Can generic expertise explain special processing for faces?

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Does face recognition involve face-specific cognitive and neural processes ('domain specificity') or do faces only seem special because people have had more experience of individuating them than they have of individuating members of other homogeneous object categories ('the expertise hypothesis')? Here, we summarize new data that test these hypotheses by assessing whether classic face-selective effects – holistic processing, recognition impairments in prosopagnosia and fusiform face area activation – remain face selective in comparison with objects of expertise. We argue that evidence strongly supports domain specificity rather than the expertise hypothesis. We conclude that the crucial social function of face recognition does not reflect merely a general practice phenomenon and that it might be supported by evolved mechanisms (visual or nonvisual) and/or a sensitive period in infancy.

Introduction

How are faces recognized? In particular, are the cognitive and neural processes that are used for identifying faces the same as or different from those that are used to recognize other objects? Evidence has shown that they can be different, with faces processed in a more holistic or configural fashion than objects [1–3] and preferentially activating the cortical region known as the fusiform face area (FFA) [4]. Recently, debate has centred on whether face processing is always different from object processing in these respects (referred to as 'domain specificity') or whether visual processing of faces only seems to be special because people have greater expertise in individuating faces than in performing within-class discrimination of other object classes ('the expertise hypothesis'). The primary aim of this Opinion article is to summarize key new evidence from multiple approaches – behavioural studies, neuropsychology, brain imaging and monkey single-unit recording – that we argue strongly favours face specificity over expertise.

What is the expertise hypothesis?

The expertise hypothesis [5] attributes putatively face-specific processing to form-general mechanisms that can potentially apply to all objects; these mechanisms are restricted to faces in most people only because the typical human adult is highly practised at identifying individual faces (e.g. Mary versus Jane) but is poor at discriminating members of other object classes (e.g. two Labrador dogs). Importantly, the hypothesis is a specific proposal about the cause of 'special' processing for *faces* (holistic processing and a face-specific, distinct neural substrate); it is not merely a statement of the uncontroversial fact that experience influences perception. Nor is it a theory about how experience affects object recognition; understanding these effects is important but orthogonal to the hypothesis, except where putatively face-specific properties are tested. Also note the explicit [5] or implicit [6] assumption of the hypothesis that expertise leading to special face-like processing can occur at any age; it is not, for example, limited to experience obtained in childhood or infancy.

The crucial prediction of the expertise hypothesis is that, in the rare circumstances where someone has trained to become a perceptual expert in another domain (e.g. a dog-show judge), then faces should no longer be unique. Instead, the hallmarks that usually differentiate face processing from object processing should also emerge for objects of expertise.

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Available online 28 November 2006.

Glossary

Holistic or configural processing: empirical evidence in standard behavioural paradigms (Figure 1) indicates that faces are recognized using a different style of computation from objects. The difference is not precisely understood, but it is established that, in comparison to objects, processing for faces involves (i) a stronger and mandatory perceptual integration across the whole (in one theory, the mechanism does not decompose faces into smaller parts [2]) and (ii) a more precise representation of the 'second-order' deviations from the basic ('first-order') shape, including precise spatial-relational information (e.g. distance from corner of left eye to tip of nose) and precise feature shape [11]. This computational style is referred to as holistic or configural processing (terminology differs among researchers), notwithstanding the use of these same terms to refer to something less stringent in other areas of vision science (e.g. the general processing of global structure that occurs in context and gestalt effects) and cognitive psychology (e.g. field dependence).

Inversion effect: performance decrement for upside-down stimuli compared with upright stimuli.

Level of expertise: ***novices*** might have general familiarity with an object class, in its usual upright orientation, but are poor at telling members of an object class apart (e.g. 20 upright Labrador dogs will all look much the same to a novice). ***Experts*** have good within-class discrimination for an object class. Most studies test real-world experts (e.g. dog-show judges [5]) who have 5–30 years of experience. Some studies use 8–10 hours of laboratory training with ***greebles***, a class of novel animal-like objects [6].

