The development of face expertise

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Recent neuroimaging studies in adults indicate that visual areas selective for recognition of faces can be recruited through expertise for nonface objects. This reflects a new emphasis on experience in theories of visual specialization. In addition, novel work infers differences between categories of nonface objects, allowing a re-interpretation of differences seen between recognition of faces and objects. Whether there are experience-independent precursors of face expertise remains unclear; indeed, parallels between literature for infants and adults suggest that methodological issues need to be addressed before strong conclusions can be drawn regarding the origins of face recognition.

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Abbreviations

ERP	event-related potential
fMRI	functional magnetic resonance imaging

Introduction

The study of the ontogeny of face recognition has a long and illustrious history, dating at least back to Darwin [1]. Interest in the topic has been rekindled recently by those studying adult face recognition. Whereas some authors remain agnostic as to whether specialization for faces is innate or learned [2], others argue that face perception is special [3] — even specified in the genome — and thus does not require experience in order to develop (see [4•]). A different view is that cortical specialization for faces results from fine-tuning by expertise of parts of the visual system especially well-suited for fine visual discrimination [5••,6••]. Support for both views is found in the developmental literature. Newborns just a few hours old often display visual preferences for face-like stimuli, suggesting an experience-independent ability [7,8]. In contrast, although six-month-old infants show different patterns of brain activity (recorded using event-related potentials [ERPs]) to faces versus objects, such differences may well result from differential experiences with these classes of stimuli (see [9,10••]). Here, we review the recent literature, looking for links between the developmental and adult work concerning the long-debated question of whether faces are special or not.

Face perception as a learned behavior

Expertise with nonface objects such as cars and birds recruits ventral temporal regions of the adult brain that are selective for face processing [6••]. This converges with studies showing that behavioral effects selectively obtained for faces in some studies [3,11] can also be found with nonface objects in experts [12,13]. These results contradict the idea of a 'module' for face recognition, because they violate Fodor's criteria of 'information encapsulation' (crucial to the definition of a module [14]) and of domain specificity (a hallmark of modular systems according to a neo-Fodorian approach [15••]). Thus, specialization for faces (functionally and anatomically) in adults could simply be the result of our experience with these objects (i.e. we recognize faces at a more specific level than most objects and we acquire a lot of expertise for such judgements throughout our lives [16]).

A corollary is that, without expertise, face processing would not be differentiated from that of other objects. However, there is evidence that faces and nonface objects are processed differently in the infant brain (for reviews, see [9,10••,17]). Unfortunately, because of methodological limitations, it is impossible to ascertain whether such 'specialness' is attributable to experience or represents an experience-independent process (see [18]).

Lessons from history

Experiments with infants and adults evaluate the putative special status of faces, and many of the methodological issues involved should be relevant for both adults and children. Studies with adults are more numerous and more easily conducted, however, so it is not surprising that methodological arguments have developed somewhat faster in this field (i.e. issues that have for the most part been addressed in adult work are starting to be raised regarding developmental studies).

One example of such problems is the influence that our belief that faces are special can have on experimental design. For example, researchers compare faces to another category of objects, or to a condition that includes many other nonface objects (F/O designs). Such designs provide evidence that, according to measure X (a behavior or a measure of neural activity), faces are processed differently from one nonface category (or the average of many). However, they ignore whether measure X also differentiates among other categories of nonface objects (this can only be tested when different object categories are also contrasted — an F/O/O design). If object categories can be dissociated, the hypothesis that measure X is sensitive to the 'faceness' of the stimuli can be questioned. Rather, it could be sensitive to another dimension on which faces score highly but other categories also vary. Two factors need to be overcome in order to see the value of the improved design. First, we often can see no reason why processing of two nonface categories should differ (making a study less likely to be conducted). Second, if a difference is obtained, we may lack an interpretation for the effect (leading to less emphasis in the literature on differences between object categories).

Despite the unexpected quality of dissociations between nonface categories, they are often obtained when designs allow them to emerge. Many early functional neuroimaging experiments used F/O designs and described how a part of the right fusiform gyrus is more active for faces than for objects ([2,19,20]). Similarly, many single-cell recording experiments in monkeys over-represent faces in their stimulus set and then find a large proportion of face-selective cells compared to object-selective cells (see [21] for a discussion). Recently, experiments using F/O/O designs have revealed differences between nonface categories around the putative 'face area'. For instance, one area was consistently more active for chairs than for faces and buildings [22••]. A single-cell recording study in humans revealed specialization for nonface categories (e.g. animals, cars and household objects) in the hippocampus, enthorinal cortex and amygdala [23•]. In this case, faces did not lead to the largest proportion of category-selective responses (e.g. in the amygdala and enthorinal cortex, more cells were selective for animals, scenes or objects, and non-emotional faces led to approximately the same proportion of category-selective response as did cars).

