adults but is not restricted in young children (i.e., no floor effects on accuracy or, alternatively, use of a reaction time measure), results seem to show quantitative *decreases* with age (figure 32.3B). Taking seriously the results of the first type of study as showing quantitative development in face perception (as is commonly done) requires also taking seriously the results of the second type of study—apparently leading to the conclusion that face perception gets consistently *worse* between early childhood and adulthood! A further requirement for valid comparison of rates of development for two stimulus types is that performance be equated for the two types in one or other endpoint age group. This is commonly not done. As one example, Mondloch, Le Grand, & Maurer's (2002) finding that sensitivity to feature changes reaches adult levels earlier than spacing changes can be attributed (McKone & Boyer, 2006) simply to the fact that the features changes were easier in adults (that is, performance on an easier stimulus set reaches adult levels before performance on a more difficult stimulus set does). Another general issue in studies comparing faces versus objects, for example, in rate of development (Golarai et al., 2007) or size of inversion effects (Carey & Diamond, 1977; Teunisse & de Gelder, 2003; Aylward et al., 2005), is that in addition to producing very mixed results, the object classes that have been tested to date (houses, scenes, sculptures, shoes) have not been well matched to faces on basic parameters, such as not sharing a first-order configuration (houses, scenes) or not being natural objects (sculptures, shoes).
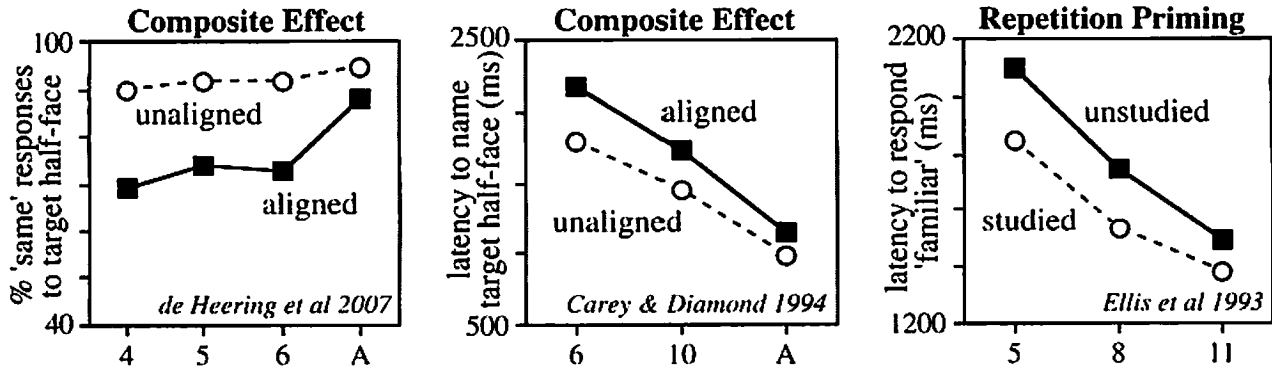
Overall, we conclude that current behavioral evidence demonstrates qualitatively adultlike processing of faces in young children but does not resolve whether processing is quantitatively mature. We note, however, that at least some evidence suggests a conclusion that is likely to be surprising to many readers, namely, that even quantitative maturity might be reached by early childhood. The three studies that appear to have the most suitable methodology, in which baselines were matched across age groups (Carey, 1981; Gilchrist & McKone, 2003) or restriction of range problems was otherwise avoided (Mondloch et al., 2007), all indicate no change in holistic processing (inversion effect: Carey, 1981; composite effect: Mondloch et al., 2007; spacing sensitivity: Gilchrist & McKone, 2003; or distinctiveness effects: Gilchrist & McKone, 2003) between early childhood (4–6 years) and adulthood (figure 32.3C).

NEURAL MEASURES OF FACE IDENTITY PROCESSING (FFA AND N170) As with behavioral studies, we discuss results of neuroimaging and ERP studies in children with respect to two issues: qualitative development and quantitative development.

