Face Perception: a Developmental Perspective

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Abstract and Keywords

This article views face perception as the ideal case study example for understanding the deeper principles underlying human neurodevelopment. It illustrates how face perception has been one of oldest battlegrounds for resolving key issues in human development. It argues that taking a developmental approach to face perception can resolve some of the major current debates in the adult face perception and cognitive neuroscience literature. Thus, face perception and development continue to be mutually informative domains of study. The work on newborns designed to test the "innate knowledge" of faces, studying the development of face perception skills during infancy and childhood, has proved to be fertile ground for domain-general theories of perceptual and cognitive development. The study reviews recent literature on the factors that contribute to the specialization of certain cortical areas for face processing. It suggests an intriguing alternative middle-ground view in this polarized debate.

Keywords: face perception, human development, cognitive neuroscience, childhood, face processing

I have little interest in face perception for its own sake. This may seem like a shocking statement coming from someone who has devoted much of his career to the topic, but it reflects the fact that I have always viewed face perception as the ideal case study example for understanding the deeper principles underlying human neurodevelopment. In this chapter I will illustrate how face perception has been one of oldest battlegrounds for resolving key issues in human development. Conversely, I will argue that taking a developmental approach to face perception can resolve some of the major current debates in the adult face perception and cognitive neuroscience literature. Thus, face perception and development have been, and continue to be, mutually informative domains of study.

Ever since Darwin's (1872) book *The Expression of the Emotions in Man and Animals* the issue of whether the exquisite face perception skills we have as adults is due primarily to phylogeny (species adaptations) or ontogeny (individual development fuelled by experience) has motivated much research. Indeed, evidence from studies of face perception abilities at different ages has provided pillars to support domain-general nature or nurture arguments in human development. For example, in one of the very first scientific studies of human infants, Fantz (1963) showed that when given a choice of looking at a schematic face or a bull's-eye pattern, newborn babies generally preferred to look at the face. A decade or so later, Goren, Sarty, and Wu (1975) systematically tested human newborns—often within the first 10 minutes after birth—on their tendency to track slowly moving patterns. They observed that human newborns would turn their head and eyes further in order to keep a simple schematic face in view, than they would for equally complex "scrambled face" patterns. Viewed from the perspective of today's scientific standards, this study raised more questions than it answered, but at the very least it has generated a whole mini-field of scientific research (some of which will be discussed later).

In addition to the work on newborns designed to test what, if any, "innate knowledge" of faces we have, studying the development of face perception skills during infancy and childhood has proved to be fertile ground for domain-general theories of perceptual and cognitive development. Basic theories about mechanisms of learning (Nelson, 2003), pubertal dips in performance (Carey et al., 1980), the longitudinal stability of childhood performance, and the functional specialization of cortical regions (Johnson, 2001; Cohen-Kadosh and Johnson, 2007), have all been at least partly based on evidence from face perception studies.

Over the past decade an increasing number of cognitive neuroscientists who study aspects of face perception in adults have realized the importance of developmental data for addressing their key issues. In a later section I will review recent literature on the factors that contribute to the specialization of certain cortical areas for face processing. For example, the debate of whether the fusiform face area is specialized for face processing due to experience and training, or due to some (p. 4) kind of innate specification, remains unresolved and controversial based on the sometimes conflicting data from adults. Data from infants and children not only allows this question to be addressed more directly, but also suggests an intriguing alternative middle-ground view in this polarized debate.

The two-process theory

Up until the late 1980s, the development of face perception was an actively researched field, but it was mainly dominated by issues in the nature versus nurture debate and related questions about the ages at which different face perception abilities might appear. After replicating the results with newborns of Goren et al. (1975), Johnson et al. (1991), and several of the key results supporting more gradual development of face processing abilities, John Morton and I proposed the "two-process" model of the development of face perception in 1991 (Johnson and Morton, 1991; Morton and Johnson, 1991; see also de Schonen and Mathivet, 1990 for a related view). The original two-process theory sought to reconcile the apparently conflicting lines of evidence about the development of face processing by postulating the existence of two systems: a tendency for newborns to orient to faces (CONSPEC), and an acquired specialization of cortical circuits for other aspects of face processing (CONLERN). This two-systems theory was partly based on my earlier animal work (e.g. Johnson et al., 1985). We hypothesized that CONSPEC serves to bias the input to developing cortical circuitry over the first weeks and months of life, thus ensuring that appropriate cortical specialization occurred in response to the social and survival-relevant stimulus of faces.

