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A critical review of the development of face recognition: Experience is less important than previously believed

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A critical review of the development of face recognition: Experience is less important than previously believed

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Historically, it has been argued that face individuation develops very slowly, not reaching adult levels until adolescence, with experience being the driving force behind this protracted improvement. Here, we challenge this view based on extensive review of behavioural and neural findings. Results demonstrate qualitative presence of all key phenomena related to face individuation (encoding of novel faces, holistic processing effects, face-space effects, face-selective responses in neuroimaging) at the earliest ages tested, typically 3−5 years of age and in many cases even infancy. Results further argue for quantitative maturity by early childhood, based on an increasing number of behavioural studies that have avoided the common methodological problem of restriction of range, as well as event-related potential (ERP), but not functional magnetic resonance imaging (fMRI) studies. We raise a new possibility that could account for the discrepant fMRI findings—namely, the use of adult-sized head coils on child-sized heads. We review genetic and innate contributions to face individuation (twin studies, neonates, visually deprived monkeys, critical periods, perceptual narrowing). We conclude that the role of experience in the development of the mechanisms of face identification has been overestimated. The emerging picture is that the mechanisms supporting face individuation are mature early, consistent with the social needs of children for reliable person identification in everyday life, and are also driven to an important extent by our evolutionary history.

Keywords: Face recognition; Development; Age of maturity; Behaviour; Functional magnetic resonance imaging; Event-related potential.

Adults can identify a specific individual face, distinguishing this person from hundreds of others despite wide variations in facial appearance that result from changes in viewpoint, lighting, emotional expression, and hairstyle. This typically requires a mere glance, belying the substantial computational

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demands that must underlie the ability. The importance of face identification skills in everyday life is highlighted by the social difficulties encountered when these skills are compromised (e.g., in developmental prosopagnosia or autism spectrum disorder; Schultz, 2005; Yardley, McDermott, Pisarski, Duchaine, & Nakayama, 2008). Adult ability to individuate thousands of faces is supported by specialized perceptual processes, typically applied to faces but not other visual objects, and by specialized neural mechanisms including face-selective regions of cortex (McKone, Kanwisher, & Duchaine, 2007). How do these processes develop?

Traditionally, our exquisite face identification skills have been viewed primarily as the result of extensive experience during infancy, childhood, and adolescence, with adult-like abilities emerging relatively late in development. From the 1970s to the mid-1990s, an extreme version of this late maturity view was dominant (*encoding switch hypothesis*; Carey & Diamond, 1977), which proposed that specialized mechanisms of face perception were not even qualitatively present until 10 years of age, and that extended lifetime experience with faces was driving this slow development (Carey & Diamond, 1994). This was taken as consistent with claimed evidence that, with enough experience (e.g., 10 years) of making within-class discriminations, other object classes (e.g., dogs) could become "special" and processed like faces (Diamond & Carey, 1986; but see Brants, Wagemans, & Op de Beeck, 2011; Harel, Gilaie-Dotan, Malach, & Bentin, 2010; McKone, et al., 2007; Robbins & McKone, 2007). From the mid-1990s on, new evidence that many aspects of face processing were qualitatively present at younger ages forced a modification of the late maturity view, with theoreticians proposing only late quantitative maturity of a subset of aspects of face perception (Mondloch, Le Grand, & Maurer, 2002). However, the driver of this late maturity was still extended experience. Thus, over the past 35 years, it has been argued that adult-like face recognition does not reach full maturity until adolescence, and that the causal mechanism for this maturity was 10 or more years of practice.

In this review, we argue that modern evidence, and careful attention to methodological issues, supports a very different conclusion. We argue the data no longer support a theory in which the only face representation present at birth is a mere orienting device (Morton & Johnson, 1991), and that good discrimination of individual faces takes many years of practice to achieve. Rather, we argue that adult expertise results from face-specific perceptual mechanisms that require at most 5 or so years of face experience to become fully mature (and possibly less), and that it also has genetic and innate contributions.

Our review begins (see following section: "Children reach adult behavioural performance levels very late in development. Why?") by noting that performance on laboratory tests of face identification improves dramatically throughout childhood and into adolescence, and evaluating two theories of why adult performance is reached so late (*general cognitive development theory* and *face-specific perceptual development theory*). The second section ("A role for nature: Genetic contributions and innateness in face individuation") reviews the evidence of innateness (defined here as "present at birth") and of genetic determinants of face recognition ability. The third section ("What effects of experience are there?") describes situations in which experience does influence face recognition, including other-race effects.

We raise several core methodological and logical errors that frequently limit the conclusions that can be drawn from developmental studies of face recognition. These include a failure to make the logical distinction between laboratory *performance* and actual ability in everyday life (*competence*); the presence of restrictions of range (including floor or ceiling effects) that prevent valid quantitative comparisons across wide age ranges; and a general observation that task difficulty has a substantial impact on the age at which the task purports the ability to be "mature". We also raise a more subtle methodological issue affecting the neuroimaging literature—namely, the potential effects of using adult-sized head coils on children in functional magnetic resonance imaging (fMRI).

We conclude that the role of experience in the development of the mechanisms of face identification has been substantially overestimated. The emerging picture is that mechanisms supporting face recognition are mature early and are also driven to an important extent by our evolutionary history.

CHILDREN REACH ADULT BEHAVIOURAL PERFORMANCE LEVELS VERY LATE IN DEVELOPMENT. WHY?

We first describe, and assess theories of, the basic developmental course of face recognition. Perhaps the most striking aspect of typical development is the late age at which performance on face tasks reaches adult levels. Despite children having many years of social interaction—across infancy with caregivers, across childhood and into adolescence with a wide variety of friends, schoolmates, and teachers—performance on laboratory face recognition tasks does not reach adult levels until adolescence. This late performance maturity occurs on both memory (Carey, Diamond, & Woods, 1980; O'Hearn, Schroer, Minshew, & Luna, 2010) and discrimination tasks usually considered "perceptual" because they minimize memory demands (e.g., same–different decision; Mondloch et al., 2002).

Before we present our review, two general points are worth making. First, although the historical explanation of late performance maturity was that core perceptual processes did not emerge until quite late in development (10 years for "holistic processing"; Carey & Diamond, 1977; Carey et al., 1980), the early behavioural research supporting this idea has been clearly refuted. It is thus unfortunate that even quite recent articles, particularly in the neuroimaging literature, have sometimes emphasized only these few early findings (e.g., Aylward et al., 2005; Golarai et al., 2007; Scherf, Behrmann, Humphreys, & Luna, 2007; Scherf, Luna, Avidan, & Behrmann, 2011).

Second, researchers almost universally refer to developmental improvement in task *performance* as an improvement in children's face recognition "*abilities*". However, it is important to emphasize that these data are all from experimental laboratory tasks. The extent to which the age-related improvement in laboratory task performance reflects improvement in real face recognition abilities, as used in everyday life, is not known. Moreover, this can be very difficult to ascertain (see section entitled "Quantitative maturity: Is there any ongoing development of face perception mechanisms beyond early childhood?").

In the remainder of this section, we describe two theories of late performance development: (a) face-specific processing matures early and ongoing task improvement reflects development of general cognitive factors; and (b) face recognition itself continues to develop late, via development of face-specific perceptual mechanisms observed in adults. We then evaluate these theories with respect to, first, the age at which face mechanisms emerge *qualitatively* (i.e., the youngest age group in which a given mechanism is present) and, second, the age at which they become mature *quantitatively* (i.e., the youngest age at which they operate at adult levels of efficiency).

The explanations

General cognitive development theory
This theory (Carey, 1981; Crookes & McKone, 2009; Gilchrist & McKone, 2003; McKone & Boyer, 2006; Mondloch, Maurer, & Ahola, 2006; Pellicano, Rhodes, & Peters, 2006; Want, Pascalis, Coleman, & Blades, 2003) proposes that perceptual coding of faces is fully mature early in development, and all subsequent development on experimental task performance results from development of other general factors. While the theory does not state an exact age that perceptual face coding reaches maturity, 5 years has been suggested as a maximum. The specific general factors that produce later task improvement are presumed to depend on the task and can include: ability to concentrate on the task and avoid distractions; ability to narrow the focus of visual attention to small stimuli; ability to use deliberate task strategies; metacognition (e.g.,

ability to know when one has successfully learned); and general perceptual development (e.g., vernier acuity as relevant to judging distances between facial features).

All these abilities develop substantially across childhood, and most improve further into adolescence (Betts, Mckay, Maruff, & Anderson, 2006; Bjorklund & Douglas, 1997; Davidson, Amso, Anderson, & Diamond, 2006; Flavell, 1985; Flavell & Wellman, 1977; Pastò & Burack, 1997; Skoczenski & Norcia, 2002). Further, all have clear potential to contribute to face task performance. To illustrate, children may fail to attend to the task on some trials due to high distractibility, which is difficult to avoid even in the most child-friendly designs. Consequently, children's accuracy will be pushed towards chance, and reaction times will be increased, even if their underlying face recognition skills were equal to those of adults. Thus, the debate between general cognitive development theory and face-specific perceptual development theory (discussed next) is not whether general cognitive development contributes to development in performance on laboratory face tasks but whether, once general cognitive factors are accounted for, there is any development in face perception per se.

Face-specific perceptual development theory

This theory (e.g., Carey & Diamond, 1977; Carey et al., 1980; de Heering, Rossion, & Maurer, 2012; Golarai et al., 2007; Mondloch et al., 2002; Scherf et al., 2011) acknowledges that infants show some early proficiency with faces, but argues that face task performance reaches adult levels late because (a) face perception mechanisms themselves continue to develop into late childhood and adolescence, and (b) the cause of this development is ongoing experience with faces. These ongoing improvements in face processing are presumed to contribute directly to improvements on face perception tasks (e.g., sequential face discrimination) and also to affect face memory (e.g., by allowing more robust encoding of novel faces, or more precise comparisons to distractors at retrieval). Researchers have raised four specific proposals about exactly what perceptual mechanisms might be developing. These are:

ability to perceptually encode novel faces; holistic/configural processing; face-space coding; and specialized neural mechanisms for faces as seen in adults. We describe each of these ideas in more detail in the following review of the development of these mechanisms.

Predictions of the general and face-specific explanations

The general cognitive development theory predicts that all key aspects of face recognition should be both qualitatively present and quantitatively mature early in childhood. In contrast, the face-specific perceptual development theory would be supported if either qualitative or quantitative development of face mechanisms was observed. We begin by considering qualitative development.

Qualitative maturity: Presence of key face-coding mechanisms early in development

In strong contrast to the early (1970s to mid-1990s) view that children under age 10 did not possess basic face mechanisms, more than 25 years of research has now tested essentially every key property of adult face recognition and has established that each is present at the youngest age tested, including even infants where investigated. Where early studies did not show an effect in a particular age group, subsequent studies have established that the failure to detect the effect resulted from methodological problems, the most common being floor effects in young children (e.g., for holistic processing assessed via the inversion effect, see Carey et al., 1980 vs. Carey, 1981; or for distinctiveness effects in face-space, see R. A. Johnston & Ellis, 1995 vs. Gilchrist & McKone, 2003). Table 1 summarizes the key findings (references follow in the review). Infant findings come from looking-time measures. Results for children 3 years and older come from studies testing children on the same tasks as adults, sometimes adapted slightly to reduce overall difficulty and avoid floor effects in the youngest age groups (e.g., children learn faces in smaller sets).

Table 1. *Core face recognition effects qualitatively present early in development*

	Newborns	Later infancy	3 years	4 years	5 years	6 years	7 years	8 years	9 years +
Basics - encoding of novel faces									
Discrimination of individual faces	☺	☺	☺	☺	☺	☺	☺	☺	☺
Recognition across view change	☺	☺				☺		☺	☺
Recognition despite paraphernalia (hats, etc)			?				☺		☺
Holistic/configural properties									
Inversion effect on discrimination	☺	☺	☺	☺	☺	☺	☺	☺	☺
Disproportionate inversion effect (faces > objects)			☺	☺	☺		☺		☺
Composite effect	?	☺	☺	☺	☺	☺		☺	☺
Composite effect faces not objects			☺	☺	☺				
Composite effect, upright not inverted		☺				☺			☺
Part-whole effect, upright not inverted				☺	☺	☺	☺	☺	☺
Part-in-spacing-altered-whole effect, upright not inverted				☺	☺				
Sensitivity to spacing changes		☺	☺	☺	☺	☺	☺	☺	☺
Inversion effect on spacing sensitivity		☺		☺	☺	☺	☺	☺	☺
Thatcher illusion, upright not inverted	☺					☺	☺	☺	☺
Perceptual bias to upright in superimposed faces							☺	☺	☺
Internal-over-external features advantage in familiar faces				☺	☺	☺	☺	☺	☺
Face-space properties									
Distinctiveness effects		☺		☺	☺	☺	☺	☺	☺
Atypicality bias			☺	☺	☺	☺	☺	☺	☺
Face-space dimensions (e.g., multidimensional scaling)				☺			☺	☺	☺
Adaptation aftereffects (figural)				☺	☺	☺	☺	☺	☺
Adaptation aftereffects (identity)					☺	☺	☺	☺	☺
Norm-based adaptation aftereffects				☺	☺	☺	☺	☺	☺
Attractiveness effects	☺	☺	☺	☺	☺	☺	☺	☺	☺
Other race effects		☺	☺	☺	☺	☺	☺	☺	☺
Neural Properties									
Fusiform Face Area				☺	☺	☺	☺	☺	☺
N170 (or precursor in infants)		☺		☺	☺	☺	☺	☺	☺
Right hemisphere advantage		☺		☺	☺	☺	☺	☺	☺
Inversion modulates neural response		☺				☺	☺	☺	☺
Face-selective cells, macaques		☺							

Note: A very wide range of core face recognition effects are present early in development. ☺ =phenomenon tested and found to be present; grey cell=not yet tested in children or babies this young; white cell=not specifically tested at this age but can be assumed to be present given presence at younger age; ?=a study has tested this, but results unclear as to whether phenomenon is present or not. Note that we have not included viewpoint tuning, which appears to undergo qualitative change in infancy at approximately 7 months (see section entitled "Coding of profile views"). The section, "Qualitative maturity: Presence of key face-coding mechanisms early in development" gives references for each result and description of tasks. "Later infancy" generally means 3 to 12 months; exact ages given in the first section.