A. Restriction of range in young children: face effects *increase* with age

Inversion Effect

100

Carey et al 1980

% correct in old-new memory

upright

inverted

50

6   10

Distinctiveness Effect

5

Johnston & Ellis 1995

d' in old-new memory

distinctive

typical

0

5   7   9   11   13   A

All plots show age in years
on x-axis;   A = Adult

B. Restriction of range in adults: face effects *decrease* with age

Composite Effect

100

% 'same' responses to target half-face

unaligned

aligned

40

de Heering et al 2007

4   5   6   A

Composite Effect

2500

latency to name target half-face (ms)

aligned

unaligned

500

Carey & Diamond 1994

6   10   A

Repetition Priming

2200

latency to respond 'familiar' (ms)

unstudied

studied

Ellis et al 1993

1200

5   8   11

C. No range restrictions: face effects are *stable* with age

Inversion Effect

100

% correct in old-new memory

upright

inverted

50

Carey, 1981

4   5   6   10

Spacing Distinctiveness

100

% correct in 2AFC memory

Gilchrist & McKone 2003

spacing changed

unaltered

50

6-7   A

Composite Effect

100

% 'same' responses to target half-face

Mondloch et al 2007
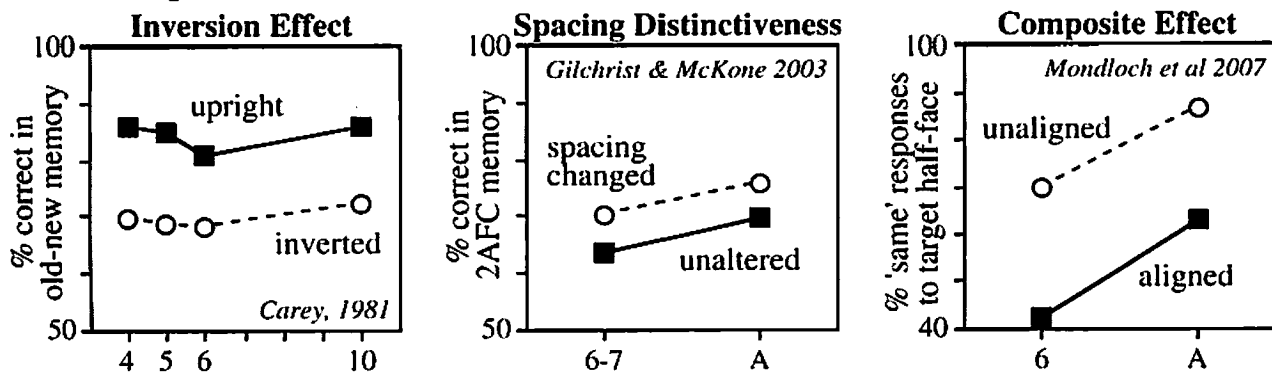
unaligned

aligned

40

6   A

FIGURE 32.3   Behavioral face recognition effects in the preschooler to adult age range. A basic finding is of overall improvement with age: higher accuracy or lower reaction time. Note that in part C, the left and middle plots show studies in which the researchers deliberately removed this trend by using smaller learning set sizes in younger children. Our major point is that apparent developmental trends in the strength of core effects (size of inversion effect, size of composite effect, ability to represent recently seen faces in implicit memory, etc.) depend on whether and how room to show effects is potentially restricted.

Three studies have used fMRI to scan children age 5 years to adult on face and object tasks, enabling these studies to track the existence and size of face-selective regions of cortex (figure 32.4). (A fourth study will not be discussed here because it used such liberal criteria to define "FFAs" that the regions that were so identified were clearly not face-selective even in adults; see figure 1d–f in that study, Gathers et al., 2004.) Considering qualitative effects, evidence of a face-selective FFA has been found in most children at the youngest ages tested. Although no FFA was revealed in young