Prosopagnosia: a severe deficit in recognizing faces following brain injury (acquired) or through failure to develop the required mechanisms (developmental). In pure cases, most probably arising from localized lesions or localized developmental irregularities, the disorder manifests without object-recognition deficits.

www.sciencedirect.com 1364-6613/$ – see front matter doi:10.1016/j.tics.2006.11.002

Faces versus objects of expertise: holistic processing
In evaluating this prediction, first we consider behavioural studies of holistic processing (see Glossary). In novices, it is accepted that face and object processing dissociate in several classic paradigms, illustrated in Figure 1. Early research indicated that the inversion effect is much more severe for faces than for other object classes, even when the tasks are matched and require within-class discrimination [7]. This difference was attributed to upright faces being processed holistically, and inverted faces and objects (in both orientations) being processed in a parts-based fashion. The disproportionate inversion effect does not demonstrate this directly. Direct demonstration was subsequently provided by two paradigms. In the part–whole effect [2], memory for a

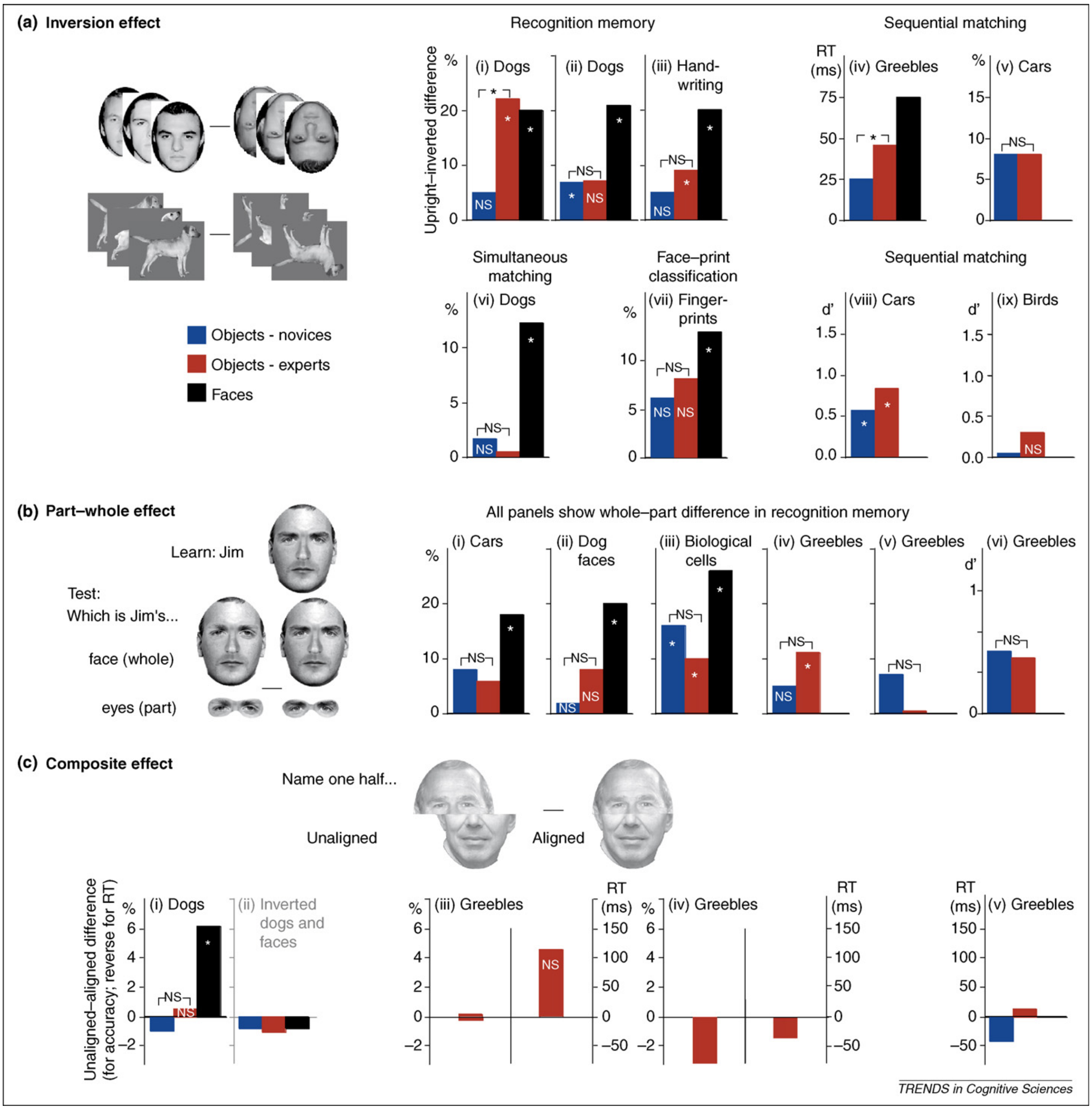

Figure 1. No holistic processing for objects of expertise. **(a)** Inversion effects [7] for homogeneous objects increase little with expertise and do not become face-like, even in a recent direct replication (see (ii) and (vi); data taken from Ref. [1]) of the classic Diamond and Carey experiment using dogs (see (i); data taken from Ref. [5]). (Instead, in most studies, experts improve relative to novices for both upright and inverted stimuli, which suggests expertise in part-based processing.) Data taken from Ref. [43] in (iii), Ref. [44] in (iv), Ref. [16] in (v), Ref. [45] in (vii) and Ref. [15] in (viii) and (ix). **(b)** The part–whole effect [2] does not increase with expertise and does not become face-like; unlike inversion, this task assesses holistic processing directly. Data taken from Ref. [46] in (i)–(iii), from Ref. [6] in (iv), from Ref. [47] in (v) and from Ref. [48] in (vi). **(c)** In another direct test of holistic processing, the composite effect [3] is not found for objects of expertise, in contrast to strong effects for upright faces. The two double-panel plots in (iii) and (iv) show cases where both accuracy (%) and reaction time (RT) were reported. Data taken from Ref. [1] in (i) and (ii), from Ref. [47] in (iii) and (iv), and from Ref. [6] in (v). Some studies measured signal-detection discriminability (d′). Abbreviations: *, $p < 0.05$; NS, $p > 0.05$. Statistical symbols within bars refer to comparison to zero; symbols above bars refer to comparison between conditions; missing bars or statistics indicate information not tested or not reported in the original study.