Basic ability to encode novel faces

As a source of face-specific perceptual development, late development in ability to encode novel faces was proposed by Carey (1992, p. 95): "young children do not form representations of newly encountered faces as efficiently as do adults". A more modern variant is that children may have specific difficulty in encoding faces in a manner that allows generalization of recognition across viewpoint change (Mondloch, Geldart, Maurer, & Le Grand, 2003).

The evidence clearly indicates that the ability to encode novel faces is present very early in

life, including cross-view recognition. Key findings are:

Discrimination of individual faces. Ability to discriminate similar faces (same age, sex, race, either without hair[1] or all with similar hair) above chance has been demonstrated using habituation-then-novelty-preference paradigms in newborns (Pascalis & de Schonen, 1994; Turati, Bulf, & Simion, 2008; Turati, Macchi Cassia, Simion, & Leo, 2006) and in older infants (e.g., 3, 6, 9 m.o.,[2] Kelly et al., 2009; Kelly et al., 2007; Pascalis, de Haan, Nelson, & de Schonen, 1998). In children, face discrimination has been demonstrated following a single learning trial in sequential matching (e.g., 3 y.o., Sangrigoli & de Schonen, 2004a), memory (e.g., 4 y.o., Carey, 1981), and implicit memory (repetition priming, 5−6 y.o., Crookes & McKone, 2009).

Recognition across view change. Recognition of a face learned in a single image generalizes to another view in newborns (between front and three-quarter, although not three-quarter and profile; Turati et al., 2008) and in older infants (3, 6, 9 m.o., Kelly et al., 2009; Kelly et al., 2007; 4 m.o., Turati, Sangrigoli, Ruel, & de Schonen, 2004; 3, 6 m.o., Pascalis et al., 1998). In children, above-chance cross-view recognition occurs in simultaneous and sequential matching (6, 8, 10 y.o., Mondloch et al., 2003; 7, 8−12, 12−15 y.o., P. J. Johnston et al., 2011), and memory (9−12 y.o., O'Hearn et al., 2010).

Recognition despite paraphernalia. Early claims suggested that children could not recognize face identity in the presence of distracting paraphernalia (hats, etc.; Carey & Diamond, 1977). However, simply making the faces larger revealed this ability (7, 10 y.o., Lundy, Jackson, & Haaf, 2001; plus similar nonsignificant trend in 3 y.o., marked as "*?*" in Table 1).

Holistic processing

Development in holistic/configural processing (henceforth referred to as holistic processing) has been heavily investigated as a potential source of face-specific perceptual development. In adults, the exact nature of holistic processing is not fully understood, but it is widely agreed (e.g., Maurer Le Grand, Mondloch, 2002; McKone & Yovel, 2009; Rossion, 2008) to (a) include strong perceptual integration of information across the whole face, (b) include processing of the "second-order" ways in which a face deviates from the basic shared first-order configuration found in all faces (i.e., two eyes, above nose, above mouth), and (c) be strongly sensitive to face orientation, with holistic processing present for upright faces but largely absent for inverted faces. One theory proposes that the key aspect of "second-order" information is exact spacing between face features (e.g., nose−mouth distance) and that spacing coding is a separate subcomponent from perceptual integration (Maurer et al., 2002); another proposes a single holistic representation of all facial information including both spacing information and second-order information about exact shape of local features (e.g., eye shape, nose size, etc.; McKone & Yovel, 2009; Tanaka & Farah, 1993; Yovel & Duchaine, 2006).

The classic theory that holistic processing did not emerge until age 10 (Carey et al., 1980) has been rejected by the evidence. There is no support for the old view that children use a feature-based method for recognizing faces. Rather, there is substantial evidence of early presence of all aspects of holistic coding (including second-order relations). Moreover, like adults', children's holistic processing disappears with face inversion. Findings are:

Inversion effect on discrimination. In adults, ability to discriminate similar faces is reduced when they are turned upside down (e.g., Yin, 1969). Although inversion effects on face recognition are not directly

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[1] Many studies exclude hair because it is a simple cue that can be used to recognize photographs without requiring face processing (e.g., prosopagnosics use hair cues in experiments even when they cannot recognize people in real life; Duchaine & Nakayama, 2006).

[2] Where a study tested separate age groups and found a clear effect present in each, we list all ages separately (e.g., "3, 6, 9" m.o.); where a study showed an effect in a combined age group but did not split by exact age, we indicate the age range of the group (e.g., "3−6" y.o.). Note, m.o. = month old; y.o. = year old.

diagnostic of holistic processing (because processing style is not directly measured in either orientation), a lack of inversion effect in development could reasonably be taken as evidence of a lack of holistic processing. However, orientation sensitivity is present throughout development. Babies discriminate faces upright but fail to discriminate the same stimuli inverted (newborns, Turati et al., 2006; 5–6 m.o., Fagan, 1972; across view change, 4 m.o., Turati et al., 2004). In children, discrimination is better upright than inverted in both short- and long-term memory tasks (3 y.o., Sangrigoli & de Schonen, 2004a; 3 y.o., Macchi Cassia, Kuefner, Picozzi, & Vescovo, 2009; 4, 5, 6, 10 y.o., Carey, 1981; 5–6 y.o., Brace et al., 2001; 7 y.o., Flin, 1985; 7 y.o., Crookes & McKone, 2009).

Disproportionate inversion effect (faces > objects). In adults, the inversion effect for faces is usually substantially larger than that for within-class discrimination of objects (for review, see McKone et al., 2007). In children, this pattern occurs in sequential discrimination (shoes, 3–4 and 5 y.o., cars, 3–4 y.o. in males only and in all 5 y.o., Picozzi, Macchi Cassia, Turati, & Vescovo, 2009; shoes 9–10 y.o., Teunisse & de Gelder, 2003) and long-term memory (labradors, 7 y.o., Crookes & McKone, 2009; houses, 10 y.o., Carey & Diamond, 1977).

The composite effect. We now turn to more direct measures of holistic processing, specifically the "perceptual integration" aspect for those favouring a subcomponents view. In adults, combining the top half of one individual (e.g., Barack Obama) with the bottom half of another (e.g., Will Smith) creates the percept of a new person. For famous faces, this results in longer naming times for a target half (e.g., top) when the halves are aligned than in a control misaligned condition (e.g., Young, Hellawell, & Hay, 1987). For novel faces, the composite effect is demonstrated by reduced accuracy in perceiving that two identical top halves, combined with different bottom halves, are the *same* when aligned as when misaligned (e.g., Le Grand, Mondloch, Maurer, & Brent, 2004).

In children, the composite effect occurs on both the naming and the same–different versions

(unfamiliar faces 4, 5, 6 y.o., de Heering, Houthuys, & Rossion, 2007; 6 y.o., Mondloch, Pathman, Maurer, Le Grand, & de Schonen, 2007; 8–13 y.o., Susilo, Crookes, McKone, & Turner, 2009; and familiar faces 6, 10 y.o., Carey & Diamond, 1994), as well as in a variant using a two-alternative forced-choice (2AFC) response (3, 4, 5 y.o., Macchi Cassia, Picozzi, Kuefner, Bricolo, & Turati, 2009). Infants also show a composite effect for top–bottom combinations (3 m.o., Turati, Di Giorgio, Bardi, & Simion, 2010; newborn results were ambiguous, hence the "?" in Table 1) and for inner–outer feature combinations (inner features of one old face combined with outer features of another old face is treated as a novel individual, 6–8 m.o., Cohen & Cashon, 2001).

Composite effect for faces not objects. In adults, the composite effect is present for faces but not other objects (e.g., dogs, Robbins & McKone, 2007). Children show this adult-like pattern (effect for faces but not cars: 3, 4, 5 y.o., Macchi Cassia, Picozzi, et al., 2009).

Composite effect, upright but not inverted. In adults, the composite effect is found for upright faces but is absent or greatly reduced for inverted faces (e.g., Robbins & McKone, 2003; Young et al., 1987). This same pattern is found in children (6, 10 y.o., Carey & Diamond, 1994), and infants (6–8 m.o., Cohen & Cashon, 2001; Ferguson, Kulkofsky, Cashon, & Casasola, 2009).

Part–whole effect, upright not inverted. The part–whole effect is also commonly taken as a reasonably direct measure of holistic integration. In the part–whole effect, memory for a face part (e.g., Bill's nose) is poorer in isolation (Bill's nose versus John's nose) than in the context of the original whole face (Bill's nose in Bill's face versus John's nose in Bill's face). Children show the adult-like pattern (Tanaka & Farah, 1993) of a whole-over-part advantage for upright but not inverted faces (4, 5 y.o., Pellicano & Rhodes, 2003; 6, 8, 10 y.o., Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998).

Part–in–spacing–altered–whole effect, upright not inverted. In this variant, memory for a face part (Bill's nose) is poorer in a spacing-altered version of the face (Bill's nose in Bill's face with the eyes shifted further apart) than in the original unaltered face. Like adults (Tanaka & Sengco, 1997), children show this effect for upright but not inverted faces (4, 5 y.o., Pellicano et al., 2006).

Sensitivity to spacing changes and inversion effect on spacing sensitivity. Changes in spacing between facial features are detected by children (3, 4 y.o., Macchi Cassia, Turati, & Schwarzer, 2011; 4 y.o., McKone & Boyer, 2006; 4, 5 y.o., Pellicano et al., 2006; 4 y.o., Mondloch & Thomson, 2008; 6, 8, 10 y.o., Mondloch et al., 2002; 6–7 y.o., Gilchrist & McKone, 2003; 8 y.o., Mondloch et al., 2006; 6–8, 8–10, 10–12 y.o., Baudouin, Gallay, Durand, & Robichon, 2010) and by infants (5 m.o., Hayden, Bhatt, Reed, Corbly, & Joseph, 2007). Inversion disrupts this performance (most of the same studies, youngest ages: 4, 5 y.o., Pellicano et al., 2006; and 5 m.o., Hayden et al., 2007).

Thatcher illusion, upright not inverted. In adults, flipping the orientation of eyes and mouth relative to the rest of the face leads to a percept of a bizarre face upright but not inverted (P. Thompson, 1980), an illusion taken as evidence of holistic processing. The illusion, and its orientation sensitivity, is found in children (6–10 y.o., Lewis 2003; 6, 7, 8, 10 y.o., Donnelly & Hadwin, 2003) and newborns (Leo & Simion, 2009).

Perceptual bias to upright in superimposed faces. Like adults (Martini, McKone, & Nakayama, 2006), children perceive an upright face more strongly than an inverted face when the two are overlaid in transparency (6–10 y.o., Donnelly, Hadwin, Cave, & Stevenage, 2003).

Internal–over–external features advantage in familiar faces. Adults' memory for familiar faces relies more on internal features than on external features such as hairstyle (Ellis, Shepherd, & Davies, 1979), a result sometimes attributed to holistic

processing. This same pattern occurs in children (4, 8, 14 y.o., Ge et al., 2008; 5–6, 7–8, 10–11 y.o., Wilson, Blades, & Pascalis, 2007).

Face-space coding

Given the clear evidence of early presence of holistic processing, recent interest has increased in *face-space* coding as a possible source of face-specific perceptual development. Face-space is a multidimensional perceptual space with the following properties: Dimensions code physical attributes that are useful in differentiating faces; each individual face is a point; the centre is the average face; and distinctive faces lie further away from the centre, while typical faces lie closer to the average (e.g., Valentine, 1991). The face-space concept has been valuable in explaining a range of phenomena (see below) not accounted for by holistic processing. Regarding development, a key assumption of standard face-space theories is that the dimensions of face-space arise through experience and that tuning continues throughout life (e.g., Goldstein & Chance, 1980; R. A. Johnston & Ellis, 1995; Valentine, 1991). Theoretically, it has been proposed that children's face-space could use fewer dimensions than that of adults, or the same dimensions but differently weighted, or could use exemplar-based coding (absolute values on dimensions) rather than norm-based coding (deviation vector from average), or could have weaker ability to update the norm of face-space based on recent experience, or could code discriminations along each dimension less finely; finally, it has been proposed that occupation of children's face-space by fewer exemplars might functionally affect face perception (Chung & Thomson, 1995; Hills, Holland, & Lewis, 2010; Humphreys & Johnson, 2007; Jeffery et al., 2011; R. A. Johnston & Ellis, 1995; Nishimura, Maurer, Jeffery, Pellicano, & Rhodes, 2008).

Again, the evidence regarding face-space coding does not indicate any qualitative development with age. That is, results show the presence of all adult phenomena at the youngest age tested. Findings are:

Distinctiveness effects. Face-space coding predicts better memory for distinctive than typical faces

(due to lower exemplar density further from the average and thus fewer confusable neighbours), but faster classification as a face for typical faces (due to closeness to average). Children show both these effects: memory advantage for distinctive faces (6–7 years, Gilchrist & McKone, 2003; 9, 11, 13 y.o., R. A. Johnston & Ellis, 1995); face classification advantage for typical faces (5, 7, 9, 11, 13 y.o., R. A. Johnston & Ellis, 1995). Children also appear to perceive distinctiveness in a similar way to adults: They can, above chance, choose the more distinctive face in a pair defined by *adult* distinctiveness ratings (4 y.o., McKone & Boyer, 2006). Distinctiveness can also be varied by *caricaturing* a face (exaggerating the way it deviates from the average, i.e., increasing the "identity strength") and anticaricaturing (reducing identity strength by morphing the face towards the average). Children judge caricatures as more distinctive than anticaricatures (6, 8, 10 y.o., Chang, Levine, & Benson, 2002). Children, like adults, are also quicker to name caricatured versions of previously learned faces than the original face or anticaricatured versions (6, 8, 10, y.o., Chang et al., 2002). Infants also distinguish caricatures and anticaricatures, with longer longest looks to the former (6 m.o., Rhodes, Geddes, Jeffery, Dziurawiec, & Clark, 2002), and distinguish average from nonaverage face length (with average preferred; 6–7 m.o., L. A. Thompson, Madrid, Westbrook, & Johnston, 2001).

