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Are Faces Special?

Elinor McKone and Rachel Robbins Oxford Handbook of Face Perception

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Abstract and Keywords

The question of "Are faces special?" has essentially referred to whether there are unique visual mechanisms for processing *identity*-related information in faces as compared to other objects. Faces provide unique information about expression, gaze direction, identity, and visual cues to speech. In the literature, however, the debate about whether "faces are special" has referred to the specific question of whether there are special *visual processing mechanisms* unique to faces, presumably deriving from the social importance of faces and developed either across the course of evolution or the course of childhood. This article provides historical background to the question and presents key theoretical findings and key methodological findings. It reviews literature on an evolved face representation, including studies of newborns, face-deprived monkeys and twins; on configural behavioral processing in object experts; and on neural processing in object novices and object experts including single-unit recording, fMRI, ERPs, TMS, and neuropsychological studies.

Keywords: faces, identity-related information, visual processing mechanism, behavioral processing, neural processing

In many ways, of course, the answer to the question "Are faces special?" is obvious. There is no doubt that faces are special *functionally*—that is, faces provide unique information about expression, gaze direction, identity, and visual cues to speech. In the literature, however, the debate about whether "faces are special" has referred to the specific question of whether there are special *visual processing mechanisms* unique to faces, presumably deriving from the social importance of faces and developed either across the course of evolution or the course of childhood. Further, because it is obvious that mechanisms involved in recognizing facial expression, eye gaze direction, and speech cues must be special to faces—these types of information are available in no other objects—the question of "Are faces special?" has essentially referred to whether there are unique visual mechanisms for processing *identity*-related information in faces as compared to other objects.

It is this question we address here. We provide historical background to the question, and then an updated review of the empirical evidence.

The theoretical proposals: faces are special

Historically, several strands can be identified to the proposal that visual representations of faces are special. First, it has been suggested that infants might be born with an innate representation of the structural form of a face (Morton and Johnson, 1991). This would make faces special, because innateness is a property that clearly cannot hold for non-face objects in general: humans can learn totally new forms of objects even as adults (e.g. new inventions such as computers or mobile phones). Second, it has been proposed that a key processing style used for recognizing faces—variously referred to as holistic, configural, or second-order relational —might be unique to faces and does not occur for other objects (Diamond and Carey, 1986; Yin, 1969). Third, it has been proposed that there might be face-specific neural representations (e.g. Kanwisher et al., 1997): common ideas are that: (1) face-

selective neurons are clustered together such that they form face-selective regions visible in functional magnetic resonance imaging (fMRI) (the fusiform face area (FFA) and occipital face area (OFA) being the most relevant for present purposes), (2) face and object regions are capable of being selectively damaged, and (3) there are face-selective event-related potential (ERP) responses (the N170 being the most relevant here).

(p. 150) The theoretical proposals: faces are not special

Two theoretical challenges have been proposed to the idea that faces are special. The first is that apparently face-specific mechanisms are in fact engaged by any within-class discrimination task (Damasio et al., 1982). The logic here is that, with faces, the task (actual or implied) is almost always to identify a face at the individual level of "Mary" or "Jane" rather than merely as "a face," while for objects the natural level of identification for most people is the general level such as "dog" rather than as individuals "Fido" or "Rex"; this could matter because within-class (subordinate level) judgments are perceptually more taxing than basic level categorization. The within-class discrimination hypothesis then proposes that apparently face-specific or face-selective mechanisms will be engaged by individual-level recognition of objects, just as they are by individual-level recognition of faces. In general, it seems well accepted that the within-class discrimination hypothesis has been disproved, and we collate the evidence against it here.

Second, there has been ongoing debate about the *expertise hypothesis* (Diamond and Carey, 1986). This is derived from the within-class discrimination hypothesis. However, rather than proposing that claimed face-specific or face-selective mechanisms are tapped by *all* within-class discrimination situations, it proposes that these mechanisms are tapped by individual-level recognition tasks only in the *special situation in which a person is an expert* at recognizing exemplars of a non-face object category (e.g. in gun dog judges for the stimulus class of Labrador dogs). The logic here is that because people typically are experts at individuating faces but not other objects, apparently face-specific visual mechanisms could in fact be expertise-specific mechanisms. People expert in within-class discrimination of objects are rare, but the case is still theoretically important: if such people show "face-specific" processing for their objects-of-expertise then this would demonstrate that this type of processing is not limited to the face structural form.

Empirical review

We now turn to evaluating the empirical evidence testing whether or not faces are special. This material overlaps with our earlier reviews and discussions (McKone, 2010; McKone, Crookes, and Kanwisher, 2009; McKone and Kanwisher, 2005; McKone, Kanwisher, and Duchaine, 2007; McKone and Robbins, 2007; Robbins and McKone, 2007), but is expanded to include a number of important new results. We will argue the latest evidence supports the view that faces are special in *all* the ways that have been proposed in the literature: that is, in terms of innate coding, holistic processing, and face-specific neural representation in adults.

An evolved face representation

Supporting the view that faces are special, recent studies have provided the first compelling evidence of an evolved and innate representation of face structure, which is involved in discriminating individual faces.

First, the ability to tell apart highly similar faces is found in newborn babies (even when the faces are novel, hair is removed, and there is a viewpoint change between habituation and test; Turati et al., 2006, 2008), and also in young monkeys raised without visual face exposure (Sugita, 2008). These results indicate individuation ability *in the absence or near absence of any prior experience* with faces. Second, *perceptual narrowing across the course of infancy* occurs for faces: experience with faces of one human race tunes out the initial ability to individuate faces of other races and other primate species (Kelly et al., 2007; Pascalis et al., 2002; Sugita, 2008). In other domains (notably language), perceptual narrowing has been taken as strong evidence of innate mechanisms that are experience-expectant. Finally, there is evidence of *heritability* of (p. 151) face recognition ability and neural mechanisms. The lifelong inability to recognize faces revealed in developmental prosopagnosia can affect multiple members of the same family (Duchaine et al., 2007; Grueter et al., 2007; Kennerknecht et al., 2008) including across three generations (Schmalzl et al., 2008). And, in the first twin study of face recognition, the pattern of fMRI

activation across visual areas in the ventral stream was more similar for monozygotic than dizygotic twins, but only when the stimuli were faces and not when they were classes for which it is clear there could be no evolutionary basis for the observed selective cortical regions (i.e. written words, and chairs; Polk et al., 2007).