face part is much more accurate when that part is presented to subjects in the whole face than when it is presented alone; in the composite effect [3], aligning two half faces of different individuals increases reaction times (or decreases accuracy) for tasks that require perception of either half independently, compared with an unaligned condition. For upright faces, these effects are strong; for inverted faces, they are absent; and for objects, in novices, they are weak (part–whole) or absent (composite) (Figure 1).

Are these classic hallmarks of face processing found for objects of expertise? Figure 1 illustrates results from all available studies. We argue that the results favour face specificity. Objects of expertise are processed in the same way as objects in novices and not in the same way as faces. One exception to this general rule is presented by Diamond and Carey [5], who found that dog experts looking at their breed of expertise showed as large an inversion effect as they did for faces. This highly cited finding has had an extensive influence on the field. However, in the 20 years since its publication, no replication of the finding has appeared in the literature. Instead, Figure 1 shows that inversion effects increase only slightly with expertise for a wide range of object classes and expert types. In a recent study [1], we used the original Diamond and Carey procedure – dog experts of 20 years' experience looking at side-on photographs of their breed of expertise – and failed to replicate the original result. Instead, we found no difference between experts and novices for the dog inversion effect. (We suspect the original finding could have been due to experts being familiar, before the experiment, with the dogs tested, which would provide an artificial boost to memory in the upright orientation.)

More direct measures of holistic processing confirm face-like holistic processing does not occur for objects of expertise. Figure 1 shows that the small part–whole effect for objects is no stronger among experts than among novices, and experts do not show a composite effect for objects, including dog experts who are looking at their breed of expertise. The 'part in original whole' versus 'part in feature-spacing-altered whole' version of the part–whole paradigm also shows no greater sensitivity to spacing changes among experts than among novices (see Ref. [1] for a review). Furthermore, we have argued elsewhere [1,8] that a non-standard task that is claimed to show holistic processing by experts [9] merely measures the inability to ignore competing response cues from notionally irrelevant information (as in the Stroop effect), rather than integration of parts into a whole at a perceptual level.

In summary, substantial evidence indicates that face-like holistic processing does not emerge for objects of expertise. These results are contrary to the core prediction of the expertise hypothesis.

Faces versus objects of expertise: neural substrates

The second question is whether identification of faces and objects of expertise engage common or distinct neural substrates.

In neuropsychological lesion studies, face recognition can be damaged independently of object-of-expertise recognition, and vice versa (Box 1). We argue that this unequivocally supports face specificity.