children by group analyses (in which all subjects are aligned in a common space; 5- to 8-years old: Scherf et al., 2007; 8–10 years old: Aylward et al., 2005), in the two studies reporting individual-subject analyses, Scherf and colleagues found an FFA in 80% of the children in 5- to 8-year-olds (albeit at a very liberal statistical threshold), and Golarai and colleagues (2007) found an FFA in 85% of children in their 7- to 11-year-old group (using a more standard statistical threshold). One study (Passarotti, Smith, DeLano, & Huang, 2007) also reported an inversion effect (a higher response to inverted
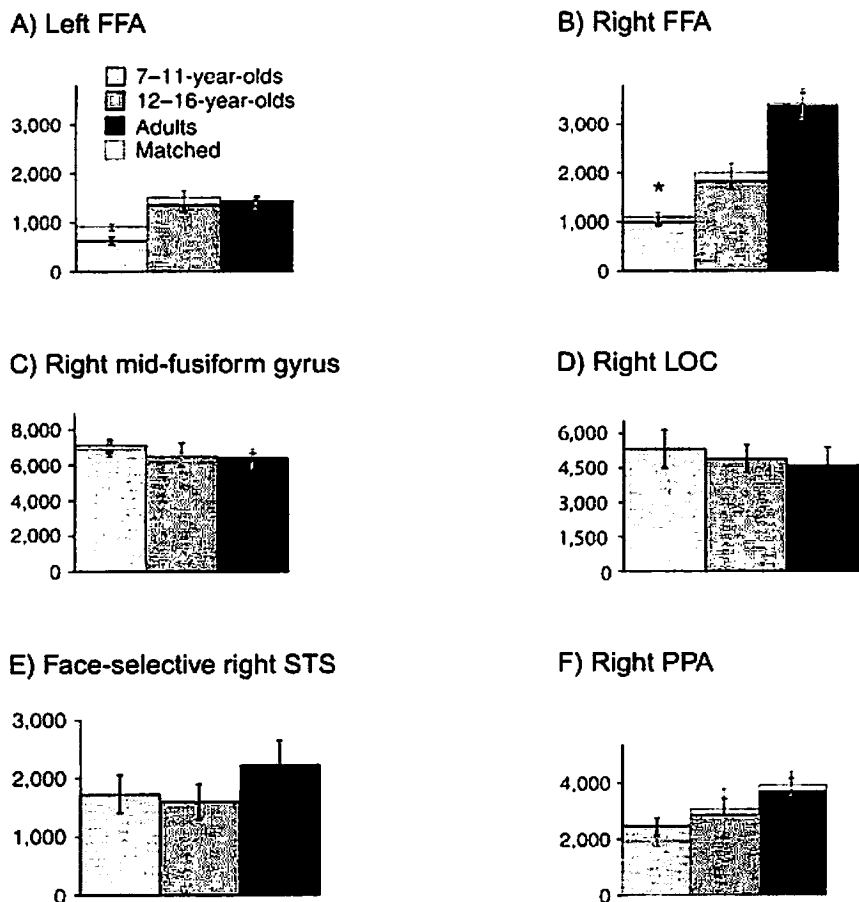
A) Left FFA

- 7–11-year-olds
- 12–16-year-olds
- Adults
- Matched

B) Right FFA

C) Right mid-fusiform gyrus

D) Right LOC

E) Face-selective right STS

F) Right PPA

Figure 32.4   Mean volume across subjects in each age group of individually defined (*A*) left and (*B*) right FFA, (*C*) anatomically defined right mid-fusiform gyrus, (*D*) functionally defined right LOC, and functionally defined (*E*) face-selective right STS and (*F*) right place-selective PPA. Red bars indicated values in subsets of subjects matched for BOLD-related confounds. (From Golarai et al., 2007.) (See color plate 47.)