To this day the putative CONSPEC mechanism occupies the middle ground between those who argue that face preferences in newborns are due to low-level psychophysical biases, and others who propose that infants' representations of faces are richer and more complex. From birth, human infants preferentially attend to some face-like patterns suggesting a powerful mechanism to bias the input that is processed by the newborn's brain. Perhaps the most controversial aspect of the two-process theory was the proposal that "infants possess some information about the structural characteristics of faces from birth" (Morton and Johnson, 1991, p. 164). Although this committed us to the view that the general configuration that composes a face was important, we did not commit to a specific representation. Nevertheless, our empirical observation from the early experiments with newborns, and evidence from other species, indicated that a stimulus with three high-contrast blobs corresponding to the approximate location of the eyes and mouth might be sufficient (Figure 1.1). In 1991 the idea that infants were born with face-sensitive information had been rejected by most in the field, largely on the basis of experiments with 1- and 2-month-old infants that failed to show any preference for static face images (see Johnson and Morton, 1991 for review). Because infants shortly beyond the newborn stage did not prefer schematic face patterns over scrambled faces, it was generally assumed that newborns could not discriminate faces from other stimuli.

Over the ensuing years, more than 20 papers on newborns responses to faces and face-like patterns have been published (see Johnson, 2005 for review). All of these studies bar one found some evidence of discrimination of face-like patterns. Several types of explanation have now been advanced for newborn face preferences that have been observed in at least five different laboratories and in the vast majority of studies conducted.

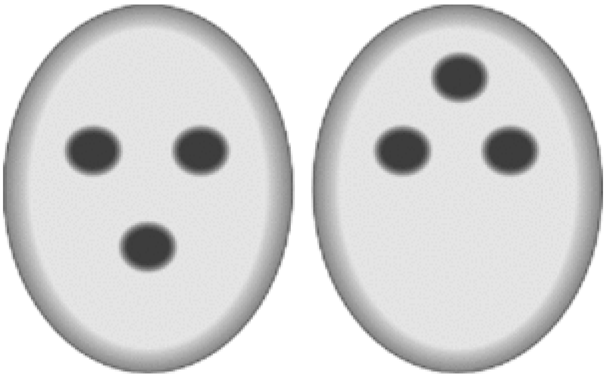

Fig. 1.1 Schematic illustration of the stimuli that might be optimal for eliciting a face-related preference in newborns. These hypothetical representations were created by putting together the results of several experiments on newborns' face-related preferences. Conclusions were combined from experiments showing the importance of the number of elements in the upper half of a bounded area or surface, the importance of a face-relevant pattern of phase contrast, and the importance of the basic face configuration as viewed at low spatial frequencies. Reprinted by permission from Macmillan Publishers Ltd: *Nature Reviews Neuroscience*, Subcortical face processing, Mark H. Johnson, **6**, 766–774, copyright 2005.

1 *The sensory hypothesis* A number of authors have advanced the view that newborn visual preferences, including those for face-related stimuli, can be accounted for simply in terms of the relative visibility of the stimuli. Different versions of this account and a detailed discussion of their merits are reviewed in an article by Johnson et al. (2008). After more than a decade of (p. 5) debate and empirical investigation about psychophysics, the upshot is that while some infant preferences for visual patterns can be predicted by the visibility of a stimulus as filtered through the limited visual system of infants, face patterns are nearly always more preferred over other psychophysically matched stimuli. That is, while the psychophysical properties of a stimulus do influence infants' looking preferences, when stimuli are carefully matched face patterns determine preference.

2 *Non-face structural preferences* This view is that newborn preference for faces can be explained by domain-general perceptual biases, such as those based on known adult Gestalt principles (see Simion et al., 2003). Simion and colleagues argue that "newborns' preference for faces may simply result from a number of non-specific attentional biases that cause the human face to be a frequent focus of newborns' visual attention" (Simion et al., 2003, p. 15). These authors still believe that the purpose of