Turning to brain imaging (fMRI) studies, the site of primary interest is the FFA, for several reasons. (i) In novices, the FFA responds at least twice as strongly to faces as to other object classes [4,10]. (ii) Its location is consistent with the critical lesion site for loss of face-recognition ability. (iii) It reflects two of the classic behavioural markers of face processing – greater sensitivity to differences between individual upright faces than differences between inverted faces [11], and holistic processing [12] – which suggests it is a locus of face-specific processing, measured behaviourally. Other face-selective regions (the occipital face area and the superior temporal sulcus) are not detectable in all subjects and seem to perform different functions [13]. Although the FFA responds selectively to faces, it does produce an above-baseline response to non-face objects in novices [4,10]. This might arise in part because limits in the spatial resolution of fMRI can conflate adjacent functional regions (each voxel sums activity over hundreds of thousands to millions of neurons). Recent scans at high resolution have indicated distinct regions selective for faces and for bodies [14], whereas earlier results at standard resolution had conflated faces and bodies. Furthermore, in monkeys, a recent study using the ultimate high-resolution method – single-unit recording within a face-selective patch in monkey cortex – found that 97% of visually responsive neurons in this region were strongly face selective (Figure 2).

The expertise hypothesis predicts that the FFA should be more strongly engaged by objects of expertise than by control objects. Eight studies have tested this prediction. Three report small but significant increases in responses to objects of expertise compared with control objects in the FFA [15,16] or a larger region centred around the FFA [17], two report nonsignificant trends in this direction [18,19] and three report no effect [10,20,21]. Controversy has surrounded the implications of these findings. We argue that the weakness and unreliability of the effects is problematic for the expertise hypothesis. The account we favour is that the effects do not reflect a special role for the FFA in processing objects of expertise but rather an overall increased attentional engagement for these stimuli. For example, car fanatics pay more attention to car stimuli than to other objects, thus elevating neural responses to objects of expertise (which produce a small response in the FFA even in nonexperts; see earlier in this section). Five studies have provided data bearing on the prediction of the attentional explanation that expertise effects for objects should be at least as large in other cortical regions as in the FFA. All five report larger effects of expertise outside the FFA than within it. This includes locations throughout the fusiform [18], parahippocampal cortex (see Figure 6 in Ref. [15]) and the lateral occipital complex, a cortical region near the FFA that is involved in processing object shape, in the three studies that have included localizers for this region [19–21]. Consistent with an attentional explanation is the finding that correlations between the FFA response to objects of expertise and behaviourally measured expertise have been shown in location-discrimination tasks but not in identity-discrimination tasks [10,15], contrary to predictions of the expertise hypothesis. Overall, the data provide no evidence for

Box 1. Neuropsychological evidence of independent neural substrates for faces and objects of expertise

It is generally agreed that prosopagnosia without object agnosia and object agnosia without prosopagnosia can occur, even when tasks are matched to require within-class discrimination for both faces and objects (see Ref. [36]). With respect to the expertise hypothesis, the question is whether the face–object dissociation still holds when the objects are objects of expertise. The expertise hypothesis predicts that ability to recognize objects of expertise should always track ability to recognize faces (e.g. if one is damaged, both should be damaged), whereas the face-specificity view predicts that objects of expertise should track other objects and dissociate from faces.

The evidence supports the face-specific view. Some individuals who have prosopagnosia show relatively pure face deficits but excellent recognition of objects of expertise. For example, following an aneurysm, RM had extremely poor face recognition but retained his expertise with cars, recognizing far more makes, models and years than controls recognized [51]. Figure I shows results from two similar cases. The converse pattern has also been reported; that is, normal face recognition but impaired recognition of former objects of expertise. Cases include MX, a farmer who could recognize faces but who could no longer recognize his cows [52], and CK, who retained perfect face recognition but lost interest in his toy-soldier collection, which numbered in the thousands [53]. No cases have been reported in which recognition of faces and objects of expertise have both been impaired while recognition of nonexpert objects is unimpaired, or vice versa.