Other experiments report differences between object categories within the 'face area' depending on the task, context and experience of the subjects. The same objects engage the 'face area' more if they have to be matched to specific rather than general labels (e.g. Saab versus car for the same picture) [24,25]. More activity is obtained in the 'face area' for objects shown in the context of other objects of the same category (e.g. birds or cars shown in succession) than for objects shown among objects of various classes [6••]. Objects (birds, cars and novel computer-generated objects such as the 'Greebles' used by Gauthier, Tarr and their colleagues [5••]) also elicit more activity in the fusiform face area (FFA) in subjects who are experts at discriminating them compared with novices [5••,6••].

The neuropsychological and electrophysiological literature also contains examples of surprising object dissociations. Prosopagnosic patient 'LH' showed superior performance with inverted faces than upright faces, a dissociation which contrasts with the typical upright advantage in normals and which was interpreted initially as a clear demonstration for a face-specific system [26]. This interpretation was questioned, however, when another patient [27], and later 'LH' himself [28•], demonstrated the same advantage for inverted shoes and houses. Similarly, many ERP studies described a potential occurring at 170 ms post-stimulus onset (the 'N170', so called because it is manifest as a negative deflection occurring 170 ms after stimulus onset) with a larger amplitude for faces than for nonface objects [29,30]. However, the interpretation of this effect has been constrained recently by an experiment showing that when activity for various object categories is compared, the N170 shows robust differences between some of them (e.g. cars and shoes) which are bigger than the difference between faces and certain other categories (e.g. faces and cars) [31•]. Crucially, even though we do not yet understand the significance of these effects with objects, these observations nonetheless directly address the implicit assumption that there is no reason for nonface categories to show differences for measures that are supposedly face-sensitive. Ultimately, our understanding of the visual system will be very different depending on whether only faces can be dissociated from other objects or whether object category differences are a pervasive pattern.

Face preferences in infants

When considering the evidence from infant studies that faces are special, it is important to ask whether the effects obtained with face-like stimuli were given a chance to emerge in tests using nonface objects. Would this change our interpretation of the effects with faces? A famous phenomenon from infant work is a preference for face-like patterns found in newborns tested as early as nine minutes after birth [7]. This argues for an experience-independent mechanism that directs attention to face-like patterns [8,17]. Such effects are typically small, and discrepant findings (see e.g. [32]) have been blamed on methodological differences such as the complexity of the stimuli or the measure of visual preference. The finding of a preference for an upright 'config' stimulus (two small black squares on top of a central one, in an oval outline) over an inverted config was replicated recently in newborns within two hours of birth [33••]. Interestingly, a preference for face-like patterns is often found after two months of age and in newborns, but it is not found in infants *between* these ages [8]. In the recent replication [33••], the config preference was not obtained at six and 12 weeks of age. Both six- and 12-week-olds showed a preference for a stimulus with only the amplitude spectrum of a face over that with only the phase spectrum of a face. Moreover, only 12-week-olds preferred a positive- over a negative-contrast face.

Thus, stimulus preferences in infants change over time. These changes are often taken as evidence for a switch from one mechanism to a different one as infants develop. One model proposes that a mechanism (largely under the control of the superior colliculi) — termed 'CONSPEC' — exists early in life, directing infants to moving objects, particularly faces [8]. As infants approach two months old, CONSPEC is replaced by 'CONLERN', a mechanism for learning differences between individual faces that is largely under cortical control. Morton and Johnson [8] coined the terms: CONSPEC is thought to be innate and provides information about biologically relevant objects, whereas CONLERN stands for a variety of mechanisms that could mediate learning of particular members of one's species. In light of these changes, it is hard to relate infant preferences to any one of the cortical face-sensitive systems studied in the adult — for example, those implicated in face discrimination or eye gaze processing [34••]. The possibility that these changes reflect learning (rather than a pre-determined unfolding of behaviors) is suggested by demonstrations of very rapid visual learning in newborns. In a study by Walton and Bower [35], newborns who were shown four briefly flashed faces (400 ms each) for only a few repetitions preferred to look at a composite of these four faces than at a composite of four new faces. This learning took place with less than one minute of exposure to the entire set of faces. Given that the difference between two composite faces is far more subtle than that between an upright and an inverted face or face-like pattern, this suggests that any face preference could be learned — and learned rapidly. It would seem important, however, to demonstrate the same learning skills with nonface stimuli.