these biases is to direct attention to faces in the natural environment of the newborn, so that they are debating the nature of the representation(s) that underlie this bias, not the existence of the mechanism itself. At this point it is useful to differentiate between face-*specific* and face-*sensitive* mechanisms. The notion of CONSPEC was never claimed to be face-specific (tuned only and exclusively to faces), but merely sufficient in the natural environment of the newborn to pick out faces from other objects and stimuli (face-sensitive). Indeed, we (Johnson and Morton, 1991) speculated that it may be possible to create "super-normal" stimuli (such as high-contrast face patterns) that would actually be preferred over a realistic human face. While the arguments advanced about non-face structural preferences accept that newborns have face-sensitive mechanisms, they argue that these biases are not adapted for that purpose, but are general biases in visual processing that, in combination, just happen to pick out faces in most natural environments. In contrast, CONSPEC is assumed to be specifically adapted for detecting conspecifics in the environment.
(p. 6) Therefore, CONSPEC would be more consistent with evidence that the biases are related (act in concert) and respond to the natural conditions in which faces are typically observed (such as the contrast patterns caused by being illuminated from above). The non-face structural preferences view has spawned much empirical research. The upshot of some of this research is that only a complex combination of different biases can explain the results (see Johnson et al., 2008). For example, a most preferred stimulus for a newborn would involve an up–down asymmetrical pattern with more elements or features in the upper half, but only when it is within a congruently shaped bounded object or area such as an oval. Related recent research indicates that this near optimal stimulus is improved further with the addition of the appropriate phase-contrast relations for a top-lit face (see Farroni et al., 2005, Figure 1). Further, these supposed different biases interact together in ways likely to be the product of one system or representation rather than being independent "non-specific" biases. Another line of research that casts doubt on non-specific structural preferences hypo-theses is evidence supporting the existence of complex face processing abilities in newborns, discussed next.

3 *Newborns have complex face representations* Some empirical results have led to the hypothesis that newborns already have complex processing of faces (for review see Quinn and Slater, 2003). These findings, usually obtained with naturalistic face images, include a preference for attractive faces (Slater et al., 1998, 2000), a preference for face patterns with the appropriate phase-contrast relations (Farroni et al., 2005), a sensitivity to the presence of eyes in a face (Batki et al., 2000), and a preference to look at faces with direct gaze that engage them in eye contact (Farroni et al., 2002). Such findings have led some authors to conclude that "…face recognition abilities are well developed at birth" (Quinn and Slater, 2003, p. 4). A fuller consideration of the details of these effects reveal that while some of them can be accounted for by the original CONSPEC notion, other experiments force the conclusion that the bias is more specific than originally hypothesized. In Figure 1.2 you will see realistic face images filtered through the appropriate spatial frequency filters to simulate newborn vision. From these images it is evident that a mechanism sensitive to the arrangement of high-contrast, low-spatial frequency components of a face would be preferentially activated by (i) the typical configural arrangement of eye and mouth regions, (ii) the presence (or absence) of open eyes, and (iii) direct versus averted gaze (see Farroni et al., 2002).

Thus, the notion of CONSPEC as a mechanism that biases newborns to attend to faces has, in my view, stood the test of time fairly well. More recent conceptions, however, suggest the mechanism is further tuned to detect potential communicative partners, such as faces that engage them with direct gaze (Farroni et al., 2002) accompanied by a smile (Farroni et al., 2007). Thus, the function originally attributed to CONSPEC now needs to be expanded: it is not just for detecting and orienting to any faces, but also prioritizes faces likely to seek social interaction with the infant. In this way, it may provide a developmental basis, not just for face perception, but also for social cognition in the brain in general.

I should note that an important caveat to many, but not all, of the above studies is that they are conducted with newborns more than 1 day old. While age (in days) is commonly reported not to have an effect on the results obtained, studies of very early learning over the first few hours of face-to-face contact need to be a priority for the future.

Fig. 1.2 How newborns see faces. (a) Realistic images of faces as viewed through the visual system of newborns at a typical distance for face-to-face interaction (~50 cm). A neutral face with direct gaze, averted gaze, and eyes closed, as well as a fearful face, are shown. These images support the view that, at close viewing distances, information around the eyes could activate the subcortical route. (b) The same realistic images of faces as viewed through the visual system of newborns, but from ~2 m. When viewed from a greater distance than in (a), or in the periphery, the configuration of shadowed areas that is characteristic of a naturally (top-) lit face could also activate the subcortical route. Reprinted by permission from Macmillan Publishers Ltd: *Nature Reviews Neuroscience*, Subcortical face processing, Mark H. Johnson, **6**, 766–774, copyright 2005.

While evidence for CONSPEC continues to strengthen and expand, there is no doubt that the notion of CONLERN was underspecified when we first proposed it in 1991. At that time CONLERN was described as “a device that acquires and retains specific information about the visual characteristics of individual conspecifics” (Johnson and Morton, 1991, p. 90). A large part (p. 7) of the reason for the lack of specificity in our original proposal, and why I did not go on to do much further research on the topic for another 4 or 5 years, was the lack of methods then available for child-friendly imaging of brain functions. My view was that without these methods we could never fully explore the mechanism(s) that underlie CONLERN. In the mid 1990s it became feasible to record high-density event-related potentials (ERPs), and, principally with Michelle de Haan, we began to exploit this method to provide evidence for the specialization of cortical processing of faces (see de Haan, Chapter 38, this volume). Some of the principles we discovered have now proved useful for functional magnetic resonance imaging (fMRI) studies of the neurodevelopment of face processing in children (see later section). Most recently, we have helped to pioneer near infrared spectroscopy (NIRS) as a method for studying cortical activation to faces and other social stimuli in infants and young children (Blasi et al., 2007; Grossman et al., 2008). Thus, the investigation of CONLERN illustrates the importance of available methods in the advancement of an area of scientific inquiry. Sometimes it is better to leave a burning question until the right methods become available for addressing it. Having said this, other researchers have made significant advances in understanding the development of the cognitive (p. 8) and perceptual aspects of face processing with behavioral studies alone (see Lee et al., Chapter 39, this volume).