Other findings are also consistent with the idea of an evolutionarily old face representation. Monkeys, like humans, show face selective cells (e.g. Tsao et al., 2006). Also, chimpanzees, monkeys, and indeed even sheep, demonstrate some key behavioral properties of face recognition found in humans, such as inversion effects that are much larger for faces than objects (chimpanzees: Parr et al., 2009; sheep: Kendrick et al., 1996), and a Thatcher illusion (monkeys: Adachi et al., 2009). (For more detailed discussion of the animal literature, see Kendrick and Feng, Chapter 34; Parr and Hecht, Chapter 35, this volume.)

Finally, evidence suggests the innate representation of face structure is specifically of the *upright orientation*. In newborns, individual-level discrimination occurs only for upright faces, and not inverted faces (Turati et al., 2006), and newborn preference for attractive over unattractive faces is also found upright but not inverted (Slater et al., 2000).

Testing the within-class discrimination hypothesis

We now turn to behavioral and neural results relevant to testing the first alternative theory to the view that faces are special, namely the *within-class discrimination hypothesis*. Crucially, all results reviewed in this section come from studies in human adults contrasting face and object recognition in tasks in which the object condition has involved, like the face condition, *recognition of the objects at the individual level*. (For example, a behavioral experiment might require learning a set of 15 Labradors followed by a memory test presenting the 15 learned Labradors paired with 15 novel Labradors.) The present section deals only with the typical situation in which participants have no particular expertise at discriminating individual exemplars of the tested object class; such participants are referred to as "novices."

A review of the results show that requiring within-class discrimination of objects does not produce face-like processing. This conclusion is derived from multiple paradigms, clearly rejecting the within-class discrimination hypothesis.

Holistic/configural processing

Considering behavioral methods first, the procedures of classic paradigms associated with holistic/configural processing for faces are illustrated in Figures 9.1 and 9.2 (also see Tanaka and Gordon, Chapter 10, this volume). These paradigms produce a strong and replicable dissociation between faces and within-class discrimination of objects.

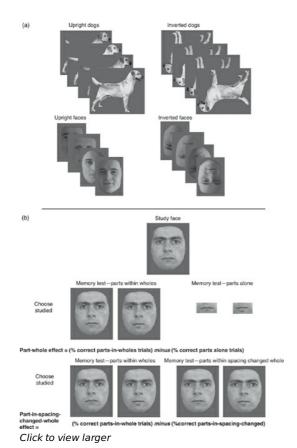


Fig. 9.1 Standards tasks: (a) inversion effect on memory or discrimination, (b) part-whole (Tanaka and Farah, 1993) and part-in-spacing-changed-whole (Tanaka and Sengco, 1997) tasks. Original faces are from the PICS (http://pics.psych.stir.ac.uk/) and CVL face databases (http://lrv.fri.uni-lj.si/facedb.html).

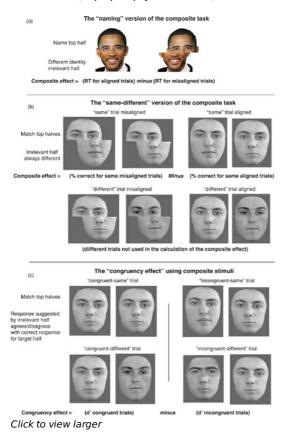


Fig. 9.2 The composite illusion together with: (a) the standard naming version of the composite task,

contrasting perception of the target half across aligned and misaligned conditions; (b) the standard samedifferent version of the composite task. (c) The Gauthier and Curby task that uses composite stimuli but measures a congruency effect rather than the composite effect. Unfamiliar faces are from the PICS (http://pics.psych.stir.ac.uk/) and CVL face databases (http://lrv.fri.uni-lj.si/facedb.html); famous faces are taken from the public domain.

First, there is a *disproportionate inversion effect* on recognition memory and perceptual matching. Inversion effects on memory (measured as the absolute difference between per cent correct for upright and per cent correct for inverted) are typically 20 to 25 percentage points for faces, and 0 to 8 percentage points for within-class discrimination of objects. Sample findings are listed in the first two data columns of Table 9.1, and similar results exists for airplanes, costumes, and stick figures (Yin, 1969), landscapes (Diamond and Carey, 1986), shoes (de Gelder et al., 1998), buildings and dog faces (Scapinello and Yarmey, 1970), houses and chairs (Boutet and Faubert, 2006), houses (Leder and Carbon, 2006), cats, dogs, and birds (Minnebusch et al., 2009), and racehorses (p. 152) (p. 153) (p. 154) (p. 155) (Crookes and McKone, 2008). Inversion effects on identification of overlearned stimuli in peripheral vision (*peripheral inversion effect*; McKone, 2004) also occur for faces but not objects (dachshund dogs; McKone, Brewer et al., 2007). Importantly, inversion effects for objects remain small or absent even for object classes in which, like faces, all exemplars share a basic "first order" configuration (i.e. cats, Labradors, dachshunds and racehorses; although see Ashworth et al., 2007, for a contradictory result using the artificial objects "greebles"). Also, the key to a large inversion effect is perception as a face: a large inversion effect occurs when an ambiguous stimulus is primed as face, but disappears when the same stimulus is primed as a Chinese character (Ge et al., 2006).

Table 9.1 Inversion decrement (upright-inverted) for faces and objects. Because there are too many studies testing faces vs objects in novices to list all of them, only studies that also tested experts on the objects are shown; all such studies are included. Studies reported various measures, including percent correct (%), d', reaction time (ms), and short-term memory capacity (K-max). For novices and experts, the significance or otherwise of each inversion effect is indicated; a separate column indicates whether the increase in the size of the inversion effect from novices to experts was significant. Studies are approximately ordered from smallest inversion effect in objects-of-expertise to largest. Adapted and expanded from Robbins and McKone (2007)

	Expert type	Task	Faces	Objects novices	Objects experts	sig of expertise increase
Dogs (Robbins and McKone, 2007, Experiment 3)	Real world	Simultaneous matching	11%	1% ^{ns}	2% ^{ns}	ns
Dogs (Robbins and McKone, 2007, Experiment 1)	Real world	Long-term memory	23%	3% ^{ns}	7% ^{ns}	ns
Fingerprints (Busey and Vanderkolk 2005)	Real world	Face/print classification	16%	6% ^{ns}	8% ^{ns}	ns
Birds (Gauthier et al., 2000)	Real world	Sequential matching	_	d'=0.05 ^{ns}	d'=.30 ^{ns}	_
Houses ^{a b} (Husk et al., 2007)	Lab trained	Sequential matching	35%	1%-	4%	_
Cars (Xu et al., 2005)	Real world	Sequential matching	_	8%-	8%-	ns