A   Study 1 : Implicit task

B   Study 2 : n-back

- 4–5 yrs
- 6–7 yrs
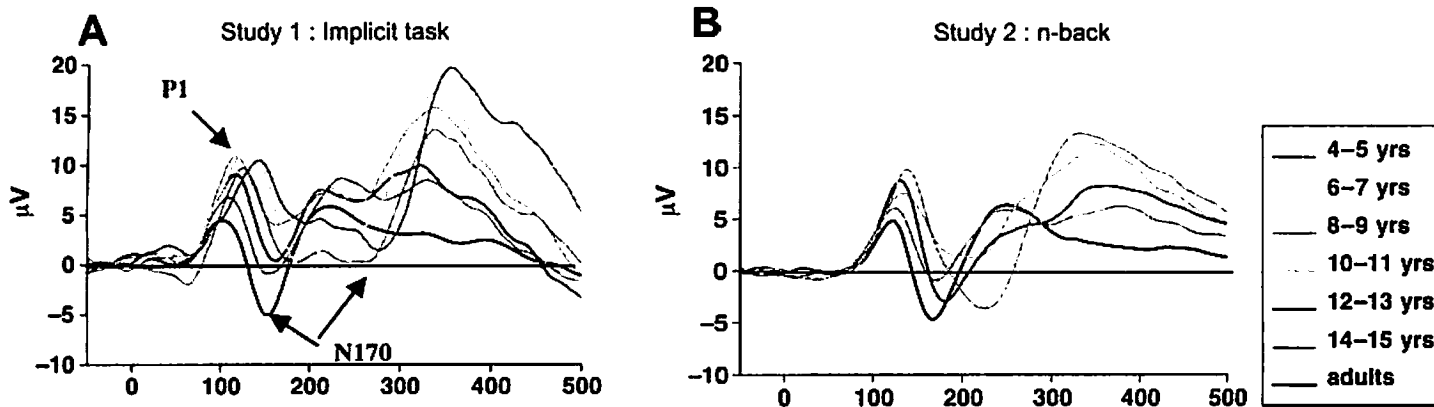- 8–9 yrs
- 10–11 yrs
- 12–13 yrs
- 14–15 yrs
- adults

Figure 32.5   ERPs from right posterior temporal scalp locations in response to face stimuli, separately for each age group. (From Taylor et al., 2004.) (See color plate 48.)

faces than to upright faces) in the region of the right (but not the left) FFA in children 8–11 years of age (and an effect in the opposite direction in adults). Regarding ERPs, young children (like infants) show both face-selective responses and inversion effects upon these (see figures 32.5 and 32.6; Taylor, Batty, & Itier, 2004). These fMRI and ERP findings in children add to the infant data to confirm that at least some form of face-specific neural machinery is established early.

Quantitatively, the neural machinery that is involved in face perception demonstrates substantial changes in face-selective neural responses continuing late into development. In all three fMRI studies, the FFA increases markedly in volume between childhood and adulthood (Aylward et al., 2005; Golarai et al., 2007; Scherf et al., 2007), even though total brain volume does not change substantially after age 5 years. These studies clearly show that the rFFA is still chang-