A subcortical route?

In Johnson and Morton’s original (1991) proposals we argued that subcortical processing was responsible for guiding the behavior of newborns toward face-like patterns. Although it was very controversial at the time, we made this proposal for a couple of reasons. First, evidence from other species indicated that inborn preferences for conspecifics are mediated by more primitive subcortical neural routes. This stands in contrast to early visual learning that is mediated by forebrain or cortical systems. Second, evidence on the maturation of the human visual system suggests that there is slower development of the cortical visual routes than the subcortical during postnatal development (e.g. Johnson, 1990). Subsequently to this and related proposals (e.g. Le Doux, 1996), neuroimaging, electrophysiological, and neuropsychological studies with adults have provided evidence for a rapid, low spatial frequency, subcortical face detection system in adults that involves the superior colliculus, pulvinar, and amygdala (see Johnson, 2005 for review). This route is hypothesized to be fast, operates on low spatial frequency visual information, and modulates cortical face processing, which led Le Doux (1996) to describe it as the “quick & dirty” pathway.

Evidence that the route is fast comes from ERP and magnetoencephalographic (MEG) studies showing that components associated with a “fast pathway” for face processing can occur at much shorter latencies than those generally associated with the “structural encoding” stage of cortical face processing (such as the N170 and M170) (Bailey et al., 2005).

Evidence that the route processes low spatial frequencies comes from fMRI studies in which the pulvinar, amygdala, and superior colliculus respond to low spatial frequency information about faces, and particularly fearful faces (Winston et al., 2003). This subcortical route was insensitive to the high spatial frequency information about faces that can activate the fusiform cortex. Finally, evidence consistent with the idea that the subcortical route modulates cortical processing comes from several functional imaging studies indicating that the degree of activation of structures in the subcortical route (amygdala, superior colliculus, and pulvinar) predicts or correlates with the activation of cortical face processing areas (George et al., 2001; Kleinhans et al., 2008). However, the causal direction of this correlation remains unknown.

What is the purpose of this putative subcortical route? The proposal that follows on from the two-process model is that it serves as a developmental basis for the emerging social brain network (see Johnson, 2005). This view assumes that newborns have widespread projections from the subcortical route to cortical structures, and as a consequence face detection initially activates widespread cortical activation of regions that will become incorporated into the adult social brain. Through the constraints imposed by architectural biases within different cortical regions, and through the process of interactive specialization discussed later, particular cortical regions become increasingly tuned for social stimulus processing. Thus, CONSPEC and the subcortical route is a critical foundation stone for each individual child to construct their cortical social brain network (Johnson, 2005).

Even if you grant that CONSPEC and the subcortical route are important for the ontogeny of face perception and the social brain, does this route have any relevance or importance for those who study face processing in adults? We have investigated this question recently (Tomalski et al., 2009a). Contrary to most cognitive and functional imaging paradigms in adults that involve foveal presentation of faces, we presented schematic face patterns similar to those used with newborns, but as briefly flashed peripheral stimuli. We observed more rapid saccadic orienting to (p. 9) flashed face-like configurations than similar patterns. Further, consistent with a subcortical basis, this effect is only evident with temporal (the visual hemifields away from the nose) rather than nasal (the visual hemifields next to the nose) visual field input (Tomalski et al., 2009b). The effect also seems be a product of fast oculomotor routes since it is not observed with manual key press responses.

While we may be able to detect subtle hallmarks of the subcortical route in laboratory experimental contexts in adults, is there any substantive consequence of this processing in the real world? Senju and Johnson (2009) marshal evidence that this route is engaged by eye contact in adults (as well as infants), and have proposed that it is one source of selective activation of cortical structures that contribute to the “eye contact effect.” The eye contact effect is defined by these authors as the phenomenon that perceived eye contact modulates the concurrent and/or immediately following cognitive processing and/or behavioral response. If this hypothesis is correct, it means that the subcortical route continues to have a vital role in social perception and cognition in adults.