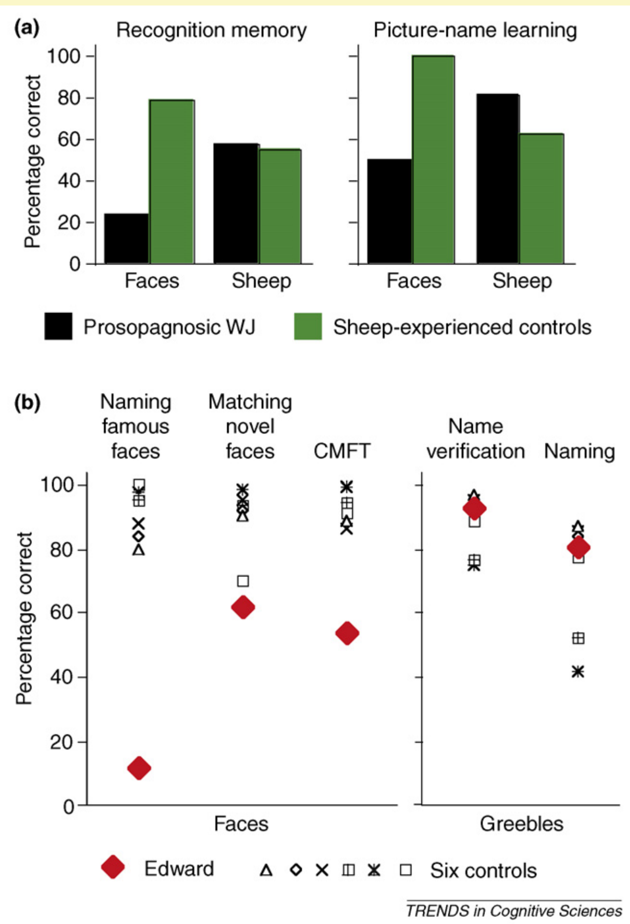

Figure I. Two cases showing that people who have prosopagnosia can become experts with other objects. **(a)** Acquired prosopagnosic WJ retired following vascular episodes and acquired a flock of sheep. Two years later, his recognition of individual sheep was as good as similarly sheep-experienced controls, despite extremely poor human face recognition [54]. **(b)** Developmental prosopagnosic Edward demonstrated severe face-recognition problems on three tasks [naming famous faces, matching novel faces and the Cambridge Face Memory Test (CFMT), which assesses memory for novel faces across changes in view], despite a lifetime of exposure to faces. However, in a training study, Edward learned to identify individual greebles at the same rate as controls, in terms of accuracy and reaction time; scores shown are accuracy in the last two blocks of training [55]. Both cases are consistent with independent neural substrates for face recognition and expertise with other objects.

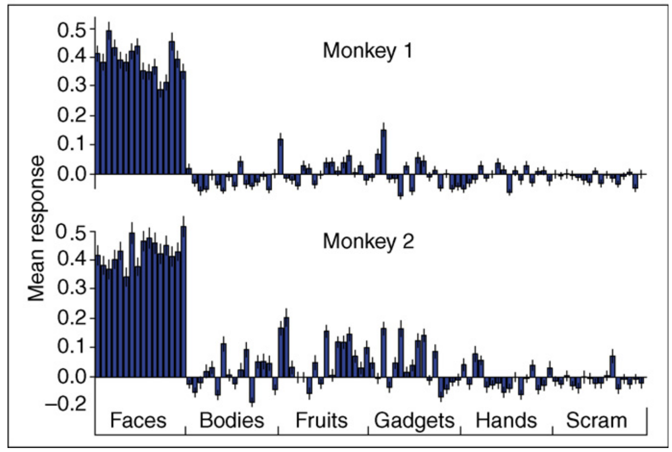

Figure 2. Responses from cells in the macaque middle face patch, located using fMRI by a standard faces-versus-objects localizer task, as used in humans. Averaged responses from all visually responsive cells in two laboratory-raised monkeys (monkey 1, 182 cells; monkey 2, 138 cells) to 96 images of human faces, human bodies, fruits, gadgets, human hands and scrambled patterns (16 images per category). All cells were highly responsive to faces; averaged responses to other categories were extremely weak, including bodies and hands with which the monkeys had as much experience as faces. Figure adapted, with permission, from Ref. [23].

the special relationship between expertise and the FFA predicted by the expertise hypothesis. Instead, fMRI studies are more consistent with the alternative hypothesis that experts pay more attention to their objects of expertise, with corresponding increases in the response of multiple extrastriate regions.

Finally, we consider the single-unit recording approach in monkeys. In this case, there are no direct tests of the expertise hypothesis, in terms of studies that directly contrast responses for faces versus objects of expertise. The most relevant data come from tests of bodies and hands, stimuli for which monkeys have had the same opportunity, and perhaps more motivation [22], to develop expertise as they have for faces. Neurons in the monkey middle face patch [23] do not respond to these stimuli (Figure 2). The point that monkeys, and humans, do not develop expertise in recognizing conspecifics (members of their own species) based on these stimuli is an important argument in favour of domain specificity, to which we return later.