		_	d'=0.44 ⁻	d'=0.87 ⁻		
Handwriting (Bruyer and Crispeels, 1992)	Real world	Long-term memory	20%*	5% ^{ns}	9%*	ns
Cars (Gauthier et al., 2000)	Real world	Sequential matching	_	d'=.57	d'=.84	_
Greebles ^a (Rossion et al., 2002)	Lab trained	Sequential matching	75ms-	25 ms ⁻	46 ms ⁻	
Cars (Curby et al., 2009)	Real world	Short-term memory capacity (Cowan's K)	0.519	0.053 ^{ns}	0.435	
Dogs (Diamond and Carey, 1986 - Experiment 3)	Real world	Long-term memory	20%	5% ^{ns}	22%	

Notes: * = p < 0.05; rs = p>0.05; reverse = trend in opposite-to-predicted direction for expertise effect; — = not tested or not reported. Means for Busey and Vanderkolk (2005) provided by Thomas Busey (pers comm, 21.7.06).

We turn next to tasks that more directly assess style of processing, in that they address, in a given orientation, whether perception involves a strong integration of information from across the face or object (i.e. holistic/configural processing) which includes access specifically to information about exact distances between parts (i.e. an aspect of "second-order relational" information). Figure 9.1b illustrates the *part-whole effect* (Tanaka and Farah, 1993), in which memory for a face part (e.g. Bill's nose) is much better in the context of the original whole face (e.g. Bill's nose vs. Jim's nose in Bill's face) than when presented alone (Bill's nose vs. Jim's nose); Figure 9.1b also illustrates the part-in-spacing-changed-whole variant, in which memory for the face part is better in the original face than when presented in a version of the original whole that includes a distance alteration in another region of the face (e.g. Bill's nose vs. Jim's nose in Bill's face with the eyes shifted slightly apart). Figures 9.2a and b illustrate the *composite effect* in which aligning the top half-face of one individual with the bottom half-face of a different individual makes it difficult to name the top half (famous face version, Figure 9.2a; Young et al., 1987) or produces an effect in which two physically same top halves appear different when aligned with two different bottom halves (novel face version, Figure 9.2b; Le Grand et al., 2004)—in both cases the control condition against which reaction time or accuracy is compared is a version of the same stimuli with the two halves misaligned.

Regarding tests of the within-class discrimination hypothesis, Table 9.2 shows that the part-whole effect for objects in novices is small, and far smaller than that for recognition of faces. Table 9.3 shows that the *part-in-spacing-changed-whole effect* for objects is absent in novices, as compared to a significant 7% effect for faces. Table 9.4 shows that the *composite effect* for objects is absent in novices, as compared to a strong effect in faces. Finally, sensitivity to the *exact spacing between internal elements* is usually much weaker in objects than in faces; for example, to match sensitivity to spacing changes in upright faces and upright houses requires much larger physical changes in the houses than in the faces (Yovel and Kanwisher, 2008).

^a In all lab training studies, results are reported for discrimination of novel exemplars of the trained class, not the trained exemplars.

^b Husk et al. (2007) created experts with a particular type of house, by training participants to discriminate very similar exemplars all sharing the same first order configuration.

A final observation is that inversion effects can be far more stable for faces than for other stimuli. Inversion effects for letter and object identification disappear rapidly with repeated trials (Corballis et al., 1978; McKone and Grenfell, 1999). In contrast, large inversion effects remain after practice for faces (but not objects) under difficult viewing conditions (e.g. peripheral presentation: McKone, 2004; noise: McKone et al., 2001), and holistic processing for faces remains impossible for inverted faces even with thousands or tens of thousands of learning trials (McKone et al., 2001; Robbins and McKone, 2003).

In summary, both indirect evidence (disproportionate inversion effect) and direct tests of processing style (part-whole, part-in-spacing-changed-whole, composite, spacing sensitivity) confirm a lack of holistic processing for individual-level recognition of objects. The only potential exception of which we are aware is human bodies, and even here the evidence is currently uncompelling. The most relevant situation is recognition of body *identity*: this does not show inversion effects when the head is removed (Minnebusch et al., 2009), although there is a strong part-whole effect for body identity with heads (Seitz, 2002). Also note that even inversion effects for body *pose* (Reed et al., 2003) have recently been shown to depend entirely on the presence of a head (p. 156) (Yovel et al., 2010). Thus, although it is possible that holistic processing might extend to cover bodies as well as faces, a reasonable alternative hypothesis is that holistic processing for bodies occurs only when the body contains a face.

Table 9.2 Results of previous studies using the Tanaka and Farah (1993) part-whole paradigm, showing size of the whole-part difference, averaged over all parts tested. All stimuli were upright unless otherwise stated. All studies including objects-of-expertise are included, as are sample extra studies that tested objects only in novices. Example results are also provided for faces. Scores are percent correct (%) or d-prime discriminability (d'). Format as for Table 9.1. Greebles are an artificial object class. Adapted and expanded from Robbins and McKone (2007)

	Faces	Inverted faces	Objects (novices)	Objects (experts)	sig of expertise increase
No objects (Pellicano et al., 2006)	13%	-2% ^{ns}	_	_	_
Houses (Tanaka and Farah, 1993)	11%	-1% ^{ns}	-2% ^{ns}	_	_
Houses (Tanaka and Sengco, 1997)	15%	0% ^{ns}	1% ^{ns}	_	_
Chairs (Davidoff and Donnelly, 1990)	11%	_	4% ^{ns}	_	_
Dog faces (Tanaka et al., 1996)	20%	_	2% ^{ns}	8% ^{ns}	ns
Cars (Tanaka et al., 1996)	18%	_	8%-	6%-	Reverse
Biological cells (Tanaka et al., 1996)	26%	_	16%	10%	Reverse
Greebles (Gauthier and Tarr, 1997)	_	_	5% ^{ns}	11%	ns
Greebles (Gauthier et al., 1998)	_	_	7%-	0%-	Reverse
Greebles (Gauthier and Tarr, 2002)	_	_	d' = 0.75 ⁻	d' = 0 68 ⁻	Reverse

Notes: * = p < .05; ns = p>.05; reverse = trend in opposite-to-predicted direction for expertise effect; — = not tested or not reported. Data from Tanaka et al. (1996) are as cited in Tanaka and Gauthier (1997).