Atypicality bias. Like adults, children perceive a 50/50 morph between a typical and a distinctive face as more strongly resembling the distinctive (atypical) "parent" (3–4, 5–6, 7–8, 9–10, 11–12 y.o., Tanaka, Meixner, & Kantner, 2011).

Face-space dimensions (e.g., multidimensional scaling, MDS). Multidimensional scaling on similarity ratings can be used to calculate the structure of the underlying perceptual face-space. MDS reveals a face-space in children similar to that of adults: Typical faces fall closer to the centre than more distinctive faces; the number of dimensions in the solutions is the same; and dimensions code similar facial attributes (e.g., nose–mouth distance, face width; 7–8, 9–10, 11–13 y.o., Pedelty, Levine, & Shevell, 1985; 8 y.o., Nishimura, Maurer, & Gao, 2009). Consistent with use of adult-like dimensions, children, like adults, choose the most distinctive of two faces when these differ only in spacing between features, or only in local features (4 y.o., McKone & Boyer, 2006).

Adaptation after-effects (figural). Face after-effects are typically explained as a shift in the perceived average of face-space to reflect the types of faces to which one has been exposed. In adults, "figural" after-effects occur with adaptation to consistent distortions of face structure: Adapting to a face with high eyes makes eyes appear low in a normal face (Robbins, McKone, & Edwards, 2007), or adapting to a centre-contracted face makes a normal face appear expanded (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003). Such after-effects occur in children (expansion, 4–6 y.o., and eye height, 4–5 y.o., Jeffery et al., 2010; expansion, 5, 8 y.o., Short, Hatry, & Mondloch, 2011; expansion, 8 y.o, Anzures, Mondloch, & Lackner, 2009; eye height, 6–12 y.o., Hills et al., 2010). As in adults, the after-effects survive change in stimulus size between adaptor and test, discounting a low-level vision explanation (4–5 y.o., Jeffery et al., 2010).

Adaptation after-effects (identity). In the identity after-effect, adaptation to one individual (e.g., Dan) makes the average face appear like its opposite in face-space (i.e., "anti-Dan", an individual with all facial attributes opposite to those of Dan), while adaptation to another individual (e.g., Jim) shifts the perceived average towards that face's opposite (anti-Jim). Like adults (Leopold, O'Toole, Vetter, & Blanz, 2001), children demonstrate identity after-effects (5, 6, 7, 8–9 y.o., Jeffery et al., 2011; 8 y.o., Nishimura et al., 2008; 8 y.o., Pimperton, Pellicano, Jeffery, & Rhodes, 2009; 8–14 y.o., Pellicano, Jeffery, Burr, & Rhodes, 2007), including with size-changes (8 y.o., Pimperton et al., 2009; 7 y.o., Jeffery et al., 2011).

Norm-based adaptation after-effects. In adults, two after-effect patterns have been used to argue that face-space uses norm-based coding (each individual coded as a deviation from the average) rather than exemplar-based coding (each individual coded via their absolute value on each face dimension without reference to an average; Rhodes & Jeffery, 2006; Robbins, McKone, & Edwards, 2007). Both norm-based patterns are shown by children. After-effects are larger from adaptors far from the average than from adaptors closer to the average (eye height, 4–5 y.o., Jeffery et al., 2010; identity, 7 y.o., Jeffery et al., 2011). And, after-effects are larger from adaptors falling along the face-space trajectory running from the target through the centre ("opposites", e.g., anti-Dan for Dan) than from adaptors lying off this trajectory ("nonopposites", e.g., anti-Jim for Dan; 8 y.o., Nishimura et al., 2008).[3]

Attractiveness effects. Like adults, children rate faces closer to the average (centre of face-space) as more attractive than faces further from the average (11, 14 y.o., Saxton, Debruine, Jones, Little, & Roberts, 2009). Like adults (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003), in adaptation studies children rate an unaltered face structure as most attractive prior to adaptation, and the most attractive stimulus shifts towards the new perceived average after adaptation (8 y.o., Anzures et al., 2009; 5, 8 y.o., Short et al., 2011). Individuals of all ages also prefer, or rate as most attractive, faces with the height of the internal feature block experienced most often by their age group (i.e., high for infants, low for young children, normal from puberty when children's faces take on adult proportions; 5 m.o., Geldart, Maurer, & Henderson, 1999; 3, 4, 9, 12 y.o., Cooper, Geldart, Mondloch, & Maurer, 2006), again suggesting ability to update a face-space average that in turn drives perceived attractiveness.

In other attractiveness effects, newborns show attractiveness preference in natural faces, driven by internal features of the face, and occurring for upright not inverted faces (Slater, Bremner, et al., 2000; Slater, Quinn, Hayes, & Brown, 2000).

Other-race effect (ORE). Adults discriminate other-race faces more poorly than own-race faces, a result often explained as tight clustering of other-race faces in face-space (Valentine, 1991). This ORE is present in children (3, 4, & 5 y.o., Sangrigoli & de Schonen, 2004a; 5–6 & 8–9 y.o., Pezdek, Blandon-Gitlin, & Moore, 2003; 6–14 y.o., de Heering, de Liedekerke, Deboni, & Rossion, 2010) and in infants aged 6 months and older (Kelly et al., 2009; Kelly et al., 2007). It has been reported in 3 m.o. but at this age was abolished with a small amount of exposure to other-race faces (Sangrigoli & de Schonen, 2004b). Adults also show *race-contingent after-effects*: Adaptation can cause observers to simultaneously perceive normal Caucasian faces as expanded and normal Asian faces as contracted (Jaquet, Rhodes, & Hayward, 2007). This indicates partially distinct neural coding of different race faces. The same effect occurs in children (5, 8 y.o., Short et al., 2011).[4]

Specialized neural mechanisms for faces

So far, we have demonstrated early qualitative presence of three key face attributes: ability to encode novel faces, holistic processing, and face-space. The fourth possible source of face-specific perceptual development is the face-selective neural mechanisms found in adults. Note that our interest here is in cortical-level mechanisms because the topic of our review is children's face individuation skills (for review of subcortical mechanisms proposed to support orientation to faces in early infancy, see Johnson, 2005). Results for children and babies support early qualitative presence of adult-like neural mechanisms.

The fusiform face area (FFA). In adults, the FFA in the midfusiform gyrus responds 2–3 times more strongly to faces than to within-class

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[3] This result holds when the opposite and nonopposite adaptors are equally dissimilar from the target and when the test trajectory for nonopposite adaptors is between nonopposite-and-target rather than opposite-and-target (8–9 y.o., Jeffery et al., 2011).

[4] Although note that contingency in 5-year-olds was driven by adaptation only to one of the races.

discrimination of objects (houses, hands, flowers, cars, birds; e.g., Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher, McDermott, & Chun, 1997). It has been the primary focus in child fMRI research because it is reliably identified in almost all adults.

Results for ages 10 and up are clear-cut. Like adults, both adolescents and preadolescents show an FFA (8–11 y.o., Passarotti, Smith, DeLano, & Huang, 2007; 9.8–12 y.o., Joseph, Gathers, & Bhatt, 2011; 10–12 y.o., Passarotti et al., 2003; 11–14 y.o., Scherf et al., 2007; 11–14 y.o., Scherf et al., 2011; 12–14 y.o., Aylward et al., 2005; 12–16 y.o., Golarai et al., 2007; 7–17 y.o., Peelen, Glaser, Vuilleumier, & Eliez, 2009). This is found even with quite small sample sizes (e.g., 10 in three of the eight cited studies) and with group-defined FFAs (Aylward et al., 2005; Joseph et al., 2011; Passarotti et al., 2003; Passarotti et al., 2007), which are less sensitive than individual-defined regions of interest (ROIs; because a region can be missed when averaging over individuals with different exact anatomical locations).

Results in younger children vary, but overall make a strong case for presence of an FFA at the earliest ages tested when the more powerful designs are used. Using group-defined ROIs and only small sample sizes, the first studies did not report an FFA (8–10 y.o. with 8, Aylward et al., 2005; 5–8 y.o. with 10, Scherf et al., 2007). However, with power improved by using either individually defined ROIs or group designs with larger sample size (thereby making group analyses less affected by individual differences in anatomical location), all recent studies have identified an FFA in mid childhood (7–11 y.o. 20, Golarai et al., 2007; 7–11 y.o. 22, Pelphrey, Lopez, & Morris, 2009; 5–9.7 y.o. 23, Joseph et al., 2011) and even earlier where tested (4–5.8 y.o. 15, Cantlon, Pinel, Dehaene, & Pelphrey, 2011; 5–8 y.o. 10, individual ROI, Scherf et al., 2007).

The N170. The adult N170 is a face-selective event-related potential (ERP) peak over occipito-temporal sensors, usually maximal on channels T5 (left hemisphere) and T6 (right hemisphere). The peak is larger for faces than for within-class

discrimination of objects. Its neural source probably includes the FFA, but also area STS (superior temporal sulcus), thought to be involved in processing the dynamic aspects of faces (e.g., gaze, expression) rather than identity (Dalrymple et al., 2011; Itier & Taylor, 2004; Sadeh, Podlipsky, Zhdanov, & Yovel, 2010).

The N170 occurs in children (4 to 14 y.o., Taylor, McCarthy, Saliba, & Degiovanni, 1999, 1999; 4 to 15 y.o., Taylor, Edmonds, McCarthy, & Allison, 2001; 4 to 10 y.o., Henderson, McCulloch, & Herbert, 2003), even when the N170 is identified in individual participants to avoid conflating it with the later N250 component (4–6 y.o., 6–8 y.o., 8–10 y.o., and older age groups, Kuefner, de Heering, Jacques, Palmero-Soler, & Rossion, 2010). In infants, N170 precursors (N290 and P400) are present and are stronger for human than for monkey faces (3 m.o., Halit, de Haan, & Johnson, 2003; 6 m.o., de Haan, Johnson, & Halit, 2003).

Right hemisphere advantage. In adults, right-handers' recognition of facial identity is more accurate following brief presentation to the left visual field, LVF (right hemisphere) than to the right visual field, RVF (left hemisphere; e.g., Ellis & Shepherd, 1975), the FFA is usually larger in the right hemisphere (rFFA) than the left (lFFA; e.g., Kanwisher et al., 1997), and the face-selective N170 is also strongest over the right hemisphere (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996).

The same right hemisphere dominance is found in development. A LVF advantage occurs for face identification in children (5, 7, 11 y.o., Young & Ellis, 1976; 7–9 y.o, Marcel & Rajan, 1975; 7, 10, 13 y.o., Young & Bion, 1980; all participants right-handed) and infants (4–10 m.o., de Schonen & Mathivet, 1990), and also for perceiving the Thatcher illusion (right-handed, 8–10 & 11–13 y.o., Anes & Short, 2009). In fMRI, right hemisphere dominance is also observed (i.e., rFFA larger than lFFA; 7–11 y.o., Pelphrey et al., 2009; 10–12 y.o., Passarotti et al., 2003; 11–14 y.o., Scherf et al., 2007; note, we evaluated only studies that reported at least 90% right-handers). In ERP, right

hemisphere dominance for the face-selective N170 is present from early childhood (all age groups 4 y.o. and up, 92% right-handed, Kuefner et al., 2010), and the infant precursor N290 shows a different magnitude to human and monkey faces only in the right hemisphere (3 m.o., Halit et al., 2003). In infant near-infrared spectroscopy (NIRS), response is stronger for upright faces than for control objects (vegetables) in the right hemisphere, but not in the left (5–8 m.o., Otsuka et al., 2007).

Inversion modulates neural response. Differential neural response to upright and inverted faces occurs in adults. It also occurs in development, although the direction of the effect does not always remain stable across age. In fMRI, the adult pattern is a higher response to upright than to inverted faces in the FFA (Yovel & Kanwisher, 2005; but see Haxby et al., 1999), but the opposite direction has been found in children (8–11 y.o., Passarotti et al., 2007). In ERPs, the adult pattern is a larger N170 for inverted than for upright faces (e.g., Bentin et al., 1996): The infant precursor N290 shows this direction (3 m.o., Johnson et al., 2005; see also Halit et al., 2003), but children aged 4–9 years show the other direction (larger N170 upright than inverted, Taylor, Batty, & Itier, 2004). In babies, the face-selective NIRS response (faces > objects) is significantly larger for upright than for inverted faces (5–8 m.o., Otsuka et al., 2007).

Face-selective cells in monkeys. Adult macaques show strong face-selective responses from temporal lobe neurons ("face cells"), which cluster into face-selective patches visible with fMRI (Tsao et al., 2006). In infant macaques, face selectivity of single units is present at the youngest ages tested (<2 m.o., Rodman, Scalaidhe, & Gross, 1993).

Individuation in fMRI. One study has tested whether children's FFA, like adults', shows discrimination of individual faces. Scherf et al. (2011) used fMR-adaptation, looking for greater blood-oxygen-level-dependent (BOLD) contrast to blocks of different-identity faces than to blocks of the same repeated face image. Results showed discrimination in the FFA in adolescents

(11–14 y.o.; specifically lFFA, but note that handedness was not reported). This was not found in 6–10 y.o., but this conclusion is questionable for reasons outlined later (see section "Evidence arguing fMRI conclusions in children younger than 10 years can sometimes be wrong, even when studies meet current 'best practice'").

Coding of profile views

We have separated out profile face views because this is the only situation where converging evidence indicates a qualitative change with age. This occurs during infancy (not childhood). Adults can recognize faces in any viewpoint, although they are slower for profiles than for front or three-quarter view (McKone, 2008). In human babies, coding of profiles has not been observed in early to mid infancy. Young babies discriminate identity in front- and three-quarter-view faces (e.g., newborns, Turati et al., 2006; 3 m.o., Kelly et al., 2009) but do not discriminate profiles (5 m.o., Fagan, 1979). Older babies do discriminate profiles (7 m.o., Fagan, 1976, Fagan, 1979). In converging evidence, face-selective neural response with NIRS (face > objects) is found for front-view faces but not profiles at 5 m.o., while older babies do show face-selective response for profiles (8 m.o., Nakato et al., 2009). Regarding generalization across views, recognition of faces in profile that were previously learned in front or three-quarter view is not found in newborns (Turati et al., 2008), it is established in 12 m.o. (Rose, Jankowski, & Feldman, 2002), and there is contradictory evidence regarding 7 m.o. (present, Fagan 1976; absent, Rose et al., 2002). Overall, these results argue for: a lack of profile coding at 5 months; followed by coding sufficient to support within-profile discrimination by 7–8 months; and extension to support generalization across views by 12 months, or perhaps earlier.