How do cortical regions come to be involved in face perception?

As discussed earlier, research on the mechanisms underlying CONLERN was delayed for several years due to a lack of necessary methods for progressing empirical research. While the use of ERPs has informed the neurodevelopment of face processing for some time now (see De Haan, Chapter 38, this volume), only in the past 5 years has fMRI been used with children on a regular basis.

Some of the hottest debates in adult cognitive neuroscience in recent years have focused on the degree to which face-sensitive markers of cortical function, such as the N170 ERP component, and activation of the fusiform face area (FFA) are selective for face processing, and how this degree of functional specificity arises in the first place (see Eimer, Chapter 17, this volume). In particular, for the FFA two opposing positions have emerged in accounting for the multitude of functional imaging data from adults. First, the "domain-specificity hypothesis" (Kanwisher et al., 1997) assumes that faces are processed in a modular and category specific fashion in the FFA. In opposition to this view is the "expertise hypothesis" that suggests that rather than being a dedicated face module, the FFA is a neural area involved in processing objects of expertise (Gauthier and Nelson, 2001). By the latter view, faces are the objects with which most adults have considerable expertise. While this debate has generated much further research with adults (see Kanwisher and Barton, Chapter 7; McKone and Robbins, Chapter 9; Scott, Chapter 11, this volume), the general question of the origin of functional specialization in human cortex is primarily a developmental issue. Specifically, the developmental question is what are the factors both intrinsic and extrinsic to the cortex that ensure that (1) we develop particular types of specialized cognitive functions relevant for our survival, such as face and language processing, and (2) these specialized functions usually end up located in approximately the same parts of cortex? The most obvious answer to these questions is that specific genes are expressed in particular parts of cortex and then "code for" patterns of wiring particular to certain computational functions. While this type of explanation appears to be valid for specialized computations within subcortical structures, a variety of genetic, neurobiological, and cognitive neuroscience evidence indicates that it is, at best, only part of the story for many human cognitive functions dependent on cerebral cortex.

I have previously outlined three viewpoints on human functional brain development (e.g. Johnson, 2001). According to a "maturational" perspective, functional brain development involves the sequential coming "on line" of a number of modular cortical regions. The maturation of a given region is thought to allow or enable advances in the perceptual, cognitive, or motor abilities of the child. As applied to the neurodevelopment of face perception, this implies that (p. 10) more complex aspects (such as "theory of mind" computations) will depend on the sequential maturation of associated cortical regions (possibly within the prefrontal cortex). This view fits best with the domain specificity hypothesis in the adult literature.

The second perspective on human functional brain development, “skill learning,” argues for parallels between the dynamic brain events associated with the acquisition of complex perceptual and motor skills in adults, and the changes in brain function seen as infants and children come to successfully perform simpler tasks. From this perspective, it has been argued that some cortical regions become recruited for processing face stimulus information because typical humans become perceptual experts in this domain (Gauthier and Nelson, 2001). This view, then, clearly fits with the expertise hypothesis in the adult literature.

A third perspective, “interactive specialization,” posits that functional brain development, at least in cerebral cortex, involves a process of specialization in which regions go from initially having very broadly-tuned functions, to having increasingly finely-tuned (more specialized) functions (Johnson 2001, 2002). A consequence of increased specialization of cortical regions is the increasingly focal patterns of cortical activation resulting from a given task demand or stimulus. By this view, some regions of cortex gradually become increasingly specialized for processing social stimuli and thus become recruited to face perception computations.

How does the empirical evidence from the neurodevelopment of face perception fit these views? The evidence available from positron emission tomography and electroencephalography/ERP studies suggests that most of the brain areas and mechanisms implicated in adult face processing can be activated relatively early in postnatal life. However, there are some additional effects, such as the activation of the inferior frontal and superior temporal gyrus in response to faces in 2-month-olds (Tzourio-Mazoyer et al., 2002), and the superior temporal sulcus generator of the face inversion effect found in 3- and 12-month-olds (Johnson et al., 2005), that do not directly map onto the mature face processing system. In addition to the extra regions involved while infants perceive faces, another important observation in the infant ERP work is that the infant face processing system possesses much broader response properties which are not yet as finely tuned to upright human faces (see de Haan, Chapter 38, this volume). This suggests that despite the gradual cortical specialization seen throughout the first year of life, the system continues to specialize well beyond infancy and into childhood.