Overall, results reviewed in this section are consistent with the view that "faces are special" compared to a very wide range of objects (with the possible exception of human bodies). Results clearly reject the within-class discrimination hypothesis.

Face selective neurons and cortical regions.

Turning to neural findings, results show the existence of strongly face-selective cells that cluster together in regions large enough to be detectable with fMRI.

In humans, multiple fMRI studies reveal face selective areas which can respond two to three times more strongly to within-class discrimination of faces than to within-class discrimination of other objects, including houses, flowers, hands, birds, and cars (for review see Kanwisher and (p. 157) Yovel, 2006). Regions identified include the FFA² and the OFA. In contrast, there are other areas of extrastriate cortex that are object-general; for example, lateral occipital complex (LOC, defined as a region responding more strongly to objects than scrambled objects) typically responds at close to equal levels for objects and faces (Op de Beeck et al., 2006). Importantly, face-selective regions are dissociated from other regions in fMRI even when, like faces, all exemplars of the object set share a basic "first-order" configuration (e.g. hands; also, houses all made from a common template, Husk et al., 2006). High-resolution fMRI also dissociates face-selective regions from regions selective for headless bodies (extrastriate body area: Downing et al., 2001; fusiform body area: Schwarzlose et al., 2005).

Table 9.3 Results of previous studies using the Tanaka and Sengco's (1997) paradigm, showing part-in-whole minus part-in-spacing-altered-whole, averaged over all parts tested. All stimuli were upright unless otherwise stated. All studies that tested objects-of-expertise are included, as is the original study that tested objects only in novices. Formatting as for Table 9.1. Adapted and expanded from Robbins and McKone (2007)

	Faces	Objects (novices)	Objects (experts)	sig of expertise increase
Houses (Tanaka and Sengco, 1997)	7%	0% ^{ns}	_	_
Greebles (Gauthier and Tarr, 1997)	_	-4% ^{ns}	0% ^{ns}	ns
Greebles (Gauthier et al., 1998)	_	1% ^{ns}	0% ^{ns}	Reverse
Greebles (Gauthier and Tarr, 2002)	_	$d' = 0.69^-$	d' = 0.64 ⁻	Reverse

Notes: * = p < 0.05; ns = p > 0.05; reverse = trend in opposite-to-predicted direction for expertise effect; — = not tested or not reported.

Monkey fMRI also reveals face-selective regions in temporal cortex (Tsao et al., 2006). Recording from one of these (the "middle face patch") revealed that, of more than 100 cells tested, 97% of visually-responsive neurons were strongly face-selective in comparison to a wide range of objects including clocks, bodies and hands (Tsao et al., 2006). Thus, when search for face-selective cells is guided by fMRI, dense clusters of colocated face cells can be identified (in contrast to early single unit studies, in which unguided electrode placement suggested face cells were more widely dispersed; e.g. Perrett et al., 1985).

Selective disruption of the network

The fact that face cells cluster into regions argues it should be possible to damage face recognition without object recognition, and vice versa. This double dissociation has indeed been demonstrated.

(p. 158) Using transmagnetic stimulation (TMS) to temporarily disrupt cortical regions in healthy adults, Pitcher et al. (2009) found a triple dissociation between within-class face, body, and object recognition in extrastriate cortex (note face and object areas located in inferotemporal cortex cannot be accessed with TMS). Participants performed discrimination tasks involving faces, bodies, and an artificial-object category while TMS was delivered over the right occipital face area (rOFA), the right extrastriate body area (rEBA), or the right lateral occipital area (rLO). Results argued category-selective areas contributed to behavioral performance solely within their preferred categories. TMS over rOFA impaired discrimination of faces but not objects or bodies. TMS over rEBA impaired discrimination of bodies but not faces or objects. Finally, TMS over rLO impaired discrimination of objects but not

faces or bodies.

We now turn to evidence from neuropsychology; that is, to cases of acquired brain injury and of atypical development. Before evaluating the evidence in this field, an important theoretical point is that pure cases of face-object dissociations would be expected to be rare. Most injuries will damage broad swathes of cortex, covering both face and object areas (and/or also damage broad swathes of connecting white matter; see Thomas et al., 2008, for the importance of white matter in prosopagnosia). Similarly, many neural development problems (e.g. a neural migration problem during a particular week of fetal development) would also be expected to damage the development of both face and object perception mechanisms. Of strong theoretical importance, however, is that pure cases *can* be identified, and that these form a *double dissociation* between face and object recognition. There exist prosopagnosics who have extremely poor recognition of faces in combination with perfectly normal within-class discrimination of objects (e.g. Duchaine et al., 2006; McNeil and Warrington, 1993; Sergent and Signoret, 1992). A few cases have also been reported of the reverse pattern (e.g. Assal et al., 1984): best known is Mr CK who was severely object agnosic but could individuate faces at normal or above-normal levels, even in very difficult formats (e.g. overlaid cartoons of multiple individuals; Moscovitch et al., 1997).

Taken together, the results of fMRI, single-cell recording, TMS, and neuropsychology make a strong case that faces are "special" in terms of tight clusterings of colocated face-selective neurons. Moreover, the results indicate dissociations not only between faces and objects in general, but also specifically between faces and other parts of the body (headless bodies, hands).

Face selective ERP/MEG response: the N170/M170

The N170 is an ERP response peaking 170 ms after stimulus onset which is stronger to faces than objects at occipitotemporal electrode sites (Jeffreys, 1996; for review see Eimer, Chapter 17, this volume); there is an equivalent M170 measured with MEG (Halgren et al., 2000; Liu et al., 2000). For our purposes, the critical finding is that the N170/M170 face-selectivity occurs even when the object exemplars are all from the same category with highly similar structural forms (for references to 17 articles containing this result, see Rossion and Jacques, 2008, p. 1962), and cannot be attributed to image variability amongst the object pictures (Rossion and Jacques, 2008). For faces, inversion produces a delay and increases the amplitude of the N170, a pattern which does not occur, or is much smaller, for objects (e.g. Rossion et al., 2000). Also, for human bodies, inversion produces delay and increased amplitude for bodies with heads, but not bodies without heads (Minnebusch et al., 2009). Results again reject the within-class discrimination hypothesis.