Summary of qualitative presence

In summary, there is broad agreement across studies that adult mechanisms of face perception are qualitatively present early in development (Table 1). In behavioural studies, this includes phenomena associated with all aspects of holistic processing (including sensitivity to "second-order relations" defined as spacing between face features), all aspects of basic

individuation (for front and three-quarter views), and all aspects of face-space coding. Indeed, research over the last 20 years has gradually pushed back the age at which all these phenomena have been observed and has now reached children of 3–4 years, in most cases, and infancy where tested. In neural studies, results are slightly more variable but are overall consistent with the conclusion: The FFA and N170 are present early; a right hemisphere advantage is present early; face-selective cells are present early; and the only partially discrepant result is that neural inversion effects, while present early, sometimes appear in the opposite direction from those in adults. The only replicated qualitative change that our review revealed is a lack of coding of faces in profile view in early infancy that emerges in later infancy.

The conclusion supported by the modern evidence is strikingly different from the early ideas of Carey et al. (1980) that basic mechanisms of face perception, such as holistic processing, were not present at all below 10 years and thus required a decade of experience to emerge. The results we have reviewed argue that much less experience is required to develop core face mechanisms. Indeed, it may be that no experience at all is required for some (e.g., holistic processing has now been demonstrated even in newborns; Thatcher illusion in Leo & Simion, 2009; also see the section entitled "A role for nature: Genetic contributions and innateness in face individuation").

Quantitative maturity: Is there any ongoing development of face perception mechanisms beyond early childhood?

To return to what explains the late age at which laboratory task performance reaches adult levels, our review so far indicates no *qualitative* development of face-specific perceptual mechanisms in the early childhood to adult range. However, to fully discriminate the general cognitive development and face-specific perceptual theories, we need to address the rather trickier question of whether there is *quantitative* development in face-specific mechanisms. For example, the question now is not merely is there an FFA in 6–10-year-olds, but is it as large as that in
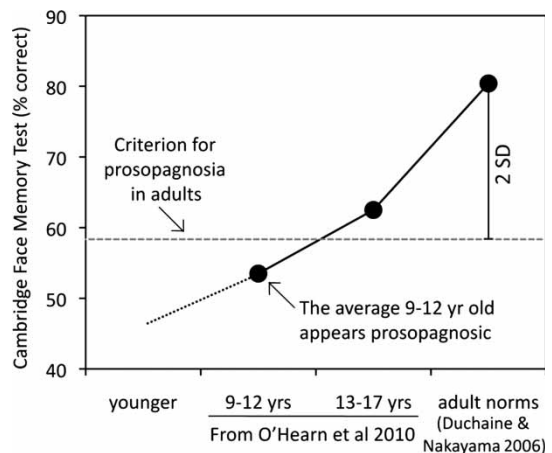

Figure 1. *Are all young children prosopagnosic? The plot illustrates that, if we were to believe that all (or even a substantial proportion of) age-related improvement on face tasks reflects improvements in face recognition, then the average child would be so poor they would be classified as prosopagnosic even at age 9–12. Note that younger children would perform more poorly again. Data are from typical developing children in O'Hearn et al. (2010), with adult norms from the larger-N control sample in Duchaine and Nakayama (2006). We use standard conservative criterion for prosopagnosia—that is, poorest 2% of population (score poorer than 2 SDs below the mean). Note: Cambridge Face Memory Test (Duchaine & Nakayama, 2006) chance score = 33%.*

adults, or not is there a composite effect in 5-year-olds, but is it as strong as that in adults?

To address quantitative change, this section first notes that "children are not prosopagnosic". Then, for behavioural, N170, and fMRI studies in turn, we summarize previous findings, describe methodological issues that invalidate the usual interpretation of many of these findings as evidence for quantitative development (although note that many studies still remain valid and useful regarding qualitative presence), and discuss the results of the studies that we argue best overcome these methodological difficulties.

Children are not prosopagnosic: Laboratory tasks dramatically underestimate children's real-world face recognition abilities

Previously, we made the point that general cognitive skills contribute to performance on laboratory face tasks and improve with age. But, how great is this contribution? Recent results from the

Cambridge Face Memory Test (CFMT)—the most valid (and reliable) method of measuring real-world face recognition ability in adults (Bowles et al., 2009; Duchaine & Nakayama, 2006; McKone et al., 2011; Wilmer et al., 2010)—argue that it is actually substantial, and that laboratory tasks dramatically underestimate children's real world face recognition abilities. Figure 1 plots results from typically developing pre-adolescents (9–12 y.o.) and adolescents (13–17 y.o., O'Hearn et al., 2010) on the adult CFMT (i.e., comparing performance of adults and children on exactly the same task, as is typical of the developmental face recognition literature). If cognitive development makes only a minor contribution to task performance, then children might perform more poorly than adults—due either to the lack of cognitive maturity or to immature face perception systems—but we would expect this disadvantage to be relatively small. This is because typical 9–12-year-olds, in everyday life, do not have significant trouble learning and remembering faces, unlike adults with prosopagnosia who have significant real-world difficulties recognizing faces of even very familiar individuals. In contrast, Figure 1 shows that, relative to adult performance, the CFMT would diagnose children's face recognition as being so poor that the average 9–12-year-old would qualify as prosopagnosic (i.e., > 2 standard deviations below the adult mean). Further, the level of apparent "disability" would be even worse in younger children (who also have no trouble learning their schoolmates).

These results argue it is not just a small amount of the age-related development on laboratory tasks like the CFMT that reflects general cognitive development, but a large amount.

Age of quantitative maturity in behavioural studies: Avoiding restriction of range shows maturity by early childhood

We now review previous quantitative findings, beginning with behavioural tasks. Almost all studies reporting behavioural measures have included statistical tests for quantitative comparison across age and have interpreted the results as theoretically meaningful: For example, if there is

a significant Age × Inversion interaction, then the authors conclude that the size of the face inversion effect increases with age, and thus holistic processing improves. There are dozens of studies including this type of analysis (a few recent references are de Heering et al., 2012; Macchi Cassia et al., 2011; Meinhardt-Injac et al., 2011). The conclusion drawn in the vast majority was that the face mechanism under investigation improved with age. Unfortunately, this conclusion is often invalid, due to a basic methodological issue.

This issue we refer to as the *restriction of range problem* (as raised by Carey, 1981; Chung & Thomson, 1995; Crookes & McKone, 2009). When attempting to cover a large age range (e.g., 5 y.o. to adults), it is rare to be able to design a task that is neither too difficult for the youngest children nor too easy for the adults. In the extreme case, of course, this can lead to complete floor or ceiling effects, where there is no potential to see any difference between conditions because performance is at chance, or perfect, in both conditions. Disturbingly, even some recent studies published in good journals have included quantitative comparisons made across groups in the presence of clear floor effects in the youngest children or ceiling effects in the adults (e.g., Macchi Cassia, Picozzi et al., 2009; Meinhardt-Injac et al., 2011); in our view, it should be automatic on the part of authors (and reviewers and readers) to avoid drawing any conclusions from the affected age groups.

Equally important, but more subtle, is that even without a complete floor or ceiling effect, there can still exist the possibility of a restriction of range problem (Figure 2). This is relevant because many of the key perceptual components of face recognition are demonstrated using differences between conditions (e.g., inversion effects, composite effects).

In Figure 2A, let's assume we have conducted a study on the size of the inversion effect on recognition memory for faces. In adults, a typical size of this inversion effect is 20% (e.g., upright = 85% correct, inverted = 65% correct). This means there is restricted range to see an adult-sized inversion effect as soon as children's upright performance
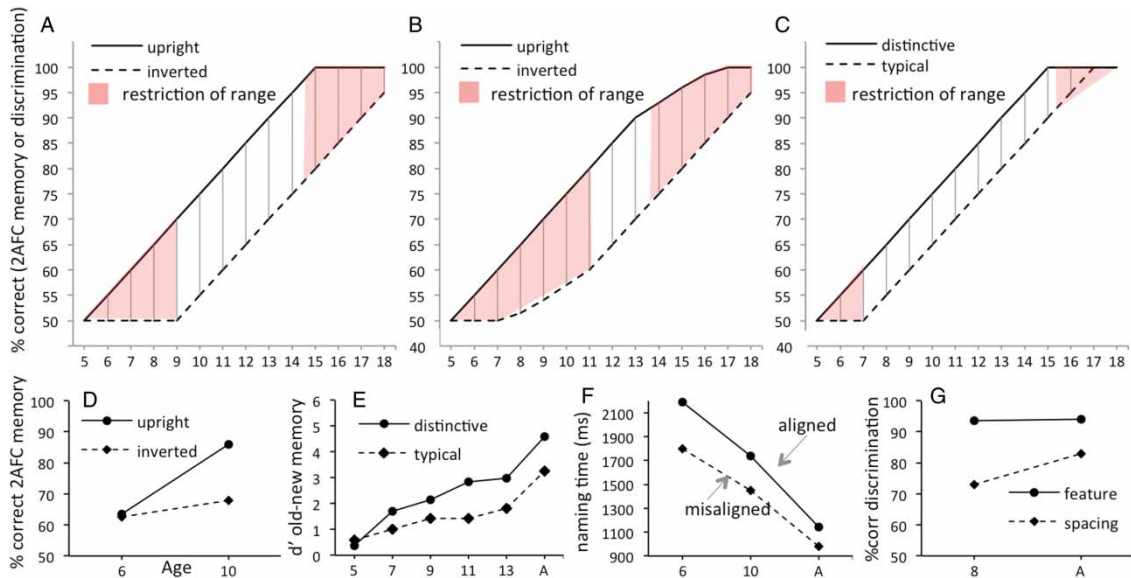
Figure 2. *The methodological issue of restriction of range in behavioural studies. (A) Assuming the underlying inversion effect on face memory (difference between upright and inverted) were a 20% reduction in accuracy, then setting the task difficulty to suit the 9−14-year-old age range leads to restriction of range to show this size of inversion effect in 5−8-year-olds and in 15−18-year-olds. This plot assumes that range becomes restricted only when one condition fully reaches chance (50% correct) or scale maximum (100%). (B) On the alternative assumption that there is some flattening out of measured values before 50% or 100% are reached, then the restriction of range problem affects even more ages (5−10-year-olds and 14−18-year-olds). (C) If the underlying difference between conditions is smaller, as is usually the case in adult studies for the distinctiveness effect (i.e., difference in memory for distinctive faces and typical faces), then the restriction of range problem affects fewer ages (5−6-year-olds and 16−18-year-olds). (D & E) Examples of real data where there is evidence of restriction of range in younger age groups that could potentially account for the Age × Condition interaction without needing to propose that the effect of interest genuinely increases in size with age. (D) In Carey et al. (1980) the inversion effect is 17.5% in the 10-year-olds. To be able to measure a difference of this size in the 6-year-olds would have required being able to measure inverted accuracy below chance. (E) A similar example for the distinctiveness effect from R. A. Johnston and Ellis (1995). The measure was d′ rather than percentage correct, so chance is 0. (F) Although we have illustrated the issue using accuracy, restriction of range also affects reaction time: Generally, two conditions will show a smaller difference between them when the overall reaction times are faster. In developmental studies, this often leads to effects appearing to be smaller in adults than in children, as illustrated for the composite effect (difference in naming times for aligned and misaligned composites) from Carey and Diamond (1994). (G) Studies arguing that one condition (e.g., detection of changes to spacing–between–features) matures later than another (detection of changes to local features) are also prone to drawing this conclusion falsely from restriction of range where the two conditions are not matched for difficulty (data from Mondloch et al., 2004). Notes: We have illustrated these issues for faces, and comparing two conditions in typically developing children, but they potentially apply widely in developmental psychology (e.g., for comparison of two types of verbal stimuli; for comparison of typically developing and atypically developing groups). A = adult; all other x-axis values are age in years. 2AFC = two-alternative forced-choice. To view a colour version of this figure, please see the online issue of the Journal.*

drops below 70% (assuming chance is 50%; i.e., upright performance of 69% in children would mean that to demonstrate an inversion drop of 20% would require being able to measure performance below chance).[5] This problem, widely ignored

in the developmental face literature, means that the difference between two conditions in one age group may falsely appear to be larger or smaller than in another simply because overall performance on the task changes with age, and so one end of the age

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[5] Thus, even showing that conditions are significantly greater than chance in the youngest group does not ensure that restriction of range has been avoided.

range or the other has a problem with restriction of range.

Unfortunately, as illustrated in Figures 2A–2C, there is no obvious way of determining when range restriction has occurred. This is partly because the exact way in which restriction might affect the functions for the two conditions being compared is unknown: For example, functions might be shaped like those in Figure 2A (straight lines until one hits chance or 100%) or like those in Figure 2B (the two functions begin to curve towards one another some distance prior to hitting chance or 100%). It is also partly because the mean accuracy level at which range restriction starts to occur will probably vary depending on the specific conditions compared: As illustrated in Figure 2C, if the memory difference between two conditions (e.g., distinctive and typical faces) is smaller, then restriction of range may not occur until more extreme age groups (cf. Figure 2A). Together, this means it is impossible to set out a rule for avoiding restriction of range; for example, it could not be said that "restriction is avoided if the mean of Condition A and Condition B is not greater than 90%, or less than 60% (in a 2AFC test)" or similar.