More direct evidence for or against these models can be gained from fMRI developmental neuroimaging studies with children while they are engaged in face processing. The interactive specialization view predicts that with development there will be increased selectivity (fine tuning) in the activation of cortical areas for specific functions such as face processing. A consequence of this more selective activation of cortical areas is that the extent of cortical tissue activated in a given task context, or in response to a particular stimulus, will decrease and become more focal as the child gets older. This contrasts with the view that such cortical functional specializations are present from birth, or that they mature in a way relatively uninfluenced by experience.

We (Cohen-Kadosh and Johnson, 2007; Johnson et al., 2009) examined the currently available developmental fMRI literature on faces with regard to two hypotheses generated by the interactive specialization approach: 1) Does cortical activation in response to viewing faces become more focal and localized during development? 2) Does the degree of functional specialization (as measured by the degree of tuning to faces) increase in specificity during development? Encouragingly, we found some consistency across the seven developmental fMRI studies conducted to date. Collectively, these studies show that while faces activate specific areas of cortex in children, these areas may occupy more extensive or slightly different regions from those seen in adults. Further, the three most recent studies show evidence of increasing tuning of face-sensitive areas of cortex (Golarai et al., 2007; Passarotti et al., 2003; Scherf et al., 2007) accompanied in some cases by (p. 11) more focal patterns of activation in older children. In general, these dynamic developmental changes in cortical activation were consistent with the predictions of the interactive specialization view. Future studies will no doubt focus more on the emergence of specialized face processing networks during development using functional and structural connectivity measures. To date, the study of face perception during childhood provides perhaps the richest data source for comparing theories of functional specialization in human cortex, illustrating once again the two-way interaction between face perception studies and developmental science.

Summary and conclusions

In this chapter, I have illustrated that face perception has been one of the most important domains of study for our understanding of perceptual, cognitive, and neurocognitive aspects of human development. Additionally, the domain of face perception is one of the oldest battlegrounds for resolving key issues in the nature–nurture debate going back to Darwin and then to the origins of empirical work on human infants in the 1960s. This viewpoint on the history of the field has, of course, reflected my personal perspective and biases. Specifically, I highlighted Johnson and Morton’s (1991) two-process theory of the development of face perception, and reviewed aspects of the theory that have stood the test of time, as well as other parts that have required modification in the light of additional empirical data.

In the next two sections of the chapter I examined how developmental thinking has influenced current research and issues on adult face perception. First, evidence for a putative subcortical route for face processing in adults has been bolstered by data from newborns where evidence suggests that cortical functioning is poor. Second, I suggested that debates about the role of expertise/experience in the activation of the “fusiform face area” could be resolved by theory and recent data from developmental fMRI studies supporting a gradual increase in functional specialization of the region.

Returning to the issue raised at the beginning of this chapter, we can now reconsider the factors, both intrinsic and extrinsic to the human cortex, that ensure that we both develop specialized processing of faces, and that this specialized function usually becomes located in the same parts of cortex in adults. With regard to developing a cortex specialized for face processing, I briefly reviewed evidence that newborns preferentially look toward faces. A number of lines of evidence suggested that this newborn preference is not mediated by the same cortical structures involved in face processing in adults, and may be due to a subcortical route for face detection. One purpose of this early tendency to fixate on faces may be to elicit bonding from adult caregivers. However, I suggest that an equally important purpose is to bias the visual input to plastic cortical circuits. This biased sampling of the visual environment over the first days and weeks of life may ensure the appropriate specialization of later developing cortical circuitry (Morton and Johnson, 1991). In addition to these findings, recent work has shown that newborns prefer to look at faces that engage them in direct (mutual) eye gaze (Farroni et al., 2002). Maintaining mutual gaze with another's face ensures foveation of that stimulus, a fact that may be relevant to the eventual location of "face areas" within the cortex (see Malach et al., 2004). Thus, I suggest, this newborn bias effectively "tutors" the developing cortex and early foveation of faces may, in part, determine the location of face-sensitive areas within cortex. In terms of the nature versus nurture issue, the research on faces has helped us understand the complex interplay between intrinsic and extrinsic factors in which each individual child's brain constructs its own specialized face-processing network. In my view headline claims about "innate face processing" (Sugita, 2009) or perceptual expertise (Gauthier and Nelson, 2001) do the field no justice in that they harp back to polarized debates from over 20 years ago. Usually, when we look more closely at the (p. 12) empirical details the subtle interweaving of nature and nurture is evident (see Maurer and Mondloch, Chapter 40, this volume). For example, the recent work of Sugita (2008, 2009) on monkeys reared without exposure to faces shows that they have abilities similar to those that have already been reported for human newborns, and that they subsequently show a process of perceptual tuning or specialization that is also very reminiscent of reports from human development (see Lee et al., Chapter 39, this volume). Sugita (2009) also speculates that the infant's proprioception or tactile contact with its own face may be important for establishing visual face perception skills, a suggestion that merits investigation with humans also.