Summary

The results reviewed in this section clearly reject the "within-class discrimination hypothesis." When within-class discrimination of faces is contrasted with within-class discrimination of objects, results show that: (1) holistic processing remains restricted to faces, (2) face-selective (p. 159) cortical regions and single neurons still occur (3) selective damage to face or object recognition is still possible, and (4) face-selective ERP responses still occur. Moreover, a number of studies have identified associations between face-selective neural phenomena and face-specific behavioral properties: in particular, the FFA demonstrates holistic processing (composite effect; Schiltz and Rossion, 2006), better identity discrimination for upright than inverted faces (Mazard et al., 2006; Yovel and Kanwisher, 2005), and identity discrimination for faces but not objects ("blobs," Yue et al., 2006). Overall, results make a compelling case that, in the typical situation in which people have no particular expertise with an object class, faces are "special."

Testing the expertise hypothesis

We next evaluate the *expertise hypothesis*. All results discussed in this section come from the situation in which faces are compared with an object class for which the participant has developed demonstrated expertise at within-class discrimination, either through many years of real world interest and experience (e.g. car, bird, or dog experts), or through several hours of laboratory training (e.g. "greeble" experts). Results refute the expertise hypothesis and again support the view that "faces are special."

Holistic/configural processing: "gold standard" tasks

Three tasks are available which can be considered "gold standards" for testing expertise hypothesis predictions about holistic processing: the part-whole task, the part-in-spacing-changed-whole task, and the composite task. We emphasize these tasks for three reasons: (1) well-established results show they produce face-specificity in object novices; (2) the tasks *directly* assess processing style (i.e. part-based versus holistic); and (3) logically, the tasks provide measures of "face-type" holistic processing (a point which will become clearer when we cover one much weaker use of the term "holistic" in a later section).

Results for all studies testing objects-of-expertise in these tasks are shown in Tables 9.2 to 9.4. Findings are straightforward, and clearly reject the expertise hypothesis.

If holistic processing emerged with expertise, then we would expect the part-whole, part-in-spacing-changed-whole and composite effects to be significant in object experts and significantly larger in object experts than in object novices. In contrast, Table 9.2 shows the part-whole effect is no larger in experts than in novices (in fact, 4/6 studies show trend in reverse-to-predicted direction); also, in a related method, detection of a small nodule in a cued region of a chest X-ray remains only slightly facilitated by a whole chest as opposed to a scrambled one in radiology experts (i.e. no more facilitated than in novices; Harley et al., 2009). Similarly, the part-in-spacing-changed effect (Table 9.3) is no larger in experts than in novices (2/3 showing trend in reverse-to-predicted direction). Regarding the composite effect (Table 9.4), a significant composite effect has never been obtained in object experts (in four published attempts plus two others mentioned in a footnote by Gauthier et al., 1998), and statistical tests comparing experts to novices have either not been conducted or show non-significant or reverse-to-predicted-direction differences in the size of the composite effect. Thus, results of the three "gold standard" tasks clearly argue that expertise with objects does not induce face-like holistic processing.

It is worth noting that, although the original results of these studies very clearly *reject* the expertise hypothesis, exactly the opposite conclusion could easily be reached by the casual reader of much of the face recognition literature. Several of the articles whose results are shown in Tables 9.2 to 9.4 have been regularly miscited as having shown evidence of holistic processing in object experts on these standard tasks when (as can be seen) they did not. Given this common miscitation, we note that we are confident we have correctly presented the original results. (p. 160) We previously presented the expertise values in Tables 9.1 to 9.4 in Robbins and McKone (2007), on which Gauthier, as the major recent proponent of the expertise hypothesis, wrote a commentary (Gauthier and Bukach, 2007): no mistakes or omissions were indicated.

Table 9.4 Results of the Young et al. (1987) composite paradigm, showing the aligned–unaligned difference for reaction times, or unaligned–aligned for accuracy; in both cases, a positive number corresponds to the direction for a positive composite effect, (i.e. aligned should be the more difficult condition). All stimuli were upright unless otherwise stated. All studies including objects-of-expertise are included, as are some sample studies that reported data for inverted faces. Formatting as in Table 9.1. Adapted and expanded from Robbins and McKone (2007)

	Task	Faces	Inverted faces	Objects (novices)	Objects (experts)	sig of expertise increase
No objects (Young et al., 1987)	Speeded naming	212 ms	9 ms ^{ns}	_	_	_
No objects (McKone, 2008)	Speeded naming	74 ms	14 ms ^{ns}	_	_	_
No objects (Robbins and McKone, 2003)	Naming twins	8.8%	-1.2% ^{ns}	_	_	_
Cars (Macchi Cassia et al., 2009)	Sequential matching	58 ms	_	0 ms	_	_
Greebles, same-family halves (Gauthier et al., 1998)	Speeded naming	_	_	_	115 ms ^{ns} 0%	
Greebles, different- family halves (Gauthier et al., 1998)	Speeded naming	_	-	-	-37 ms ^{reverse} - 3% ^{reverse}	
Greebles, same-family halves (Gauthier and Tarr, 2002)	Speeded naming	_	_	-42 ms ⁻	12 ms ⁻	_ a
Dogs (Robbins and McKone, 2007)	Simultaneous matching	6.1%	-3.5% ^{ns}	-0.8% ^{ns} 0.8% ^{ns b}	0.7% ^{ns}	ns Reverse

Notes: * = p < 0.05; ns = p > 0.05; reverse = trend in opposite-to-predicted direction for expertise effect; — = not tested or not reported.

^a Across 5 sessions (we show only session 1 = novices, session 5 = experts), there was a close-to-significant interaction between session and aligned vs. unaligned. This did not reflect an increase with expertise: the composite effect started close to zero, strangely became more negative in sessions 2-4, then returned to close to zero. The 12 ms composite effect in experts was in the context of 35 ms SEMs for the aligned and unaligned conditions.

b Results for two independent groups of subjects.

Holistic/configural processing: attempts to discredit the standard tasks

Several articles by Gauthier and colleagues have tried to discredit two of the "gold standard" tasks, suggesting that the part-whole and composite effects are not good measures of holistic perceptual (p. 161) integration (despite their wide acceptance as such in the face literature). Regarding the part-whole effect, Gauthier and Tarr (2002) argued that the effect may arise from the general memory advantage which arises from match as opposed to mismatch in stimulus format between study and test: study-test match is greater in the whole condition (whole at study, whole at test) than in the part condition (whole at study, part at test). In response, we have pointed out (Robbins and McKone, 2007) that, although there may indeed be some contribution of general memory-match effects on this task (see Leder and Carbon, 2005), Gauthier and Tarr's (2002) proposal fails to mention that inverted faces produce no whole-over-part advantage despite the degree of study-test match in the whole and part conditions being the same as for upright faces, and also provides no explanation of why the part-whole effect is consistently so much larger for faces than for objects. To our minds, these findings imply that the large part-whole effect for upright faces can only be attributed to holistic processing.