Turning to empirical findings, Figures 2D–2F illustrate three examples where restriction of range almost certainly occurred. Our observation is that the literature contains many cases like D and E, where there is potential restriction of range in the young age groups. Such studies typically find a larger difference between the conditions at older ages (e.g., Carey et al., 1980; de Heering et al., 2012; R. A. Johnston & Ellis, 1995). However, interpreting these studies as good evidence that the effect of interest genuinely increases with age implies that one would also need to accept as equally valid the conclusion of the (fewer) studies that have potential restriction of range present in the older age groups. As illustrated by one example in Figure 2F (Carey & Diamond, 1994; also see Ellis, Ellis, & Hosie, 1993; de

Heering et al., 2007; Macchi Cassia, Picozzi et al., 2009), such studies typically find that the difference between the conditions of interest gets smaller with age; if this result were to be taken as valid in the way that the patterns in D and E have automatically been assumed to be valid, then the conclusion would be that face perception mechanisms (e.g., holistic processing) weaken with age. Most researchers have been rightly hesitant to draw this conclusion.

Another case where restriction of range is a potential issue is where the interest is not in comparing the difference between two conditions at each age, but instead in asking which of two conditions develops faster or matures (reaches adult levels) first. Example questions have been whether there is "special" development for faces, compared to nonface objects, and whether children have late maturity of discriminating "second-order relations" in faces (spacing between features, as opposed to local feature shape). Here, restriction of range can become a problem where the two conditions being compared are not matched in difficulty at one end of the age range,[6] because results are open to the interpretation that it is simply the easier condition which reaches adult level first because this condition approaches ceiling performance at an earlier age (e.g., Golarai et al., 2007; Mondloch, Dobson, Parsons, & Maurer, 2004; Mondloch et al., 2002).

Because a very high proportion of the literature is affected by one or more of these methodological problems, we argue that most studies do not, in fact, address the question of whether face-specific mechanisms develop quantitatively with age.

So, what happens when these problems are avoided? We plot results of studies that have done so in Figures 3–5. These studies avoided potential problems associated with restriction of range via various methods. Some (indicated with green dot; Figures 3A & 3B) compare rate of development for faces versus objects where stimulus sets are matched for difficulty (e.g., by matching performance in the youngest age groups).

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[6] Matched accuracy requires that two conditions have equivalent means *and* that these means are not approaching ceiling or floor. It is not sufficient to show that two conditions have near-perfect accuracy in adults (e.g., 97% versus 99%): The "matching" (unless also present on reaction times) could reflect simply a ceiling effect.

Others (red dot; Figures 3C, 3D, 3F, 3M & 4B) experimentally matched performance across ages in a "baseline" condition (e.g., upright faces, for an inversion study), for example by using longer presentation times, or smaller learning set sizes, for the younger age groups. Others used exactly the same procedure across the adults and children, and the conditions of interest just happened to produce no sign of restriction of range across the ages tested (blue dot ; Figures 3E, 3G-I, 3K & 4A), or show some suggestion of possible restriction of range but had no significant Age × Condition interaction (pink dot ; Figures 3J & 3L). Others (yellow dot; Figures 4C-L) used methods not prone to restriction of range because the measure is not accuracy (where children's poorer concentration can push scores artificially towards chance); rather, there is no "right answer", and participants choose the face or identity that best matches their perception (atypicality bias; and shifts in face perceived as most normal in adaptation after-effects).

Inspection of Figures 3–5 indicates a remarkable convergence of results. In contrast to the classic interpretation of the literature, findings suggest that face perception mechanisms are not only qualitatively present in early childhood, but also quantitatively mature at an early age. This includes *ability to perceptually encode a novel face*, where Figures 3A–3B do not support the face-specific perceptual development theory prediction that performance should improve more steeply with age for faces than for a comparison object class (Crookes & McKone, 2009; P. J. Johnston et al., 2011),[7] and

Figure 3C shows no change in the amount of implicit memory (repetition priming benefit) for novel faces between 5–6 years and adult (Crookes & McKone, 2009). It also includes all aspects of *holistic/configural processing*. Beyond the earliest age tested (generally 4–7 years), results show: no increase with age in the *inversion effect* for faces (Figures 3D–3E); no increase with age in the *disproportionate inversion effect* for faces versus objects (Figures 3F–3G); no increase with age in the *composite effect* (Figure 3H; there is no floor effect because chance is not 50%); no significant increase with age in the *part–whole effect* (Figures 3I–3J); no increase with age in the *inner face advantage* in identifying personally familiar faces (Figure 3K); and no increase with age in *sensitivity to spacing* between features (Figures 3L–3M).

Results also imply no quantitative change in *face-space*. This includes the ORE (Figure 4A; Pezdek et al., 2003; also Sporer, Trinkl, & Guberova, 2007) and memory enhancement arising from increased *distinctiveness* (spacing distinctiveness, Figure 3M; local feature distinctiveness such as making eyebrows bushier, Figure 4B). From 5–6 years, the *atypicality bias* (extent to which a 50% morph looks more like the distinctive rather than the typical parent) does not increase (Figure 4C; bias was weaker in 3–4-year-olds); this argues that exemplar density varies with distance-from-centre to the same degree in children and adults. In adaptation after-effect experiments comparing children and adults on exactly the same tasks (Figures 4D–4L), children's ability to update face norms based

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[7] We review studies where the object class is theoretically similar to faces (animate objects with exemplars sharing a first-order configuration). Interestingly, however, face memory might develop faster than memory for houses or scenes (which activate different brain areas from discrete objects, i.e., the parahippocampal place area). In two studies, accuracy was similar for faces and houses/scenes in the youngest age group (and above floor), making comparison of developmental trends valid. Both these studies found stronger development for faces than houses (across 6 to 10 years, Carey & Diamond, 1977) and scenes (across 7–11 to 12–16 years, Golarai et al., 2007). Our conclusion that there is no development of face-specific mechanisms is based on the presumption that discrete objects form a better control class for faces than do houses/scenes. The results reviewed do not rule out the possibility that mechanisms common to both faces and objects might develop at a different rate than those used to code houses and scenes.

[8] Children do show a larger after-effect than adults for an asymmetric manipulation of eye height that breaks the first-order face configuration (Hills et al., 2010). This could suggest greater flexibility in the range of faces that can be coded (see "Effects of age and early experience on the flexibility of tuning to different face subtypes"), but it could arise from mid-level-vision responses to the vernier offset of the eyes: vernier offset is less precisely coded in children than in adults (Skoczenski & Norcia, 2002) and could plausibly produce after-effects.

on recent exposure is as strong as adults': After-effects are no weaker in children (eyes up−down symmetrically, Figures 4D and 4L, Hills et al., 2010; Jeffery et al., 2010; expanded Figure 4E, Jeffery et al., 2010; Dan−anti-Dan, Figures 4F−4K, Jeffery et al., 2011; Nishimura et al., 2008; Nishimura, Robertson, & Maurer, 2011; Pimperton et al., 2009). The only possible age effect in Figure 4 is a slightly larger identity after-effect in 5−7-year-olds than in 8-year-olds and adults (Jeffery et al., 2011; note that figural after-effects are not larger in 4−6 y.o. than in adults, Jeffery et al., 2010).[8] Further, the amount by which identity after-effects are larger for far-from-average adaptors than for close-to-average adaptors is equal in 7-year-olds and adults (Figure 4J, Jeffery et al., 2011), indicating equal reliance on norm-based rather than exemplar-based coding, plus equal sensitivity to differences in distinctiveness (80% vs. 40% identity strength adaptor). The amount by which after-effects increase as presentation time of the adaptor is increased is equal in 8-year-olds and adults (Figure 4K, Nishimura et al., 2011), indicating equal sensitivity to build-up of adaptation and arguing that children can update face norms as rapidly as adults. And the amount by which the figural after-effect (eyes up−down) generalizes across identity change in the face (i.e., reduction when adaptor and test differ in identity compared to when they are the same in identity) is equal for 6−12-year-olds and adults (Figure 4L, Hills et al., 2010), arguing that the overlap in neurons coding two different face identities is the same in children as in adults.

Finally, we consider whether detection of *spacing changes* matures later than that of *feature changes* (Mondloch et al., 2002). Post 8 years of age, it is now widely agreed that improved spacing sensitivity is not specific to faces nor based on face experience: it occurs at the same rate for houses and (nonexperienced) monkey faces as for human faces (Figure 5, Mondloch et al., 2006; Robbins, Shergill, Maurer, & Lewis, 2011). Younger than 8 years, there is still controversy: McKone and Boyer (2006) found 4-year-olds were equally sensitive to spacing and feature changes; Mondloch and Thomson (2008) argued that the lack of delay for spacing could have been because the spacing changes were, according to their physical measurements, outside the normal range in natural faces; however, in response, we note that Mondloch and Thomson did not compare the *feature* changes to physical norms, and McKone and Boyer equated *perceived* spacing and feature changes, so both were comparably normal.

In summary, across all these studies comprising 26 separate findings from multiple different laboratories there is now strong evidence arguing that the core behavioural mechanisms of face perception reach early quantitative maturity.[9] Regarding the exact age, 4−5 years seems a reasonable upper age limit from the figures (although note that some phenomena have not been tested below 6−8 years).

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[9] In conflict, a recent adult study appears to suggest very late quantitative maturity: Germine et al. (2011) reported face memory peaks at 32 y.o. Because general cognitive function should not change over 20−32 years, this appears to imply that the amount of lifetime experience with faces is a key driver of face recognition ability. However, the "age" effect could reflect a confound with the ORE. Data were internet-collected via the http://www.testmybrain.org site. Face stimuli were Caucasian. Participants' race or country of origin were not recorded, and they could have participated from anywhere in the world. More recent data from test-mybrain (2011 sample, four years later than the original; L. T. Germine, personal communication, August 26, 2011) reported the country in which participants grew up. Grouping participants into majority-Caucasian countries (US, Europe, etc.) or other countries (Asia, Africa, etc.), results showed noticeable variation across age in proportion from majority-Caucasian countries. In some age ranges, this could not explain face recognition performance (e.g., recognition declined across 34−65 years despite proportion-Caucasian increasing). However, across the crucial 20−32-year-old range, proportion-Caucasian increased significantly with age (from approximately .71 at 20 years to .81 at 32 years, $r = .61$, $p = .027$). If this confound was present in the original sample, then the improvement in face recognition between 20 and 32 could have reflected reduction in the ORE (noting that this would also predict the observed changes for upright and not inverted) rather than an age/experience effect.
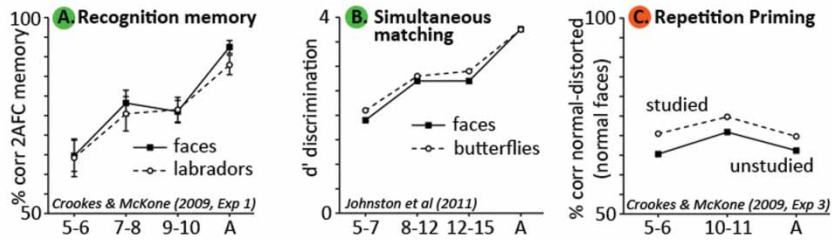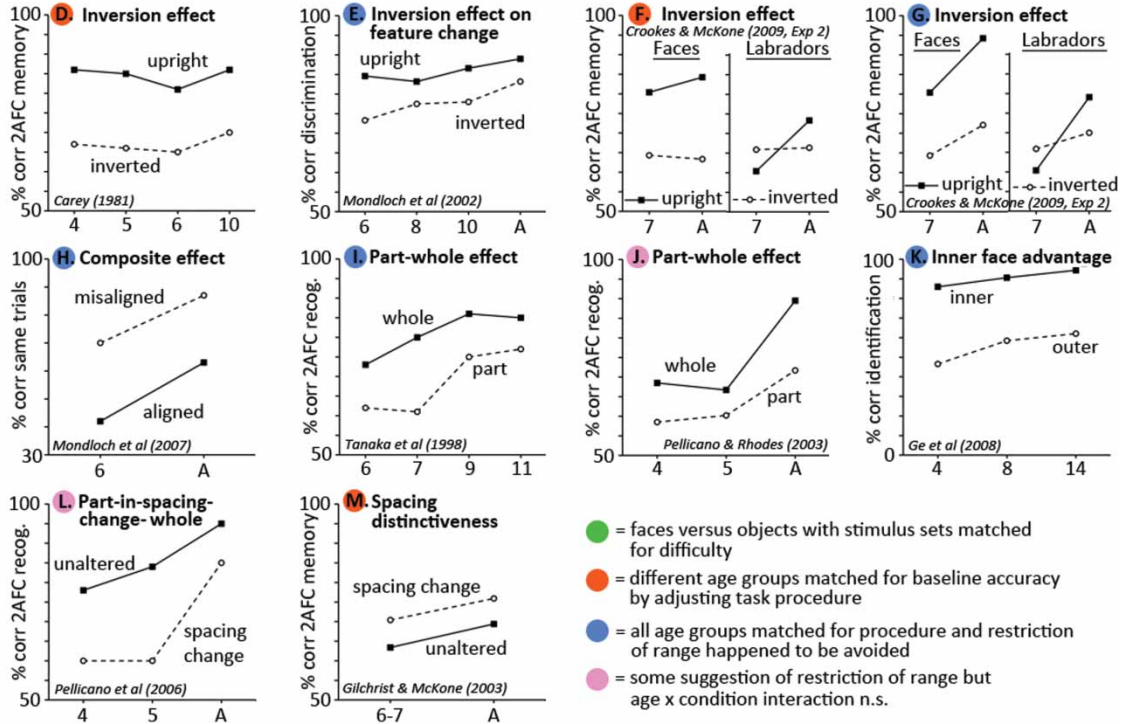
Figure 3. *Results of behavioural studies avoiding restriction of range problems for novel face encoding and holistic processing. Results imply early quantitative maturity of face-specific perceptual mechanisms. (A−C) For novel face encoding: Discrimination increases with age at the same rate for faces and difficulty-matched object classes, and repetition priming does not change across age. (D−M) For holistic/configural processing, all standard effects are as large in young children as in older groups. (See the section entitled "Age of quantitative maturity in behavioural studies: Avoiding restriction of range shows maturity by early childhood" for details of studies.) Coloured dots indicate the method used to avoid restriction of range issues: (A & B) faces versus objects with stimulus sets matched for difficulty; (C, D, F, M) different age groups matched for baseline accuracy by adjusting task procedure; (E, G, H, I, K) all age groups matched for procedure and restriction of range happened to be avoided; (J & L) some suggestion of restriction of range but age × condition interaction n.s. All plots show age in years on the x-axis; A = adult. 2AFC = two-alternative forced-choice. To view a colour version of this figure, please see the online issue of the Journal.*