What of the future? I believe that face perception will continue to be an important domain for our understanding of general issues in developmental science and vice versa. The application of theories based on typical development to developmental disorders with known atypicality in face processing such as autism, Williams syndrome, and developmental prosopagnosia (Webb et al., Chapter 43; Behrmann et al., Chapter 41; Duchaine, Chapter 42, respectively, this volume), will be a critical application of our basic research. Multimodal imaging offering good temporal and spatial resolution will be critical for discriminating between different theories of the emergence of cortical specialization for face perception (Grossman et al., 2008). Computational and neural network modeling of the emergence of specialization for face perception will be an essential bridge between brain and cognition (see Cottrell and Hsiao, Chapter 21, this volume). Moving from static and schematic to realistic and dynamic face images, presented in both foveal and peripheral visual fields, will be important to ensure that we are not just studying the brain responses to pictures of faces, rather than the real thing. Finally, studying how specific neural circuitry becomes tuned to face perception within the richer context of social cognition and interaction will help us unravel the complex dynamics between babies' experience of interaction with others, and their abilities to detect and analyze the signals from their faces.

References

Bailey, A.J., Braeutigam, S., Jousmaki, V., and Swithenby S.J. (2005). Abnormal activation of face processing systems at early and intermediate latency in individuals with autism spectrum disorder: a magnetoencephalographic study. *European Journal of Neuroscience*, **21**, 2575–2585.

Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J., and Ahluwalia, J. (2000). Is there an innate gaze module? Evidence from human neonates. *Infant Behavior & Development*, **23**, 223–229.

Blasi, A., Lloyd-Fox, S., Everdell, N., *et al*. (2007). Investigation of depth dependent changes in cerebral haemodynamics during face perception in infants. *Physics in Medicine and Biology*, **52**, 6849–6864.

Carey, S., Diamond, R., and Woods, B. (1980). The development of face recognition: a maturational component? *Developmental Psychology*, **16**, 257–269.

Cohen-Kadosh, K. and Johnson, M.H. (2007). Developing a cortex specialized for face perception. *Trends in Cognitive Science*, **11**, 367–369.

Darwin, C. (1872). *The expression of emotion in man and animals.* London: John Murray.

de Schonen, S. and Mathivet, E. (1990). Hemispheric asymmetry in a face discrimination task in infants. *Child Development*, **61**, 1192–1205.

Fantz, R. (1963). Pattern vision in newborn infants. *Science*, **140**, 296–297.

Farroni, T., Csibra, G., Simion, F. and Johnson, M.H. (2002). Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences* (USA), **99**, 9602–9605.

Farroni, T., Johnson, M.H., Menon, E., Zulian, L., Faraguna, D., and Csibra G. (2005). Newborns' preference for face-relevant stimuli: Effects of contrast polarity. *Proceedings of National Academy of Sciences*, **102**, 17245–17250.

Farroni, T., Menon, E., Rigato, S., and Johnson, M.H. (2007). The perception of facial expressions in newborns. *European Journal of Developmental Psychology*, **4**, 2–**13.**

(p. 13) **Gauthier, I. and Nelson, C.** (2001). The development of face expertise. *Current Opinion in Neurobiology*, **11**, 219–224.

George, N., Driver, J., and Dolan, R. (2001). Seeing gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *NeuroImage*, **13**, 1102–1112.

Golarai, G., Ghahremani, D.G., Whitfield-Gabrieli, S., et *al.* (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neuroscience*, **10**, 512–522.

Goren, C.C., Sarty, M., and Wu, P.Y.K. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics*, **56**, 544–549.

Grossman, T., Johnson, M.H., Lloyd-Fox, S., et *al.* (2008). Early cortical specialization for face-to-face communication in human infants. *Proceedings of the Royal Society B*, **275**, 2803–2811.

Johnson, M.H. (1990). Cortical maturation and the development of visual attention in early infancy. *Journal of Cognitive Neuroscience*, **2**, 81–95.

Johnson, M.H. (2001). Functional brain development in humans. *Nature Reviews Neuroscience*, **2**, 475–483.

Johnson, M.H. (2005). Sub-cortical face processing. *Nature Reviews Neuroscience*, **6**, 766–774.

Johnson, M. and Morton, J. (1991). *Biology and cognitive development. The case of face recognition.* Oxford: Blackwell.