Regarding the composite effect, the argument (Gauthier and Bukach, 2007; Richler et al., 2008) is that the composite effect in the same-different version of the task arises at a decisional level rather than a perceptual level. Again, however, Gauthier and colleagues have failed to mention two key points: (1) making a decisional-perceptual distinction requires analyzing *different* trials in the composite procedure and this is invalid because, while there is a clear prediction that holistic processing will make aligned harder than unaligned for "same" trials, the predicted direction of any effect on "different" trials will vary depending on the similarity of the non-target halves (see Robbins and McKone, 2007, p. 54); and (2) on the *naming* version of the task, in which the issue of decisional bias does not arise, the composite effect is also present for faces (Young et al., 1987) and not for objects (greebles, Table 4).

Overall, we see no reason to discount the results of the "gold standard" holistic processing tasks, which clearly support the view that faces are special.

Holistic/configural processing: disproportionate inversion effect

We now turn to results for objects-of-expertise in other tasks which have been suggested to be measures of "holistic processing," but in which we believe the link between the task and holistic processing is either more tenuous or entirely absent.

We first consider the classic disproportionate inversion effect. Valentine (1988) pointed out many years ago that the fact that an inversion effect is larger in one condition (e.g. faces) than in another (e.g. objects) does not per se show that this arises from holistic processing: the task does not address processing style in either orientation (as do part-whole, part-in-spacing-changed-whole, and composite). For *faces*, research has subsequently made a very strong case that the large inversion effect on memory and discrimination *does* derive from holistic processing. However, this does not guarantee that the origin of any large inversion effects for *other objects* must derive from holistic processing. Many authors now explicitly state that the inversion effect is merely indirect evidence for holistic processing (e.g. Michel et al., 2006), and D. Maurer et al. (2002) explicitly noted that the mere presence of an inversion effect is not diagnostic of holistic/configural processing in the absence of more direct evidence.

Do results for objects-of-expertise show even indirect support for holistic processing, using the inversion effect? If inversion effects for objects-of-expertise reflect holistic processing, the expertise hypothesis predicts that studies should find an increase in the size of the inversion effect with expertise. Table 9.1 shows that this result is found only very occasionally. Instead, the findings are highly variable. Inversion effects for objects in experts range from nothing to an inversion effect as large as that for faces. Four tests have found only small and non-significant inversion effects in experts that are only very slightly and non-significantly larger in experts than in novices (dogs with both memory and sequential matching: Robbins and McKone, 2007; fingerprints: Busey and (p. 162)

Vanderkolk, 2005; birds: Gauthier et al., 2000); similarly, a fifth test found no change in inversion effect at all with expertise on a per cent-correct measure (cars: Xu et al., 2005). Next, three tests have found either significant inversion effects in experts, or a significant novice-expert difference, but with the inversion effects for objects-of-expertise remaining fairly small: the effect was either strikingly smaller than for faces (4% houses vs. 35% faces in

Husk et al., 2007; 9% handwriting vs. 20% faces in Bruyer and Crispeels, 1992), and/or the difference from objects in novices was not great in numerical terms (cars in Gauthier et al., 2000; also the d' measure in Xu et al., 2005). Next, one study produced a quite large inversion effect in experts, with the effect for objects 85% larger in experts than in novices, and 60% the size of that for faces (greebles, Rossion et al., 2002). Finally, two studies have produced very large inversion effects for objects of expertise, equal in size to the inversion effects for faces (dogs, Diamond and Carey, 1986; cars, Curby et al., 2009). Taken together, these studies argue there is some effect of expertise on inversion effects for objects which is typically small, but can sometimes be very large.

What explains the variability across studies? The expertise hypothesis could account for it if the variable driving the size of the inversion effect was the experts' level of expertise. However, results in Table 9.1 contradict this interpretation: for example, the dog experts in Robbins and McKone (2007) had a mean of 23 years experience (and were as good at discriminating dogs as faces), yet showed no inversion effect; while, at the other extreme, the greeble experts in Rossion et al. (2002) had only a few hours of laboratory training, yet showed quite a sizeable expertise-related change in the inversion effect.

Alternatively, the expertise hypothesis could perhaps account for the variability if it were proposed that expertise effects on holistic processing emerge only with expertise specifically in *individual*-level discrimination (an idea proposed by Wong et al., 2009) noting that several studies with small inversion effects tested bird and car experts and these people typically have expertise at discriminating class exemplars at the "subordinate" rather than individual level (e.g. Mazda 626 vs. Mazda 323, not a particular Mazda 626). Again, however, Table 9.1 contradicts this hypothesis: small inversion effects have been found in people highly expert in individual-level discrimination of labradors (Robbins and McKone, 2007) and fingerprints (Busey and Vandervolk, 2005); and, one of the two findings of extremely large inversion effects was obtained with car experts (Curby et al., 2009).

We thus conclude that results of inversion effect studies do not provide even indirect support for the expertise hypothesis: level of expertise does not appear to correlate with the size of the inversion effect; and nor does expertise specifically in individual-level discrimination.

This does leave us with an interesting open question, however, which is what *does* explain the variability in inversion effects? Robbins and McKone (2007) suggested that the large inversion effect in Diamond and Carey (1986) could have been explained if the experts in that study had been pre-experimentally familiar with *the particular dog images* (but not the face images) used as stimuli (this was plausible given the source of the participants and stimulus images). However, this critique does not apply to Rossion et al. (2002), where the test stimuli were all novel greebles. Also, although in Curby et al. (2009) some of the particular car images could plausibly have been pre-experimentally familiar to participants, this is equally true of all the other car studies which produced only small inversion effects in experts. We therefore suggest it may be worthwhile exploring the effect of other variables in future studies. For example, for faces, the size of the inversion effect is affected by distinctiveness (Valentine, 1991). Perhaps, if object recognition inversion effects are also affected by distinctiveness, and we make the plausible assumption that experts are more sensitive to distinctiveness than novices, then we could potentially explain why inversion effects vary across studies in experts (but not novices) by hypothesizing that the particular stimulus sets used in particular studies happened to comprise items that were either more (p. 163) distinctive or more typical exemplars of their class. Importantly, this explanation requires no reference to the concept of holistic processing.