Age of quantitative maturity in neural mechanisms

This leaves us only with the neural underpinnings of face recognition to consider as possible sources of face-specific development. In our previous reviews (Crookes & McKone, 2009; McKone, Crookes, & Kanwisher, 2009), we noted an apparent difference between the developmental literature on behaviour, suggesting early quantitative
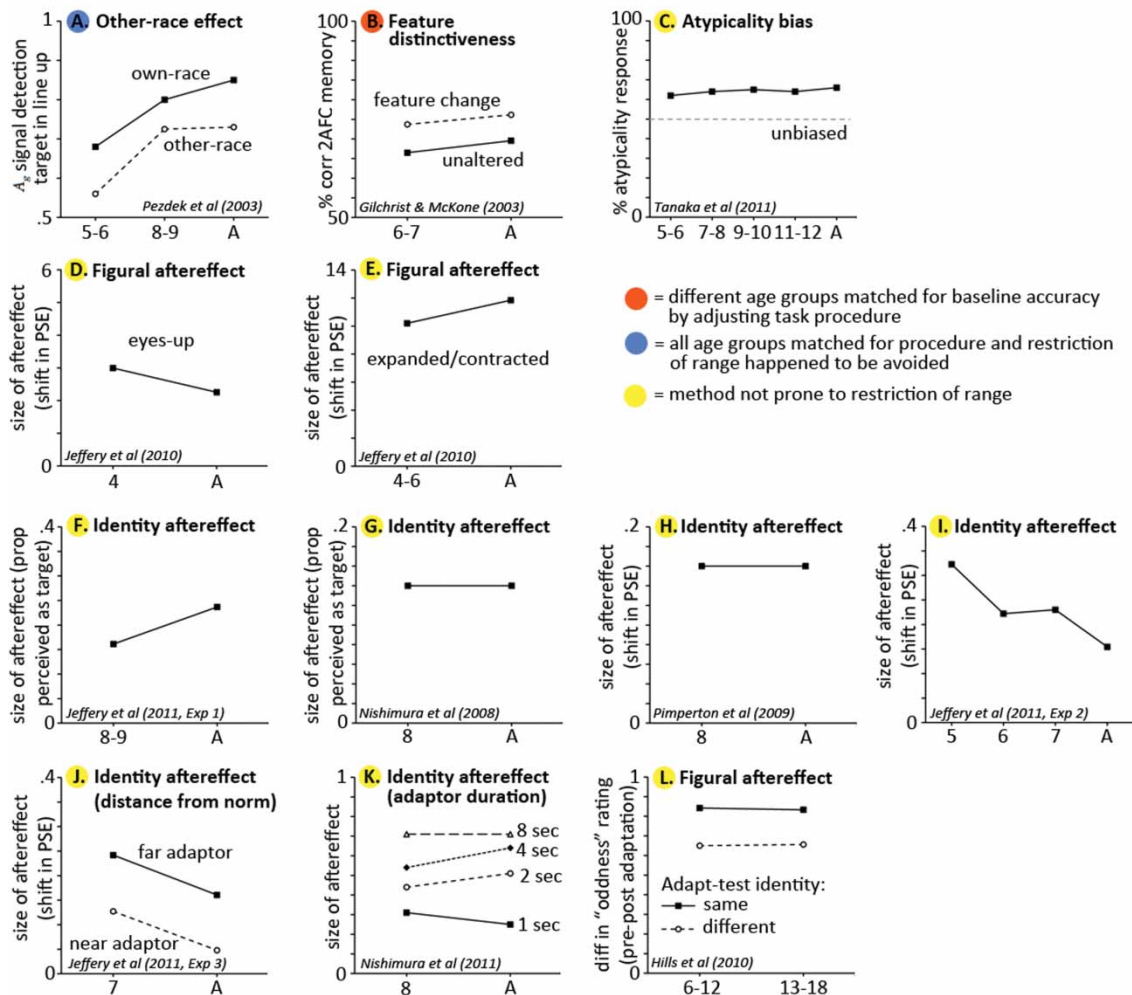
Face-space coding

Figure 4. *Results of behavioural studies avoiding restriction of range problems for face-space coding. Results again imply early quantitative maturity of face mechanisms. Across all plots, the only significant changes with age were in identity after-effect studies testing children 7 years and younger; these ages demonstrated larger identity after-effects than adults, not smaller. Coloured dots indicate the method used to avoid restriction of range issues: (B) different age groups matched for baseline accuracy by adjusting task procedure; (A) all age groups matched for procedure and restriction of range happened to be avoided; (C–L) method not prone to restriction of range. (See the section entitled "Age of quantitative maturity in behavioural studies: Avoiding restriction of range shows maturity by early childhood" for details.) All plots show age in years on the x-axis; A = adult. 2AFC = two-alternative forced-choice. PSE = point of subjective equality. To view a colour version of this figure, please see the online issue of the Journal.*

maturity, and the results for neural mechanisms, which suggested late maturity. Recent evidence has largely resolved this discrepancy for the N170, but not fMRI.

N170 studies. Prior to 2010, studies of the N170 all indicated quantitative change across early childhood to late adolescence, with good agreement regarding its form: N170 *latency* decreased by
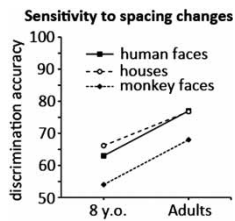
Sensitivity to spacing changes

Figure 5. *Age-related changes in sensitivity to spacing between parts (e.g., distance between eyes or between two windows) are not face-specific or driven by face experience after 8 years of age. Rate of improvement with age is the same for experienced face type (human), nonexperienced face type (monkey), and nonface objects (houses). Plot combines data from Mondloch, Maurer, and Ahola (2006; human and monkey faces, using sequential same–different task) and Robbins et al. (2011; houses, using delayed match-to-sample task).*

∼100 ms between 4–5 years and adulthood, with the steepest decrease before 10 years of age; *amplitude* had a "U" shaped developmental trajectory, smallest for children 10–11 years of age, and larger both younger and older; and *topography* was marked by a dominant posterior positivity rather than negativity in children, becoming adult-like in the midteenage years (4 to 14 y.o., Taylor et al., 1999; 4 to 15 y.o., Taylor et al., 2001; 4 to 10 y.o., Henderson et al., 2003). The N170 also sometimes appeared double-peaked in

young children, having both an early (N170a) and a later (n170b) peak (Taylor et al., 2004), in contrast to adults' single N170 peak.

However, Kuefner et al. (2010) pointed out that ERP latency, amplitude, and topography can change due to age-related changes in any number of general factors unrelated to perceptual processes or even brain function (e.g., skin conductivity; skull thickness; head size; electroencephalography signal-to-noise ratio; attention). They used a higher density of channels than previously to improve signal-to-noise in young children, controlled for age-related variations in the P1, avoided grand averaging to isolate the N170 response from that of the preceding P1 and the later N250 (peak confound can occur when there is large interindividual and intertrial variance, and young children's data are grand-averaged), and examined face-specificity by testing car stimuli. Results showed that none of the previously reported age-dependent changes in latency, amplitude, or topography of the N170 were specific to faces. The effect of age on the N170 for faces was the same as that for cars, on both latency (Figure 6A) and amplitude. Results also implied that the previously reported "N170b" was in fact the N250, and that this confound accounted for the apparent large (100-ms) decrease in "N170"

Neural mechanisms for faces
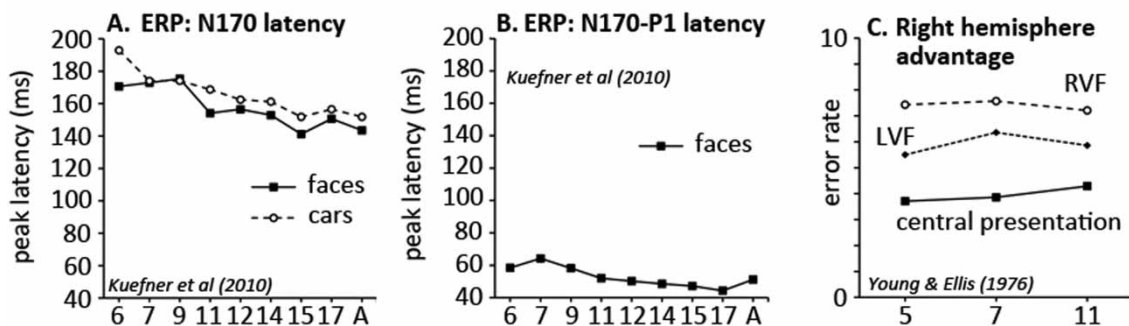
Figure 6. *Results of neural studies avoiding methodological problems that support early quantitative maturity of face-specific mechanisms. (A) Latency of the N170 peak over right occipitotemporal areas (electrode P08). (B) Results of subtracting out age differences in latency of P1 (i.e., N170 latency minus P1 latency). (C) Right hemisphere advantage in visual field (left visual field, LVF; right visual field, RVF) study that avoided restriction of range by equating baseline accuracy for central presentation. (See the section entitled "Age of quantitative maturity in neural mechanisms" for details.) All plots show age in years on the x-axis; A = adult. ERP = event-related potential.*

latency with age in previous studies: Latency reduction with age was much smaller for the true N170 (Figure 6A), and indeed when further isolated from age-related changes in P1 the face N170 latency was found to decrease by only 10–15 ms between 4 and 9 years (and no more after that; Figure 6B). Finally, the latency advantage for faces compared to cars did not change with age (Figure 6A). Overall, Kuefner and colleagues found that the electrophysiological markers of face-sensitive perceptual processes do not change throughout development, from 4 years to adulthood.

Right hemisphere bias. Also consistent with early neural maturity, the degree of right hemisphere bias for face recognition does not increase quantitatively after early childhood. Considering studies that reported at least 90% right-handers: Kuefner et al. (2010) found that the amount by which N170 amplitude was larger over the right hemisphere than the left hemisphere showed no systematic developmental trend from age 6; a visual field study equating baseline accuracy (longer presentation times for younger children) found no change in degree of LVF advantage over 5 to 11 years (Figure 6C, Young & Ellis, 1976); and fMRI studies found that, if anything, the strength of the right hemisphere bias decreased with age (Scherf et al., 2007; only rFFA and not lFFA observed in 7–11 y.o., Pelphrey et al., 2009).

fMRI studies of the FFA. Both size and selectivity of the FFA have been of interest: *size* because increases are predicted by gradual construction of functionally specific regions of cortex (constructivist view, Quartz, 1999); and *selectivity* (i.e., amount by which response is higher to faces than control objects) because increases are predicted by the theoretical perspective that redundant and irrelevant neuronal connections exist from birth and are gradually eliminated on the basis of experience (Changeux & Danchin, 1976). All fMRI studies to date have reported an increase in FFA size with age (Aylward, et al., 2005; Golarai, et al., 2007; Golarai, Liberman, Yoon, & Grill-

Spector, 2010; Joseph, et al., 2011; Passarotti, et al., 2003; Passarotti, et al., 2007; Peelen, et al., 2009; Pelphrey, et al., 2009; Scherf, et al., 2007; Scherf, et al., 2011)—up to three-fold larger in adults than children—that extends into adolescence (e.g., smaller even in 13–16 y.o. than in adults, Golarai et al., 2007). One study also found that rFFA size was correlated with behavioural face recognition memory performance (and not with place or object memory), separately in children and adolescents although not in adults (Golarai et al., 2007). Several studies have reported increased selectivity of the FFA, sometimes revealed as increased magnitude of FFA response to faces without change in its response to objects (Golarai, et al., 2007; Golarai, et al., 2010; Joseph, et al., 2011; Peelen, et al., 2009; Scherf, et al., 2007) and in one study revealed as decreased response of the FFA to nonface stimuli (Cantlon et al., 2011).

While these findings appear to support face-specific perceptual development, there are potentially serious methodological issues. As we noted earlier, many studies (Aylward et al., 2005; Joseph et al., 2011; Passarotti et al., 2003; Pelphrey et al., 2009) rely exclusively or primarily on group analyses, rather than individual-subject analyses. Group analyses are problematic because an apparent difference in FFA volume between children and adults could result from a difference in variability of anatomical location, even if the volumes of FFA measured individually were identical between children and adults (for direct evidence that group analyses can underestimate volume or selectivity of functional regions, see Saxe, Brett, & Kanwisher, 2006; Scherf et al., 2007).

Another issue, potentially affecting even the individual-subject analyses, is that signal-to-noise ratio is likely to be lower in young children. This is partly because children might move their heads more, but also due to a previously unnoted problem—namely, the use of adult-sized head coils to collect fMRI data on child-sized heads. Of the 10 previous studies, 3 explicitly report using an adult head coil (Golarai et al., 2007, 2010; Pelphrey et al., 2009), and we presume the

remaining studies also did so because, to the best of our knowledge, these groups do not possess a paediatric coil. It has recently been shown that, because children's heads are smaller (and hence farther from the coil) than adults' heads, adult coils have low signal-to-noise ratio over time (tSNR) for scanning children (Keil et al., 2011). tSNR is the most important metric for sensitivity in a given fMRI acquisition protocol (e.g., Triantafyllou, Polimeni, & Wald, 2011); it measures fluctuations from thermal and physiological noise sources and is defined as mean intensity of an ROI or pixel in a resting functional time-series divided by its standard deviation across time. The fact that tSNR in an adult head coil increases with head size (and thus age) of the participant raises the possibility that even individual-analysis studies, with good control for head movement, may have underestimated the volume (and perhaps selectivity) of the children's FFA.