To summarize, we argue that there is clear evidence of different neural substrates for faces and objects of expertise based on neuropsychological cases, and consistent evidence from fMRI and single-unit recording. In the three studies that reported small expertise effects in the FFA, evidence suggests that these effects arise from attentional confounds.

But isn't there other evidence for the expertise hypothesis?

We now briefly describe, and discard, two other arguments that are sometimes made to support the expertise hypothesis. The first concerns development of face recognition in children. Early evidence claimed that children needed ten years of experience of faces to develop the hallmarks of adult holistic processing (see Ref. [24]). This was taken as strong support for the expertise hypothesis [5] (although, logically, late emergence could reflect maturational processes). However, this early evidence was rapidly refuted. All the classic holistic effects of faces have now been demonstrated in children as young as four years, including the inversion effect [24], the composite effect [25], the part–whole effect [26] and sensitivity to exact spacing between facial features [27]. There is even evidence that these effects can be quantitatively mature in early childhood [26,28]. Seven-month-old babies also show holistic-processing effects [29]. Thus, developmental results do not provide support for the expertise hypothesis. (The early emergence of holistic face processing also disposes of the idea that experts might show face-like processing for objects if they were 'more' expert: if babies and young children show clear effects for faces, then surely the ten or more years of experience should be sufficient for significant effects to emerge.)

Second, some have argued in favour of the expertise hypothesis because face recognition is sensitive to experience. For example, holistic processing is affected by race of the face [30] and by training with other-race individuals [31], and FFA activation is sensitive to race [32]. However, such findings are not evidence that learning has taken place within a generic expertise system. The effects are consistent with tuning within face-specific mechanisms.

Other important facts about face recognition

Several other facts about face recognition will be important for the development of a detailed domain-specific theory.

First, exposure to faces in early infancy is essential to develop holistic processing. People born with dense bilateral cataracts blocking all pattern vision input who have them removed at 2–6 months of age show no composite effect at 9–23 years, despite substantial post-cataract exposure to faces [33]. Revealingly, deficits arise with deprivation to the right but not the left hemisphere [34].

Second, six-month-olds can discriminate individual monkey faces but nine-month-olds, like adults, have lost this ability [35]. This loss of an initial ability with non-experienced face types, rather than just improved ability for experienced types, is similar to the loss of initial ability seen in language for discriminating nonexperienced phonemes.

Third, all typically developing humans choose to individuate conspecifics based on the face, rather than some other body part. Despite extensive opportunity to develop expertise with, for example, hands or body shape, adults fail to do so, remaining poor at identifying these stimuli compared with faces – the classic observation is that bank robbers cover their faces rather than cover other body parts. Neural substrates supporting body and hand recognition also differ from those supporting face recognition [4,14,23,36,37].

Fourth, a genetic component is implicated in some cases of developmental prosopagnosia – that is, it seems to run in families [38].

Explanatory theories

So, what is the origin of special processing for faces? Clearly, it is not generic expertise: if it were, then objects of expertise should be processed in the same way as faces, and they are not. Instead, some variant of face specificity is implicated, given evidence that the adult visual system contains specific mechanisms that are tuned to faces as a structural form.

We suggest two general possibilities, which differ in whether they include an innate representation of face structure. Within an 'experience-expectant innate template' theory, we propose that four components would be necessary to explain the major extant findings. First, an innate template would code the basic structure of a face (e.g. this might take the form of eye blobs above nose blob above mouth blob, as in the Morton and Johnson CONSPEC theory [39]). Second, the template must provide the developmental impetus not just for good face recognition [39] but also for the emergence of holistic processing and the grouping of face-selective neurons seen as the FFA in adults. Third, the activation of the template must rely on appropriate input during a sensitive period in early infancy, without which it would no longer function. Fourth, following a typical infancy, the coding of face structure must remain general enough to enable holistic processing to be applied to initially nonexperienced subtypes of faces after practice (e.g. other-race faces), but must be permanently tuned to the upright orientation of faces; this is supported by evidence that adults cannot learn holistic processing for inverted faces (Figure 3). This theory proposes that a face template has developed through evolutionary processes, reflecting the extreme social importance of faces. At the same time, the visual system has maintained an independent and more flexible generic system suitable for recognizing any type of object (including objects that are recent in evolutionary timescales). This theory is consistent with the results we have reviewed. We also know of no results inconsistent with it.