A
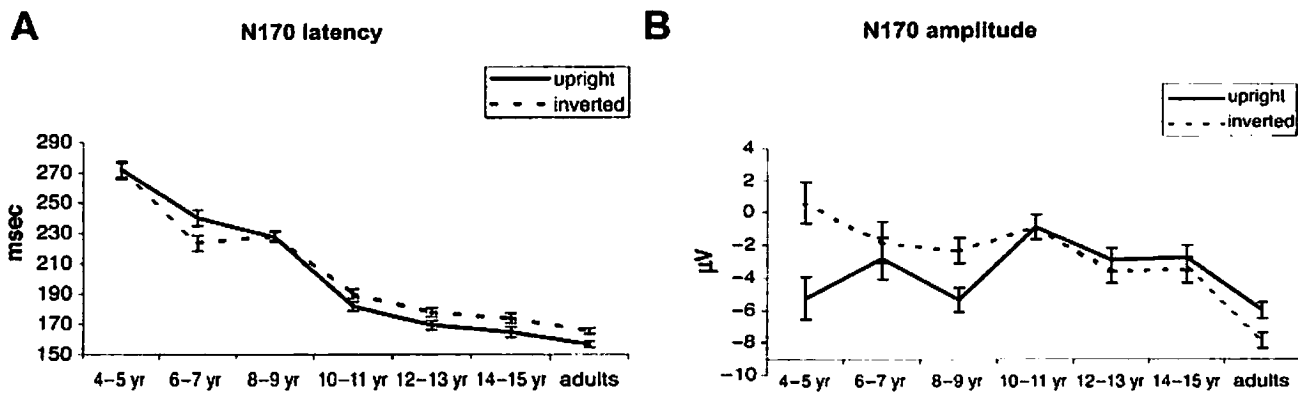### N170 latency

B
N170 amplitude

FIGURE 32.6 Mean N170 latency (left) and amplitude (right) for upright and inverted faces as a function of age. (From Taylor et al., 2004.)

ing late in life—certainly after age 7 and in some studies much later.

Comparing fMRI data across children and adults is fraught with potential pitfalls. Children move more in the scanner and are less able to maintain attention on a task. These or other differences between children and adults could in principle explain the change in volume of the rFFA. However, notably, control areas that are identified in the same scanning sessions do not change with age. For example, object-responsive regions and the scene-selective "parahippocampal place area" in the right hemisphere or rPPA (Epstein & Kanwisher, 1998) did not change in volume from childhood to adulthood (Golarai et al., 2007; Scherf et al., 2007), although somewhat surprisingly, Golarai and colleagues found that the lPPA did increase in volume with age. These findings reassure us that the changes in the rFFA with age are not due to across-the-board changes in the ability to extract good functional data from young children.

Golarai and colleagues (2007) asked how changes in the rFFA relate to changes in behavioral face recognition over development. Right FFA size was correlated (separately in children and adolescents but not in adults) with face recognition memory but not with place or object memory. Conversely, lPPA size was correlated (in all age groups independently) with place memory but not with object or face memory. This double dissociation of behavioral correlations clearly associates the rFFA with changes in face recognition measured behaviorally.

ERP findings are consistent with the evidence from fMRI that the cortical regions that are involved in face recognition continue to change well into the teenage years. Face-related ERPs show gradual changes in scalp distribution, latency, and amplitude into the mid-teen years (figures 32.5 and 32.6). Both the early P1 component and the later N170 component show gradual decreases in latency from age 4 to adulthood. Regarding neural inversion effects, late developmental changes are found with both fMRI and ERP

(see figure 32.5), including a reversal of the direction of the inversion effect between children and adults in both methods (Taylor et al., 2004; Passarotti et al., 2007). Future research might best approach this question not just by measuring mean responses to upright versus inverted faces, but also by using identity-specific adaptation to ask when the better discrimination of upright than inverted faces seen in adulthood emerges (Yovel & Kanwisher, 2005; Mazard et al., 2006).

COMPARING DEVELOPMENT FOR BEHAVIORAL AND NEURAL MEASURES   Taking the findings from the 4-to-adult range together with the infant literature, we can draw the following conclusions. First, the results regarding qualitatively adultlike face processing appear to agree well across behavioral and neural measures; that is, just as all behavioral face recognition effects have been obtained in the youngest age groups tested, face-selective neural machinery as revealed by fMRI, ERPs, NIRs, and single-cell recording has also been found in the youngest children and infants tested. Nonetheless, fMRI data are not available for children younger than 5-8 (pooled together), and the ERP studies in infants and children often go in opposite directions from those in adults. For example, the inversion effect on the N170 switches polarity between childhood and adulthood, as shown in figure 32.6, despite maintaining the same polarity in behavior.