The newborns in the Walton and Bower [35] study demonstrated a familiarity preference and were reportedly tested in an 'alert' state. This is interesting because newborns and one-month-olds have been found recently to shift from a familiarity preference before feeding to a novelty preference after feeding, this effect being attributed to higher arousal before feeding [36•]. A prevailing view is that infant preferences for familiar stimuli reflect a failure to completely encode stimuli. In contrast, evidence of memory *per se* is inferred only when infants prefer the *novel* stimulus. In the case of the Walton and Bower study, this could mean that infants never fully learned (remembered) the four faces initially presented. However, in order to fully understand the interaction between arousal and memory in infants, one would need to dissociate the effect of arousal during the learning and testing phases. Obtaining the same interaction when arousal is manipulated only at test would argue against the classical interpretation of novelty and familiarity effects.

If face specialization is learned, do we have a model for its development? Recent neural network modeling shows that specialization of a face-processing module can arise in a system initially nonspecialized for categories in part of the network receiving low-spatial-frequency information [37••]. This happened when the network was trained to discriminate between faces at the individual level while performing categorization on objects at a more general level (e.g. book versus cup versus can). This is merely a demonstration of how specialization for faces can arise through experience, but it should be noted that the basic ingredients of this model seem ecologically valid. Infants may indeed be biased rapidly to process faces at the individual level as they learn to discriminate their mother's face from other faces, and the infant's visual world is one that is limited to low spatial frequencies [38].

Studies of newborn preferences are, to a large degree, conducted according to F/O designs in the same manner as has been prevalent in the adult literature. F/O/O designs could change the manner in which we interpret newborn preferences for face-like patterns. When such preferences are investigated in older infants (i.e. three- and four-month-olds), reliable preferences have been found for cats over horses, tigers over cats, chairs over tables and mammals over birds [39]. Although there may be no obvious reason to expect such O/O dissociations in newborns, such unexpected effects have been found in adults when tests allowed them to emerge and they force us to reassess our assumptions.

Categorization and discrimination

Category preferences in infants are not easy to relate to adult processing, because adults are typically not tested for what stimuli they prefer. It would seem easier to relate infant categorization and discrimination skills to similar processes in adults, as there is little evidence that these infant processes are not simply the precursors of homologous ones later in life. Given the functional plasticity observed in the adult [5••], can we expect that the infant perceptual system be any less flexible and capable of learning across multiple categories?

In familiarization–novelty preference procedures, three- to four-month-old infants can discriminate and categorize cats and dogs and appear to do so using information centered on the face and head [40]. Although this could be taken as evidence for a face bias, infants can also do this on the basis of head silhouettes (with no internal detail), but not body silhouettes alone [41••]. It is possible that the head region contains particularly diagnostic cues to distinguish between these two categories [42]. This shows clearly that categories can be differentiated by infants without the use of a 'CONSPEC' mechanism for crude internal features of faces [8]. It raises the question of whether stimulus preferences play a necessary role in the development of later-learned discrimination abilities [8].

In adults, face-like processing can be recruited for many domains, such as cars or birds, dogs or Greebles [5••,12,16]. Perhaps no head-start is required for a category to recruit expert recognition processes of the sort we have for faces? A recent study [43••] found abnormalities in the right fusiform region of autistic adults for face but not object identity judgements, despite no obvious anatomical abnormality in this part of cortex. A right fusiform abnormality in autism was confirmed in a later study [44], where it was also found for sex and emotion judgements. One hypothesis is that autistic people lack the expertise that would have specialized this region of their brain for faces; that is, faces in them lacked the proper 'head-start'. This work suggests that there may be mechanisms present in normally developing children that are necessary to develop face expertise.

Another syndrome receiving attention recently is prosopagnosia acquired as a result of damage to ventral temporo-occipital cortex in infancy [4•]. In one case, Adam — a 16-year-old who sustained brain damage at one-day of age (although exactly which regions were damaged at that time remains unknown) — showed profound impairments in tasks with pictures of faces. There was also a more moderate deficit with common objects. Farah *et al.* [4•] concluded that 'the distinction between face and object recognition, and the anatomical localization of face recognition, are explicitly specified in the genome'. However, the neuropsychological evidence obtained from Adam would not be considered strong evidence of a face-specific deficit in an adult patient. In particular, his ability to process visually similar nonface objects was not assessed [45] and his response times were not considered [46]. In addition, as there is clear evidence for specialization for faces in a consistent region of the adult brain, it should be expected that damaging this region of the brain would impair the development of face recognition — even if it is only because this part of the visual system would be the best suited for learning to discriminate visually similar objects. An analogy is that abnormalities in parts of the brain that are important for acquiring reading skills may cause developmental dyslexia, even without reading being explicitly specified in the genome [47].