A second variant is that domain specificity for faces is due entirely to biased exposure to faces in early infancy that arises from some factor other than an innate face template. This 'infant experience plus other factor' theory would explain the evidence that holistic processing is restricted to (upright) faces in adults by arguing that faces are the only homogeneous stimuli for which individual-level discrimination is practised during the sensitive period; importantly, the mechanisms supporting this expertise in the infant brain would be necessarily different from those supporting general object expertise in the adult brain. This theory can explain many of the other findings reviewed earlier in this article. For example, heritability of developmental prosopagnosia could arise if there is a genetic abnormality in the 'other factor', rather than in a face template. We have no clear idea what the other factor might be, but possibilities include: faces being presented close enough to infants so they are in focus more often than other stimuli; preference for stimuli that have more elements in the upper half of the visual field [40]; preference for moving stimuli that produce synchronous sound; or infants' prenatal familiarity with their mother's voice [41,42]. All these proposals have potential difficulties: the faces-in-focus idea does not

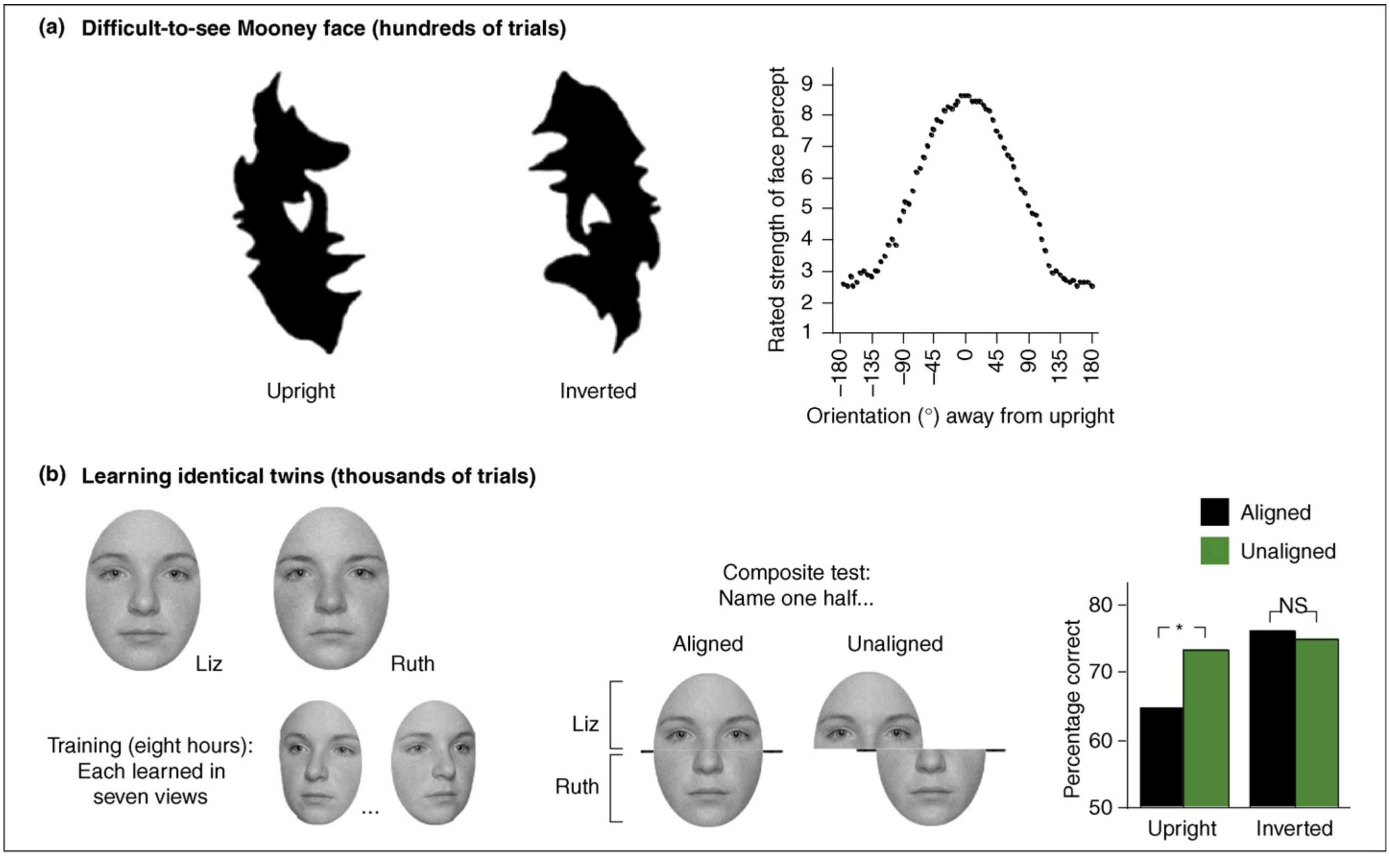

Figure 3. No learning of holistic processing for inverted faces. Both methods illustrated isolate the holistic contribution to face recognition by minimizing the usefulness of information from single local features. **(a)** For this difficult-to-see high-contrast 'Mooney' face, approximately 80% of people perceive the face upright (hint: young attractive female, lit from top right) but not inverted. If the inverted face is not seen within the first few trials, our observation is that it is never seen at all. The plot shows rated strength of the face percept for different orientations averaged over 580 trials [49]. Reproduced, with permission, from Ref. [49]. **(b)** After eight hours of training to distinguish identical twins (2200 trials), subjects who learned the twins inverted showed no aligned–unaligned composite effect, despite a composite effect in control subjects who learned the twins upright. Instead, inverted subjects identified the twins by differences in the way they had combed their eyebrows [50]. Adapted, with permission, from Ref. [50].

provide a natural explanation of the heritability of developmental prosopagnosia; real heads do not have more elements in the upper half; and deaf people are not generally prosopagnosic. However, it remains logically possible that some factor other than an innate template could be the origin of face specificity.

Concluding remarks

Resolution of the debate about whether faces are 'special' is of substantial theoretical importance. In psychology, researchers need to know why faces have special status in regard to crucial social interactions (e.g. parent–infant attachment). There could be no role for critical early infancy effects [33,42] or an evolved representation of face structure [39] if face recognition reflected merely a generic practice phenomenon. Similarly, researchers who are attempting to understand the computational principles of face recognition need to know whether models, particularly of the holistic aspect of face recognition, must be general enough to be applicable to any structural form or whether they can be limited to the (presumably simpler) case of the structural form of faces.