Holistic/configural processing: definition as merely a generic failure of selective attention

In claiming support for the expertise hypothesis, one approach by Gauthier and colleagues has been to weaken the definition of holistic processing from the traditional face-literature definition—that is, some form of very strong perceptual integration (Tanaka and Gordon, Chapter 10, this volume)—to merely any failure of selective attention (specifically, "obligatory processing of all features of an object, when subjects are instructed to attend selectively to one feature while ignoring others," Gauthier et al., 2003, p. 1). Corresponding tasks (e.g. Gauthier et al., 2003; Wong et al., 2009) have then relied on measuring a *congruency effect* (see Figure 9.2c). In a sequential same-different task, using some form of composite stimuli, two conditions are contrasted in which the response suggested by matching the to-be-ignored half is either consistent with the response suggested by the target half (e.g. the non-target bottom halves are the same when the target top halves are the same; congruent trials) or inconsistent with the response suggested by the target half (e.g. the non-target bottom halves are different when

the target top halves are the same; incongruent trials). The difference between congruent and incongruent trials is then taken as the measure of "holistic processing."

This congruency measure can sometimes produce patterns in objects of expertise that are similar to patterns in faces: that is, patterns in which failures of selective attention to parts are strong for faces, weak or absent for objects in novices, and significantly stronger for objects in experts than in novices (cars: Gauthier et al., 2003; novel objects ziggerins: Wong et al., 2009). In other cases, however, the results do not show face-like patterns (e.g. a strong congruency effect in *novices* for misaligned greebles, Richler et al., 2009; or no expertise influence on the congruency effect, Hsiao and Cottrell, 2009).

Even where face-like patterns are obtained, however, the question is whether this should be taken as evidence of claimed "special" processing for objects of expertise. We argue not. The selective attention approach weakens the definition of holistic processing to such an extent as to make it of no theoretical value in the present context. Under the Gauthier definition, practically any two things one cared to test would be processed "holistically": for example, the Stroop effect would be interpreted as showing that ink color and word identity are processed together "holistically," despite the fact that color and word form/names are clearly *not* integrated at a perceptual level. Thus, the congruency effect revealed for car experts in Gauthier et al. (2003; or for ziggerins in Wong et al., 2009) is, to our minds, not an expertise effect on *face*-like holistic processing; instead, it merely shows that competition for attentional resources from the to-be-ignored half is stronger when subjects are experts with the object class. This seems unsurprising. (As an analogy, the Stroop effect would not occur for English readers if the written word was in Chinese.) Consistent with our explanation, the circumstances in which the congruency effect in experts weakens or disappears (when the non-target half is either flipped upside down or misaligned to one side; cars, Gauthier et al., 2003; ziggerins, Wong et al., 2009) correspond to a circumstance known from the spatial attention literature to disrupt global processing and facilitate attention to parts (i.e. sudden discontinuities in the outline suggest the presence of "two things" not "one thing").

We thus conclude that the results of the *congruency effect* tasks do not demonstrate *face*-like processing for objects of expertise, but instead reflect general Stroop-like attentional phenomena. The theory that "faces are special" remains intact.

(p. 164) Face selective neurons and cortical regions

No single-cell recording studies have addressed the question of whether face-selective cells respond strongly to objects-of-expertise. The available evidence regarding cortical location of face-selectivity and expertise comes from fMRI. These studies have focused on the FFA.

The expertise hypothesis predicts that the FFA should be more strongly engaged by objects of expertise than by objects for which the participant is a novice; also, where expertise levels are high, activation should approach face levels. Twelve studies have reported relevant data. One failed to properly localize the FFA, reporting a significant expertise effect in a larger region centered around the FFA that would be expected to include much object-general cortex (greebles: Gauthier et al., 1999). Of those that localized the FFA, only two found small but significant increases in responses to objects of expertise compared with control objects in the FFA (cars and birds: Gauthier et al., 2000; cars: Xu et al., 2005), and one a significant correlation between level of behavioral expertise and FFA activation (chest X-rays: Harley et al., 2009). Two report non-significant trends towards expertise effects in the FFA (Lepidoptera: Rhodes et al., 2004; novel polygon-based objects: Moore et al., 2006) and four report no change with expertise (cars: Grill-Spector et al., 2004; "blobs": Yue et al., 2006; novel objects: Op de Beeck et al., 2006; dance actions: Calvo-Merino et al., 2005). Another study failed to find a change in the degree of overlap between the FFA and a "greeble selective fusiform area" with expertise training (Kung et al., 2007). Finally, Liu et al. (2008) found activity in the right FFA was substantially greater for faces than for a non-face class for which their subjects were highly expert at individual-level discrimination (Chinese characters).

Thus, most studies find that the FFA is not strongly activated in response to objects-of-expertise. Even more compellingly, some studies have examined expertise effects in cortical regions *not* selective for faces. Of six relevant studies, all have found larger effects of expertise in these regions than in the FFA (Calvo-Merino et al., 2005; Gauthier et al., 2000; Moore et al., 2006; Op de Beeck et al., 2006; Rhodes et al., 2004; Yue et al., 2006). Overall, then, the results indicate a dissociation between the FFA and areas related to object expertise, rather than

the strong association predicted by the expertise hypothesis.

Why does the FFA sometimes show greater activation in experts than novices? For many of the studies reviewed, a plausible idea (Xu et al., 2005) 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, bird experts will find birds more interesting than novices, and will thus pay more attention to bird stimuli than to other objects. This will elevate neural responses to objects of expertise, which produce a small response in the FFA even in nonexperts (possibly because limits in the spatial resolution of fMRI can conflate adjacent functional regions). This idea is consistent with evidence that greater attention raises BOLD response and that hemodynamic signals in the FFA include late responses that can be modulated by feedback connections (Furey et al., 2006). It is also directly supported in cases where correlations between FFA response to objects of expertise and behaviorally measured expertise have been shown in *location*-discrimination tasks, where subjects are free to attend to item identity as they wish, but not in *identity*-discrimination tasks, where all subjects, regardless of intrinsic interest level, are forced to attend to item identity (Grill-Spector et al., 2004; Gauthier et al., 2000; also see Kung et al., 2007).