Second, the evidence for quantitative development is less clear. It might be that the improvements with age on behavioral tasks do reflect ongoing development of face perception itself; if so, this could agree neatly with the increasing size of the FFA. As we have noted, however, findings such as those shown in figures 32.3B and 32.3C suggest that behavioral face perception could be fully mature early and that ongoing behavioral improvements with age reflect changes in other, more general, cognitive factors. This view would produce an apparent discrepancy—behavioral maturity arising well before maturity of relevant cortical regions— that would need to be resolved. If this is the case, two ideas

	Newborns / deprived	<= 3 months	Later infancy	4 years	5 years	6 years	7 years	8 years	9 years	10 years	11 years	Adults
Behavioral Properties												
Ability to discriminate individual faces	☺	☺	☺	☺	☺	☺	☺	☺	☺	☺	☺	☺
Inversion effect on discrimination (looking time or recognition memory)	☺	☺	☺	☺	☺	☺	☺	☺	☺	☺	☺	☺
Composite-like effect, upright not inverted			☺									☺
Composite effect				☺	☺	☺	☺	☺	☺	☺	☺	☺
Part-whole effect, upright not inverted				☺	☺	☺	☺	☺	☺	☺	☺	☺
Part-in-spacing-altered-whole effect, upright not inverted				☺	☺	☺	☺	☺	☺	☺	☺	☺
Sensitivity to spacing changes	☺		☺	☺	☺	☺	☺	☺	☺	☺	☺	☺
Inversion effect on spacing sensitivity			☺			☺	☺	☺	☺	☺	☺	☺
Perceptual bias to upright in superimposed faces							☺	☺	☺			☺
Distinctiveness effects				☺	☺	☺	☺	☺	☺	☺	☺	☺
Adaptation aftereffects				☺	☺				☺	☺	☺	☺
Attractiveness preference, upright not inverted	☺											☺
Neural Properties												
Face-selective cells, macaques		☺										☺
Face-selective ERPs		☺		☺	☺	☺	☺	☺	☺	☺	☺	☺
FFA present				☺	☺	☺	☺	☺	☺	☺	☺	☺
Some type of inversion effect on neural response		?	☺	☺	☺	☺	☺	☺	☺	☺	☺	☺
Perceptual Narrowing												
Looking time discrimination of other race/species faces	☺	☺	X									X

FIGURE 32.7 For each property of face processing, we indicate for each age group whether that property is *qualitatively* present (☺), debatable (?), not present (X), or not yet tested (gray). Deprived = monkeys deprived of face input from birth. Note: All references can be found in text except inversion effect on spacing sensitivity aged 6 years to adult is from Mondloch et al. (2002) and adaptation aftereffect aged 9 years to adult is from Pellicano, Jeffery, Burr, & Rhodes (2007).

might be worth exploring. It might be that the measured size of the FFA in children is affected by top-down strategic processing that (for some unknown reason) affects faces and not objects. Another possibility is that the FFA might play some role in the long-term storage of individual faces (e.g., it shows repetition priming; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005; Williams, Berberovic, & Mattingley, 2007) and that the increased size of the FFA could arise simply because people continue to learn faces across life; this idea would have to propose that the number of new faces learned is much greater than the number of new objects.

Conclusion

For decades, conventional wisdom has held that face recognition arises very slowly in development and that experience is the primary engine of this development. The new evidence that we have reviewed here refutes this hypothesis. Impressive face recognition abilities are present within a few days of birth and are present in monkeys who have never seen faces before. Some form of inherited genetic influence is also indicated by Polk and colleagues' imaging study of twins and by the fact that developmental prosopagnosia can run in families. Qualitatively, behavioral findings indicate establishment of all adultlike face recognition effects by 4 years at the latest and in infancy wherever tested; the striking breadth of this evidence is summarized in figure 32.7. The available evidence also indicates early initial establishment of face-selective neural machinery at the cortical level (again see figure 32.7). It is not, however, that experience plays no role in development. Perceptual narrowing of the range of facial subtypes for which discrimination is possible reveals a destructive role for experience. Further, there is a requirement for early-infancy input (consistent with a critical period) for the development of holistic face processing but (mysteriously) not face discrimination.

Three major questions remain for future research. First, it will be critical to determine whether face perception per se improves quantitatively after age 4 years or whether instead improvement in performance after this age reflects improvement in domain-general mechanisms. Second, if face perception itself does improve quantitatively after age 4, what role does experience play in this improvement? A final critical challenge will be to understand the relationship between cognitive and neural development, especially the substantial increase in the size of the FFA.

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