Johnson, M.H., Bolhuis, J.J., and Horn, G. (1985). Interaction between acquired preferences and developing predispositions during imprinting. *Animal Behaviour*, **33**, 1000–1006.

Johnson, M.H., Dziurawiec, S., Ellis, H., and Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, **40**, 1–19.

Johnson, M.H., Griffin, R., Csibra, G., et *al.* (2005). The emergence of the social brain network: Evidence from typical and atypical development. *Development and Psychopathology*, **17**, 599–619.

Johnson, M.H., Grossman, T., and Farroni, T. (2008). The social cognitive neuroscience of infancy: illuminating the early development of the social brain functions. *Advances in Child Development and Behavior*, **36**, 331–372.

Johnson, M.H., Grossmann, T., and Cohen-Kadosh, K. (2009). Mapping functional brain development: Building a social brain through Interactive Specialization. *Developmental Psychology*, **45**, 151–159.

Kanwisher, N., McDermott, J., and Chun, M.M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, **17**, 4302–4311.

Kleinhans, N.M., Richards, T., Sterling, L., et *al*. (2008). Abnormal functional connectivity in autism spectrum disorders during face processing, *Brain*, **131**, 1000–1012.

Le Doux, J. (1996). *The Emotional Brain: The Mysterious Underpinnings of Emotional Life*. New York: Simon & Schuster.

Malach, R., Avidan, G., Lerner, V., Hasson, U. and Levy, I. (2004). The cartography of human visual object areas. In N. Kanwisher and J. Duncan (eds.), *Attention and Performance XX: Functional Neuroimaging of Visual Cognition*, pp. 195–204. Oxford: Oxford University Press.

Morton, J. and Johnson, M.H. (1991). CONSPEC and CONLERN: A two-process theory of infant face recognition. *Psychological Review*, **98**, 164–181.

Nelson, C.A. (2003). The development of face recognition reflects an experience-expectant and activity-dependent process. In O. Pascalis and A. Slater (eds.), *The development of face processing in infancy and early childhood: Current perspectives*. pp. 79–98. New York: Nova Science Publisher.

Passarotti, A.M., Smith, J., DeLano, M. and Huang, J. (2007). Developmental differences in the neural bases of the face inversion effect show progressive tuning of face-selective regions in the upright orientation. *Neuroimage*, **15**, 1708–1722

Quinn, P.C. and Slater, A. (2003). Face perception at birth and beyond. In O. Pascalis and A. Slater (eds.), *The development of face processing in infancy and early childhood: Current perspectives*. pp. 3–12. New York: Nova Science Publisher.

Scherf, K.S., Behrmann, M., Humphreys, K., and Luna, B. (2007). Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. *Developmental Science*, **10**, F15–F31.

(p. 14) **Senju, A. and Johnson, M.H.** (2009). The eye contact effect: mechanisms and development. *Trends in Cognitive Science*. **13**, 127–134.

Simion, F., Macchi Cassia, V., Turati, C., and Valenza, E. (2003). Non-specific perceptual biases at the origins of face processing. In O. Pascalis and A. Slater (eds.), *The development of face processing in infancy and early childhood: Current perspectives*. pp. 13–26. New York: Nova Science Publisher.

Slater, A., Von der Schulenburg, C., Brown, E., and Badenoch, M. (1998). Newborn infants prefer attractive faces. *Infant Behavior and Development*, **21**, 345–354.

Slater, A., Quinn, P.C., Hayes, R., and Brown, E. (2000). The role of facial orientation in newborn infants' preference for attractive faces. *Developmental Science*, **3**, 181–185.

Sugita, Y. (2008). Face perception in monkeys reared with no experience to faces. *Proceedings of the National Academy of Sciences* (USA), **105**, 394–398.

Sugita, Y. (2009). Innate face processing. *Current Opinion in Neurobiology*, **19**, 39–44.

Tomalski, P., Csibra, G., and Johnson, M.H. (2009a). Rapid orienting toward face-like stimuli with gaze-relevant contrast information. *Perception*, **38**, 569–578

Tomalski, P., Johnson, M.H., and Csibra, G. (2009b). Temporal-nasal asymmetry of rapid orienting to face-like stimuli. *Neuroreport*, **20**, 1309–1312.

Tzourio-Mazoyer, N., de Schonen, S., Crivello, F., Reutter, B., Aujard, Y., and Mazoyer, B. (2002). Neural correlates of woman face processing by 2-month-old infants. *Neuroimage*, **15**, 454–461.

Winston, J.S., Vuilleumier, P. and Dolan, R.J. (2003). Effects of low-spatial frequency components of fearful faces on fusiform cortex activity. *Current Biology*, **13**, 1824–1829.

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