In this article, we have argued that a clear resolution of the debate is implied by the data. Converging evidence from four approaches shows that cognitive and neural mechanisms engaged in face perception are distinct from those engaged in object perception, including objects of expertise.

We have proposed two variants of a domain-specificity theory. To discriminate between these, we suggest future research should concentrate on developmental prosopagnosia and typical infancy. In developmental prosopagnosia,

Box 2. Questions for future research

- What are the patterns of deficit in developmental prosopagnosia (e.g. severity of disorder; face detection versus identity versus expression problems) and how do these relate to neural and genetic abnormalities?
- Do infant animals that have been brought up with atypical stimulus exposure patterns – for example, inverted rather than upright faces, or non-conspecifics – develop holistic processing for those stimuli? (Ethically, these studies cannot be conducted in humans because of the possibility of interference with normal development of upright face processing.)
- In developmental prosopagnosia, is there a common deficit in a nonface factor that might normally draw newborns' attention to faces (e.g. attention to mother's voice)?
- What are the computational or coding advantages of closely packing face cells into a common cortical location?
- How face-like does a stimulus have to be to activate face-specific cognitive and neural mechanisms?
- What processes of neural development produce the adult FFA?
- Do the different face-selective regions differ from each other functionally and are any of these regions homologous across humans and monkeys?
- Computationally and neurally, what might a face 'template' look like and how would it perform holistic processing?

understanding patterns of face versus 'other factor' problems in the disorder should cast light on whether there is an innate face representation. Patterns of inheritance and genes are also of great interest. With respect to typical infancy, an innate face template predicts that an infant monkey preferentially exposed to, for example, dogs or inverted faces would fail to learn holistic processing for those stimuli and could still develop holistic processing only for upright faces. By contrast, if early experience alone is the key factor, it should be possible for infants to learn holistic processing for nonface objects. Questions for future research are outlined in Box 2.

Acknowledgements

Supported by grants ARC DP0450636 (E.M.), EY13455 (N.K.) and ESRC RES-061-23-0040 (B.C.D.). We thank Romina Palermo for part–whole stimuli in Figure 1 and Chris Baker, Lucia Garrido, Gillian Rhodes, Rachel Robbins and Doris Tsao for comments on the manuscript.

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