Our best hope for understanding how the infant system develops into an adult expert face recognizer may lie in detailed studies of the intermediate stages of development. Most of the work on infants' recognition of faces is based on behavioral studies, such as infants' preferences for one face over another. However, this tells us little about the underlying neural substrate for face recognition. Accordingly, Nelson and colleagues [9,10••] conducted a series of studies in which they recorded ERPs as infants were presented with familiar and unfamiliar faces (see e.g. [9]) and objects [10••]. From this work, three important points have been discovered about six-month-old infants. First, they show more right (over left) occipito-temporal activity to faces versus objects (with objects being more bilaterally represented). Second, there is a particular component of the ERP called the P440 component that is shorter in latency to faces than it is to objects (and which has been thought to be a developmental precursor to the N170 component observed in adults). Third, there is differential brain activity to familiar versus unfamiliar faces *and* objects. Unfortunately, in these investigations, no control was exerted over exposure to faces (which would be likely to require an unfeasible deprivation study); thus, the degree to which this pattern of activity depended on exposure to faces (particularly as newborns were not tested) remains uncertain.

Conclusions

Findings from the adult and infant literatures are not easily reconciled, and at least four different interpretations need to be considered:

1) Face perception in infants and adults relies on the same mechanism, already modular at birth.

2) There is a modular mechanism for face processing at birth that becomes more general with development.

3) There is a modular mechanism for face processing at birth that is different from a more general mechanism implicated in adult face recognition.

4) There is a general mechanism at birth that is recruited for faces very early in development. The same or a different mechanism in adults can be recruited for recognition of other categories.

The first hypothesis is not supported by the adult literature on expertise — behavioral and neural signatures of face-specific effects can be obtained with nonface objects in expert subjects, so the mechanism for face processing, at least in adults, cannot be truly modular [5••,6••]. The second hypothesis suggests a modular system that becomes increasingly general. Although this is a possibility, it would be the first instance of such a developmental pattern. In brain and cognitive development, there is generally a gradual 'modularization' rather than the other way around [48]. Furthermore, given that the input domain for cognitive and perceptual systems generally *narrows* with development, we may want to leave open the possibility of a general-to-modular progression in development of face processing [49••]. Thus, one possibility is that although adults can learn to recruit a face-processing system for nonface objects, the effort required is more than it would be at a younger age. By analogy, as we grow older it becomes more difficult to acquire another language, although we can do so with enough effort. To test this hypothesis, we would need to compare the rate of perceptual learning in infants and adults, which is complicated by the profound differences in the visual system at different developmental stages.

The last two options both build on recent evidence on adult expertise to argue for a system in adulthood that is not modular and that can be recruited by expertise for discriminating objects from visually similar categories [16]. The first of these options is akin to the traditional CONSPEC/CONLERN theory [8]. As we have reviewed here, this model should be preferred only if appropriate control evidence becomes available from infants. First, we need to demonstrate convincingly that face preferences cannot be learned, as the infant visual system has been shown to learn extremely rapidly [35,50••]. Second, unless more F/O/O comparisons are performed with infants, the differences found between faces and objects may be inappropriately interpreted. That is, a face preference may be only one of several category preferences present in the newborn, including some that are unlikely to be innate. If this were the case, it would suggest that we need a better understanding of the newborn visual system and how its limitations influence the complex task of making sense of the visual world.

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

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This is an excellent review of the concepts related to modularity. A neo-Fodorian approach is described and it is shown that domain-specificity is most important as a criterion of modularity. It is also suggested that we abandon the idea that modules cannot be 'assembled' from subprocesses.

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•• **recognition**. *Infant Child Dev*, in press.

This paper reviews the literature on whether faces are accorded special status by the brain. After briefly summarizing what is known about face processing in adult human and nonhuman primates with and without brain damage, the author reviews extensively the literature on the ontogeny of face perception. A model (adapted from the field of speech perception) of how infants come to become expert at recognizing faces is offered.

50. Maurer D, Lewis TL, Brent HP, Levin AV: **Rapid improvement in the**
•• **acuity of infants after visual input**. *Science* 1999, 286:108-110.

This is a study of visual acuity in children who have undergone congenital cataract removal. Acuity improves significantly after as little as one hour of visual input, suggesting that the newborn's visual system responds quickly to visual stimulation and is especially plastic at this early age.