Importantly, some studies have reported control areas to argue that low tSNR in children was not the source of the increase in FFA size. Considering individual-subject analyses, results are mixed regarding the parahippocampal place area (PPA) with some studies finding increased size with age (Scherf et al., 2011; lPPA in Golarai et al., 2007) and some not (Scherf et al., 2007; rPPA in Golarai et al., 2007). Regarding areas that code discrete objects rather than places or scenes, Peelen et al. (2009) found the fusiform body area (FBA) did not increase in size, and object-area lateral occipital complex (LOC) is also developmentally stable (Golarai et al., 2007, 2010; Scherf et al., 2007). Demonstrating age stability of a control area nicely rules out many potential confounds (e.g., head movement) as the origin of the smaller FFAs in children observed in these studies. However, it does not necessarily rule out lower tSNR in children arising from head coil size. This is particularly the case for the LOC. For a given head coil size, tSNR is lower for brain regions further from the coil than for those closer to the coil (Keil et al., 2011). This could mean that the effect of adult head coil size on children's small heads could be more severe for medial regions (e.g., FFA, FBA) than for lateral regions (e.g., LOC). Potentially, this could explain why the FFA appears to increase with age while the LOC remains stable; that is, there is little negative effect of using an adult head coil on the LOC because it is sufficiently close to the coil regardless of head size.

Overall, from this discussion, we would not like to conclude that there is not a genuine change in the size and/or selectivity of the FFA with age; this remains a possibility from the presently available evidence. But on the other hand, given the methodological issues, we would not like to conclude there *is* genuine change in the FFA with age. This is particularly the case because, as we next discuss, there is evidence arguing that fMRI in young children can sometimes produce nonsensical conclusions due to lack of sensitivity.

Evidence arguing that fMRI conclusions in children younger than 10 years can sometimes be wrong, even when studies meet current "best practice"

Scherf et al. (2011) examined whether the FFA was capable of making individual-level discriminations between faces, using fMR-adaptation (difference between different-face and same-face blocks). Importantly, the study made strong efforts to collect good fMRI data in children, including individual-subject analyses, independently defined ROIs, matching children and adults for head motion, and good alignment between anatomical and functional scans.

Results showed no face individuation in children aged 6–10 years in the FFA. Critically, however, a whole-brain analysis was also included, and no fMR-adaptation was revealed anywhere in the entire brain (see Figure 7). This contradicts known evidence that the brains of 6–10-year-olds *can* adapt to individual faces: Both repetition priming and adaptation after-effects are found, at adult strength, in this age range (Figure 3C, Figures 4D–4L; also note that fMR-adaptation can be observed, for other stimuli, in 4-year-olds, Cantlon, Brannon, Carter, & Pelphrey, 2006). Interpreting Scherf et al.'s (2011) lack of fMRI discrimination as genuinely reflecting the ability of children's brains to discriminate faces would also
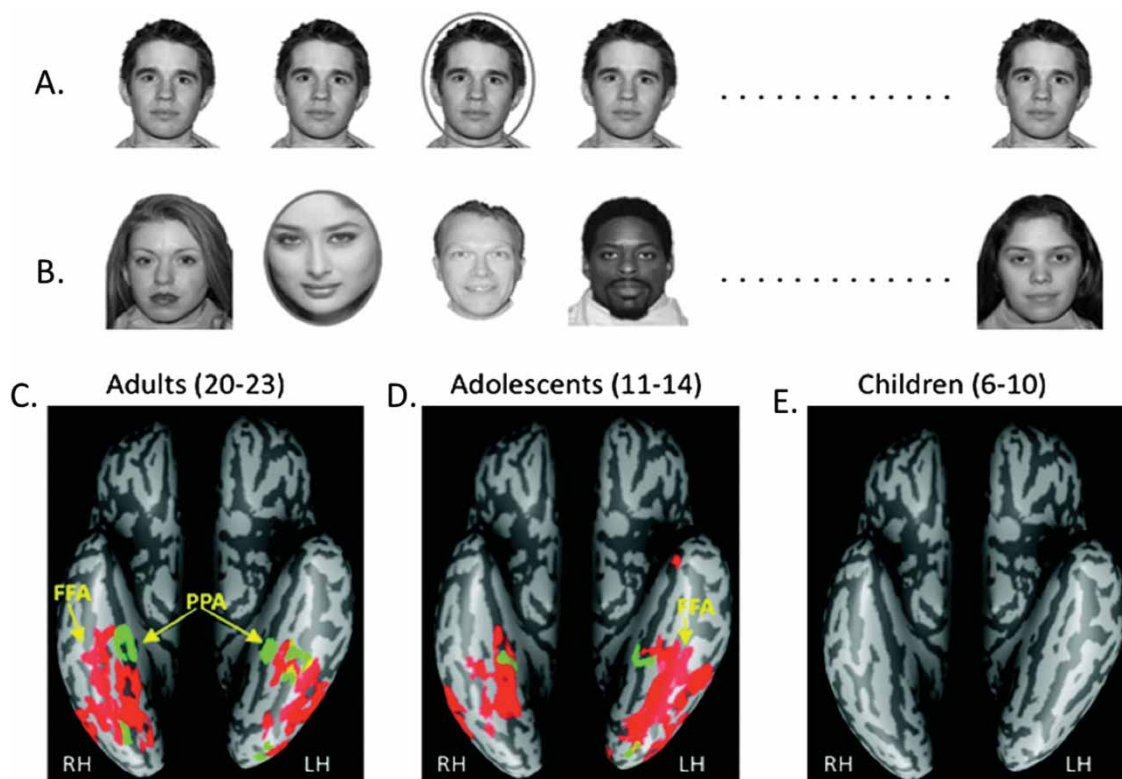
Figure 7. *Evidence that even a well-controlled functional magnetic resonance imaging (fMRI) study can fail to reveal an effect that other evidence suggests must be present in children. Stimuli and results from Scherf et al. (2011). (A, B) Face stimuli used to examine individual-level face discrimination via fMRI-adaptation. In separate blocks, participants viewed consecutive images of (A) identical faces or (B) different faces, pressing a button when a circle surrounded the stimulus. (C−E) Results of whole brain voxelwise analysis evaluating individual-level adaptation effects within each age group in the adaptation task. Individual-level adaptation was computed as different > identical for faces (red) and houses (green) in separate contrasts (p > .025, corrected). Scherf and colleagues report that adults and adolescents (left fusiform face area, FFA, only for adolescents) exhibited selective individual-level adaptation for faces in the fusiform gyrus, which was centred on the classic FFA region. Children failed to exhibit individual-level adaptation in any region, inconsistent with behavioural adaptation and excellent behavioural ability to discriminate faces at this age and the expectation that even primary visual cortex should be able to discriminate the faces in (B). To view a colour version of this figure, please see the online issue of the Journal. From "'What' Precedes 'Which': Developmental Neural Tuning in Face- and Place-Related Cortex", by K. S. Scherf, B. Luna, G. Avidan, and M. Behrmann, 2011,* Cerebral Cortex, 21, *pp. 1963−1980. Copyright 2011 by Oxford University Press. Adapted with permission.*

appear to make the absurd prediction that children aged 6−10 go about their daily lives unable to tell apart even dramatically different faces (variation in sex, race, expression, presence or absence of hair; Figure 7B). However, contrary to Scherf et al.'s (2011) suggestion that their result "converges with several behavioral studies" (p. 1975), the lack of neural discrimination disagrees strongly with behavioural discrimination. Mondloch et al. (2002)

found that 6−10-year-olds averaged 87% correct for discriminating successive static images even of very similar faces (all Caucasian women, all the same age, all wearing a shower cap) presented for only 200 ms (cf. 800 ms per face in Scherf et al.).

We thus suggest the Scherf et al. (2011) study provides evidence that fMRI data in young children can fail to detect effects that should be present. This cannot be due merely to the sample

size (Scherf et al. used the same *N* in older groups, in which fMRI adaptation was clearly found; Figure 7) and so demonstrates a lack of sensitivity, perhaps due to low tSNR in children. The fact that even a decently controlled experimental design leads to conclusions that are probably incorrect leads one to have serious doubts about the interpretation of other fMRI face results in children under 10 years (i.e., a region is absent, smaller, or less selective than in adults) as reflecting immature neural processing of faces.

Summary of quantitative maturity

We have argued the results of behavioural, N170, and hemispheric difference measures support the general cognitive development theory of late task improvements, with no change in face-specific perceptual processing beyond the age of perhaps 4–6 years. The number of behavioural studies avoiding the problem of restriction of range has increased substantially in the last 2–3 years (see Figures 3 and 4). The new findings of these studies, together with better controlled N170 data, support early maturity of face-specific mechanisms including ability to perceptually encode a novel face, holistic processing (including spacing sensitivity), face-space coding, and rapid face processing. Overall, these findings make a strong case that the ability to recognize faces quickly and accurately does not depend on extended experience over many years, as proposed by Carey et al. (1980; although note that we do not rule out some important effects of experience, e.g., during infancy; see the sections entitled "Coding of profile views", "Innateness: Critical period", "Innateness: Perceptual narrowing", "Effects of experience during infancy").

At present, fMRI results appear discrepant with those of the other techniques. Some or all of this discrepancy may be due to methodological issues—such as scanning children in an adult-size head coil—which mean that fMRI studies to date may have underestimated the size or selectivity of the FFA in children. However, the discrepancy could also reflect a genuine difference. If so, one possible explanation is that an increasing FFA size reflects the number of individuals with whom a participant is

familiar, and that average FFA size increases across development simply because adults have met, and stored the faces of, more people than children have. Under this interpretation, storing more faces in the FFA would require more neurons, and these might be taken over for this purpose from surrounding areas of body or object-general cortex. Another idea is that measured FFA size might be determined by top-down processing as well as bottom-up face perception, and that children engage in this top-down processing less readily. Both of these ideas are empirically testable: for example by comparing same-age participants with low versus high number of known individuals (e.g., from small country-towns versus large cities), or on tasks with low versus high top-down demands (e.g., passive viewing versus 3-back matching) to see whether these variables affect measured FFA size.

A ROLE FOR NATURE: GENETIC CONTRIBUTIONS AND INNATENESS IN FACE INDIVIDUATION

The review so far indicates that experience with faces plays a weaker role in our ability to recognize faces than traditionally believed. Complementing this finding, there is now clear evidence of a role for "nature" in face individuation. This includes both *genetic* contributions and *innate* contributions (in the sense of being present at birth). Note that genetics and innateness are independent issues because genetically influenced processes can occur late in development (e.g., onset of puberty; onset of dyslexia when children learn to read) rather than necessarily at birth. The evidence comes from studies of twins, families, neonates, visually deprived monkeys, critical periods, and perceptual narrowing.

Genetic contribution to individual differences in ability: Twin and family studies

Twin studies demonstrate that individual differences in face recognition have a heritable genetic

component. Twin studies use the logic that differences in a cognitive ability are heritable if the correlation is higher for monozygotic twins (identical twins, who share 100% of their genes) than for dizygotic twins (fraternal twins, who share an average of 50%). Results show heritability of face individuation, for fMRI activation pattern across the ventral visual stream (Polk, Park, Smith, & Park, 2007) and for behavioural discrimination (Wilmer et al., 2010; Zhu et al., 2010). Results also indicate face-specific heritability: There is heritability for holistic processing (face inversion and composite effects, Zhu et al., 2010), no heritability for recognition of houses or inverted faces (Zhu et al., 2010), and no heritability of ventral stream activation patterns for stimuli unlikely to have any special evolutionary status (written words and chairs, Polk et al., 2007). Independence of the face heritability from the heritability of general cognitive abilities (i.e., intelligence, or "*g*") is also indicated: Singleton studies show very low correlation between face memory and verbal memory or IQ (Bowles et al., 2009; Wilmer et al., 2010; Zhu et al., 2010). The twin studies also show that the heritable contribution to face recognition is large (specifically, 100% of familial resemblance is genetic, i.e., monozygotic correlation equal to twice or more times the dizygotic correlation; Wilmer et al., 2010; Zhu et al., 2010). The contribution of nonfamilial environment was significant but modest in both studies (see McKone & Palermo, 2010).

Also consistent with heritability is the fact that developmental prosopagnosia—a lifetime inability to recognize faces without any known brain injury—can run in families across generations (Grueter et al., 2007; Kennerknecht, Pluempe, & Welling, 2008; Schmalzl, Palermo, & Coltheart, 2008). Again arguing for face-specificity, this can occur independent of intelligence (Dobel, Bölte, Aicher, & Schweinberger, 2007; Duchaine, Germine, & Nakayama, 2007) and sometimes coexists with normal within-class discrimination of objects (Lee, Duchaine, Wilson, & Nakayama, 2010).

These results argue that face-specific individuation plus the component mechanism of holistic processing both have a component derived from genetic differences between individual people, heritable across generations.

Innateness: Neonates and visually deprived monkeys

Visual abilities present immediately after birth, or in monkeys deprived of all face input, cannot be derived from experience and so reveal *genetic influences* (on average face recognition ability, not individual differences) in isolation from any visual learning. Table 1 shows that human newborns individuate and holistically process faces. Babies in these studies were 1−3 days old, giving a maximum of perhaps 12 hours of visual experience of any kind (newborns sleep 16 hours per day plus have their eyes shut during breastfeeding and crying). It seems unlikely that the small amount of face experience would be sufficient for a purely learning-based system to support the level of fine discrimination ability observed.

Sugita (2008) raised macaques with no exposure to faces (human caregivers wore full face masks), but otherwise normal visual experience in a complex environment. On their first experience with faces, at age 6−24 months, the monkeys could discriminate very subtle differences between individual faces (both spacing and feature changes).

Together, these results strongly imply that face individuation and holistic processing abilities are present at birth, without experience.

Innateness: Critical period

Another source of evidence for neural systems being present at birth can be a *critical* (or *sensitive*) *period* (Sengpiel, 2007), in which environmental input of the appropriate stimulus type is required within a specified period after birth to avoid the system being taken over for other purposes. In the textbook example, cats are born with cells tuned to all line orientations, but if raised in an environment containing only vertical lines, they lose neural and behavioural sensitivity to horizontal lines.

For faces, patients born with dense cataracts disrupting all pattern vision (and subsequently removed) show, later in life, normal recognition of same-image faces (Ostrovsky, Andalman, & Sinha, 2006; Putzar, Hötting, & Röder, 2010). However, despite many years of post-cataract-removal exposure to faces, they show impaired performance on cross-view recognition (Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002; Putzar et al., 2010) and no face composite effect (Le Grand et al., 2004). Further, patients with left-eye-only or bilateral cataracts—which produce a deficit of early input to the right hemisphere due to the wiring of the infant visual system—show a deficit in processing spacing information in faces, while patients who had had right-eye-only cataracts do not (Le Grand, Mondloch, Maurer, & Brent, 2003), a pattern predicted by the normal role of the right hemisphere in holistic processing.

Taken together, the results indicate some form of critical period in infancy for individuation of faces across views, and for holistic processing.

Innateness: Perceptual narrowing

A final phenomenon associated with innate abilities is perceptual narrowing across infancy, in which an ability present in younger babies disappears in older babies. Perceptual narrowing is best known in language (e.g., Kuhl, Tsao, & Liu, 2003): Infants are born able to discriminate phoneme boundaries from all languages in the world (e.g., English and Mandarin), but from age 6–12 months lose this ability for nonexperienced languages (English for a child from a monolingual Mandarin-speaking family). This type of result is used to argue that a representational capacity (e.g., for faces) is present at birth, that this can initially be applied to a wide range of stimuli from the class (e.g., a wide range of face subtypes), and that its range gets restricted during the first several months of life to include only the kinds (i.e., face species, or races) seen in this period.

Perceptual narrowing occurs for faces. Infants younger than approximately 6 months can

individuate faces of races (Asian, Caucasian, African)—and, indeed, species (monkey and sheep faces)—that they have never experienced: Nonexperienced types are then gradually "tuned out", with this process complete at 9 months (Kelly et al., 2009; Kelly et al., 2007; Pascalis, de Haan, & Nelson, 2002; Scott & Monesson, 2009; Simpson, Varga, Frick, & Fragaszy, 2011). Sugita's (2008) monkeys also showed perceptual narrowing, with initial ability to individuate human faces disappearing after a month of exposure to only macaque faces.

Holistic processing also undergoes perceptual narrowing. Using the Cohen and Cashon (2001) version of the composite effect, holistic processing occurs for both own and other-race faces in young infants (4 m.o. Caucasian babies looking at Caucasian and African faces) but only for own-race faces in older infants (8 m.o., Ferguson et al., 2009).

Together, these results argue that babies are born with a broadly tuned ability to represent individual faces, and holistically code them, without experience. The fact that young human babies can individuate nonhuman primate and indeed sheep faces suggests that the underlying representation is rather old in evolutionary terms and might, for example, include all mammal faces.

Summary of genetics and innateness

Overall, these results provide a compelling array of evidence that there are both genetic and innate contributions to face recognition. Importantly, evidence from all techniques—heritability, newborns, critical periods, and perceptual narrowing—now supports such contributions for face individuation, and also for one of the key supporting mechanisms long presumed to be "special" to faces—namely, holistic processing. Regarding the breadth of the innate representation, the individuation for monkey and sheep faces in humans, and of human faces in monkeys, argues that this ability emerged quite some time ago in evolution and is possibly part of a general

conspecific recognition mechanism available to all mammals.

It is interesting to note that, to date, possible genetic or innate contributions to face-space coding have received essentially no investigation. Attractiveness effects have been reported in newborns (Slater, Bremner, et al., 2000; Slater, Quinn, et al., 2000) but stimuli were natural faces that did not vary specifically in terms of distance from the average face, making it difficult to tie the result specifically to face-space. Theoretically, it has been almost universal in the literature to assume that face-space develops entirely from lifetime exposure. In fact, however, no studies have tested this assumption (i.e., there are no twin studies, no perceptual narrowing studies, etc.). We suggest that it remains plausible that face-space may have genetic contributions or be present in some form at birth. It would be valuable for researchers to test this hypothesis in future.

WHAT EFFECTS OF EXPERIENCE ARE THERE?

So far we have emphasized situations in which ongoing lifetime experience with faces does not influence face recognition. We now briefly summarize situations in which experience does have an effect. We do not, of course, propose that infants are born with a fully operational face recognition system that requires no experience at all to mature. Instead, we argue that current results leave it open that quantitative and indeed qualitative change in core face coding could take place across infancy and/or into the uninvestigated preschool years; and also that later experience can fine-tune adult face recognition for particular individual faces, or particular subsets of faces.

Effects of experience during infancy

One effect of experience across infancy is a *qualitative change in viewpoint effects*, with identity information coded in front- and three-quarter-view faces from birth, but coding of profile views

emerging only after mid infancy (section entitled "Coding of profile views"). This raises an intriguing idea. Adult macaques have face-selective cells organized in a three-stage process of increasing view-invariance across three posterior-to-anterior face patches (Freiwald & Tsao, 2010). If, of view-specific cells, fewer are selective for profiles than for other views, then the baby findings might reflect a gradual development of a similar pathway, ultimately achieving view-invariance of neural coding.

Second, *perceptual narrowing* occurs across infancy (section entitled "Innateness: Perceptual narrowing"). The perceptual narrowing described so far represents a *loss* of ability with experience; that is, younger babies can do something (individuate faces of nonexperienced races and species) that is lost in older babies as a consequence of experience in the first months of life. In language, the likely functional reason for the loss of discriminability in nonexperienced categories is to fine-tune the system towards experienced categories and thus improve discrimination within the native language (Kuhl et al., 2006). Perceptual narrowing for faces might similarly enhance ability to discriminate commonly experienced face subtypes—that is, discrimination of own-species own-race faces might be initially crude and subsequently improve concurrent with the loss of ability to discriminate other-species and other-race faces. Potentially consistent with this prediction, Humphreys and Johnson (2007) found that the physical difference between faces required to produce novelty preference was smaller in 7-month-olds than in 4-month-olds. Unfortunately, however, there was no control stimulus (e.g., inverted faces), so it is unclear whether this reflects improvement in tuning of face mechanisms across infancy, or general improvement in vision or memory.

Finally, the type of perceptual discriminations an infant is required to make affects whether or not a face subtype is spared from perceptual narrowing. Perceptual narrowing is prevented for experienced face classes only where the experience involves individual-level categorization (e.g., monkeys are individually named) and not basic-level categorization (monkeys are experienced but

are all labelled "monkey"; Pascalis et al., 2005; Scott & Monesson, 2009). This implies that the reason babies remain able to individuate human faces across infancy in everyday life is that they have regularly experienced people being identified at the individual level.

Effects of experience 12 months to 3 years

Although we have argued that the current literature implies full quantitative maturity of face recognition by 4–5 years of age (at least in behaviour and ERP), we emphasize that there is nothing to rule out important quantitative improvements occurring between infancy and 4 years. It is generally not possible to quantitatively compare children aged 0–3 years to adults on the same tasks. Indeed, there are almost no data at all on face recognition between 12 and 36 months (note the jump from later infancy straight to 3 years in Table 1), because this intermediate age range is notoriously difficult to test.

In language—the other key ability supporting crucial social interaction in children—there is dramatic change in ability over the first 36 months of life. Potentially, the same could be true of face recognition. This means that an important task for developmental researchers is to develop face tasks suitable for assessing face-coding mechanisms in the 12–36-month age range.

Effects of age and early experience on the flexibility of tuning to different face subtypes

Clearly, experience can influence the relative ability to code different subtypes of faces, as demonstrated in the other-race effect. We emphasize, however, that the early quantitative maturity of face-specific mechanisms that we have argued for (see Figures 3–5) refers to *own*-race face recognition ability. Thus, we do not see any evidence that the good discrimination for own-race faces is a result of experience with own-race faces after 4–5 years of age. However, it seems plausible that the adult ORE is a result of the lack of experience with other-race faces prior to 4–5 years. Experience with other-race faces during adulthood may then become important and improve other-race

performance, but, importantly, this does not indicate late experience-related changes in ability to code faces per se, but instead in ability to apply established mechanisms to a different subset of faces.

It is also possible that the degree to which experience with other-race faces may facilitate discrimination might change across development. At 3 months, the decrement for other-race faces observed in one study was rapidly overcome by just a few trials of experience (Sangrigoli & de Schonen, 2004b). There is also evidence of flexibility into middle childhood: Korean children adopted to Caucasian countries at 3–9 years of age, and expected to have a deficit for Caucasian faces at adoption, show good memory for Caucasian faces when tested several years post adoption (de Heering et al., 2010; Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005; although see Sugita, 2008, for a potentially contradictory finding in macaques). And, in language, flexibility to "relearn" a language tuned out in infancy appears higher in children than in adults; for example an English-speaking 5-year-old relocated to France will become a fluent speaker with perfect grammar and accent, but even extensive exposure as an adult to a non-native language is usually insufficient to attain native-speaker levels of proficiency. Therefore, flexibility of the face system may be higher earlier in development than later.

Interestingly, in adulthood the degree to which experience can improve discrimination of certain face types might rely on reactivating latent effects of exposure from early childhood. Macchi Cassia, Kuefner et al. (2009) found that adults with recent experience of infants (first-time mothers) showed inversion effects for infant faces, but only if they also had had younger siblings when they were children (i.e., both early childhood and adult experience with infant faces). Further, women who had had younger siblings, but were not mothers (i.e., early childhood experience only) did not show inversion effects for infant faces. This study argues that experience with a face subtype in early childhood can lie dormant until reactivated by further experience in adulthood. An analogy from language would be that

an English speaker who has lived for a while in France as a child can subsequently forget most of their French but still relearn it as an adult with good accent and grammar, whereas an English speaker who has had adult-only experience of French does not achieve the same outcome.

Age-independent effects of experience

Finally, some effects of experience can occur at any age and are thus unrelated to any particular developmental stage. In *familiarity effects*, adults continue to learn new faces throughout life. This improves perceptual discrimination: Matching the correct face photograph to a low-resolution video image is more accurate for familiar than for unfamiliar faces (Bruce, Henderson, Newman, & Burton, 2001; Burton, Wilson, Cowan, & Bruce, 1999). *Adaptation after-effect*s (section entitled "Face-space coding") also indicate purely experience-based changes in the responses of perceptual representations of faces, as do *training effects* on ability to discriminate trained and novel faces (e.g., in an adult prosopagnosic, DeGutis, Bentin, Robertson, & D'Esposito, 2007). Crucially, however, there is no evidence that these types of experience alone produce any fundamental qualitative change in face processing either neurally or cognitively: Holistic processing, face-space effects, and FFA activation all occur strongly for both familiar and unfamiliar faces (Carbon et al., 2007; Kanwisher et al., 1997; Le Grand et al., 2004; Webster & MacLin, 1999; Young et al., 1987).

Summary of effects of experience

The important conclusions regarding the effects of experience are that (a) there are some, (b) it seems likely that these might be stronger earlier in development than later, although learning of faces continues throughout life, (c) after 4–5 years they affect recognition ability for certain subtypes of faces rather than improving overall face recognition ability per se (which is already mature for own-race faces), and (d) we currently have no

information at all as to at what age face perception reaches maturity in the 0 to 4 years age range.

CONCLUSION AND FUTURE DIRECTIONS

Conventional wisdom has long held that face recognition develops slowly, with experience as its primary engine. The modern findings support almost a complete reversal of this view. The data no longer support a theory in which the only face representation present at birth is a mere orienting device, and good individual-level face discrimination takes many years of practice to achieve. Rather, infants are born with a rich capacity to represent the structure of upright faces, and this supports face individuation, and holistic processing, rather than merely drawing attention to faces. Inherited genetic influence is also indicated, from twin studies, on both behaviour (individuation ability and holistic processing) and the pattern of ventral stream responses to faces. Qualitatively, findings indicate that all adult-like face recognition processes are present at the earliest ages tested (typically 3–4 years and in many cases infancy); the striking breadth of this evidence is summarized in Table 1. Further, face processes appear quantitatively fully mature early, by perhaps 5 years, as indicated by evidence from a now substantial set of behavioural and ERP studies that have avoided methodological problems common in previous literature (Figures 3–5). Regarding experience, there are substantial effects during infancy, including perceptual narrowing and a critical period for holistic processing and cross-view recognition. Post infancy, it seems plausible that there are ongoing effects of experience on quantitative performance in children younger than 4 years, although direct investigation is lacking. However, continuing experience beyond this age does not produce continuing improvements in face recognition at least for our most frequently experienced face types (i.e., own-race, own-species faces).

Our conclusions may depart dramatically from the traditional view of protracted development of

face individuation skills but they are entirely consistent with children's real-world need for face recognition. Crucially, the demands placed on children's face individuation skills do not differ substantially from those placed on adults' skills. Children would struggle socially if they could not distinguish numerous individuals from early in childhood. These social demands are particularly important as children enter school where they need to quickly learn many new faces. Children's laboratory test scores at this age suggest that, like adult prosopagnosics, they would struggle to learn these new people. Yet they do not. Further, it makes evolutionary sense to have a face system capable of rapid, accurate face recognition from an early age to support social development and, ultimately, survival.

Our review has also highlighted a number of areas for future research. First, behaviourally, it is imperative to develop face tasks suitable for the notoriously difficult 12-to-36-month age range. To be of theoretical value, these tasks need to allow valid quantitative comparison of face effects to be made with older children, rather than merely qualitative demonstration of effects known to exist in infants. Second, concerning behavioural studies in children four years and over, it would be valuable to investigate whether the developing cognitive mechanisms that we have argued drive improvement in laboratory face tasks contribute at all to face recognition performance in naturalistic settings (i.e., where social interest would be expected to drive attention to faces, concentration, etc.). Third, the current conflict between behaviour and fMRI regarding the age of quantitative maturity of face perception mechanisms needs to be resolved. Importantly, this is no longer a conflict between behaviour and brain (N170 results have now been shown to be consistent with our behavioural conclusions), but instead fMRI results conflict with those from behavioural, ERP, and right hemisphere advantage studies. We have suggested at least two possible approaches: Test children in child-sized head coils to match tSNR across age groups and see whether the age-related changes in the FFA disappear or hold up; and test the hypothesis that FFA size is related to the number of faces known to the observer (e.g., compare

children from small country-town schools and large city schools). Finally, in terms of innate and genetic contributions to face recognition, there has been no investigation of face-space coding. Data about this domain would be valuable in clarifying whether the effects of human's evolutionary history are apparent not only on face individuation ability, holistic processing, and ventral stream response to faces, but indeed to all aspects of face recognition.

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