One study, however, provided good evidence against an attentional explanation, and so requires more detailed consideration. Using novice and expert radiologists, Harley et al. (2009) found that behavioral performance during scanning on a radiograph abnormality diagnosis task correlated positively with level of FFA activation, and negatively with activation of voxels (in LO) selective for radiographs. This could potentially indicate a role for the FFA in expert processing (p. 165) of radiographs. An alternative explanation, however, arises from the fact that the voxel resolution used in the study cannot discriminate between responses from the true FFA and the neighboring fusiform body area (higher resolution is required; see Schwarzlose, et al., 2005). Given that chest radiographs show body parts and not faces, and that radiologists are trained to associate radiographs to real bodies, it seems plausible that the expertise effects arose from body-selective neurons not from face-selective neurons. In support of this interpretation, the location of the strong LO activation apparent for the radiographs appears to correspond closely to the typical location of the extrastriate body area (e.g. see figure 6 in Arzy et al., 2006); thus, it is possible that the expertise effect in the Harley et al. study represents expert radiologists increasing their reliance on the FBA, and decreasing their reliance on the EBA, relative to first-year intern radiologists.

In summary, the data provide no compelling evidence for the special relationship between expertise and the FFA predicted by the expertise hypothesis (and in many cases no evidence at all). Instead, fMRI studies are more consistent with the view that "faces are special."

Selective disruption of the network: TMS and neuropsychology

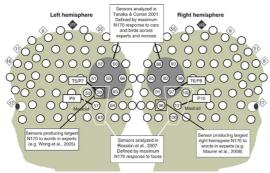
There are no TMS studies of objects-of-expertise. Regarding neuropsychology, the expertise hypothesis states that the same "special" neural mechanisms used for recognizing faces are also used for recognizing objects-of-expertise. It thus predicts that damage to, or atypical development of, these mechanisms should *always* damage both face recognition *and* object-of-expertise recognition; in contrast, evidence that objects of expertise dissociate from faces would reject the expertise hypothesis and support the view that faces are special.

Few studies have tested this prediction (for the obvious reason that few individuals with acquired prosopagnosia happened to be experts in another object class prior to their brain injury), but results refute the expertise hypothesis. Some individuals show extremely poor face recognition but excellent recognition of objects of expertise: following brain injury, RM retained his expertise with cars (Sergent and Signoret, 1992); WJ lost face recognition but learned to individuate sheep (McNeil and Warrington, 1993); and developmental prosopagnosic Edward learned greeble expertise at completely normal levels (both accuracy and reaction time; Duchaine et al., 2006). In the other half of the double dissociation, individuals have lost recognition of former objects-of-expertise, but retained face recognition: cases include MX, a farmer who could recognize faces but no longer recognize his cows (Assal et al., 1984), and CK, who retained perfect face recognition but lost interest in his toy-soldier collection, which numbered in the thousands (Moscovitch et al., 1997). No cases have been reported in which recognition of faces and objects of expertise have both been impaired while recognition of non-expert objects is unimpaired, or vice versa.

Face selective ERP/MEG response: the N170/M170

Several studies have shown that an N170 response can be altered by expertise with non-face stimuli. This includes increased amplitude in experts compared to novices (birds and cars: Tanaka and Curran, 2001; greebles: Rossion et al., 2004; fingerprints: Busey and Vanderkolk, 2005; words in both alphabetic and character-based scripts: Wong et al., 2005), and the emergence of a time delay in peak amplitude for inverted relative to upright stimulus orientations (greebles: Rossion et al., 2002; fingerprints: Busey and Vanderkolk, 2005).

Perhaps the most relevant question here is whether or not these effects derive from the same neural generators as the N170 to faces. The N170 is a complex ERP response that provides far from a pure measure of face-selective cortical regions. A recent review of source localization studies (Rossion and Jacques, 2009) concludes the N170 over occipitotemporal sensors most likely (p. 166) derives from an equivalent dipole combining neural processes in and between multiple regions activated in interlocked time-courses, some of which are face-selective (including OFA and FFA) and some of which are object-general (e.g. the lateral occipital complex, LOC).



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Fig. 9.3 Approximate scalp locations reported in N170 expertise studies of faces, objects (cars, birds) and words (both alphabetic and character-based languages). Numbers refer to sensor numbers in the 128-channel Geodesic Sensor Net $^{\text{T}}$. Corresponding values in the 10-20 system are indicated for T5, T6, P9 and P10

If objects-of-expertise activate "face" neural generators, a minimum prediction is that the spatial distribution on the scalp of the N170 to objects-of-expertise should shift towards that of faces and away from that of objects in novices. However, in general results favor the view that this does not occur, consistent with the idea that "faces are special." Xu et al. (2005), using MEG, found face selective sensors showed absolutely no magnitude increase in the car M170 response in experts compared to novices. Tanaka and Curran (2001) found significant expertise effects on car and bird N170 amplitudes but, crucially, the result was obtained from a selection of sensors that barely overlaps with the sensors usually used in face N170 studies (see Figure 9.3); moreover, scalp distribution data showed no suggestion of a shift towards a more face-like distribution of the peak sensors with expertise. Two other studies have measured at T5 and T6, sensors for which the N170 is highly face-selective. Rossion et al. (2002) found the development of an inversion delay with greeble expertise occurred in the left hemisphere (T5) but not the right hemisphere (T6), in contrast to the bilateral occurrence of this delay for faces (Rossion et al., 2000). Busey and Vanderkolk (2005) found the opposite pattern of an inversion delay in fingerprint experts in the right but not left hemisphere; but, the study also showed no amplitude increase in the right hemisphere (T6) with fingerprint expertise (i.e. not a face-like pattern). Further, neither of these studies reported the expertise effects on any other sensors, and so it cannot be determined whether (p. 167) the scalp distribution for objects-of-expertise matched that for faces (i.e. expertise effects on object processing may have been larger at other sensors). Turning to word studies, experts with a given word script show a strong left hemisphere bias in amplitude of the word N170 including for character-based scripts (U. Maurer et al., 2008a,b; Wong et al., 2005), in contrast to a more bilateral pattern in novices (U. Maurer et al., 2008b), and in contrast to the typical right hemisphere bias for the N170 to faces. Even within the right hemisphere the word N170 responses are strongest at a different sensor location from that which typically produces the largest face N170 (sensor 96, rather than 97/T5; U. Maurer et al., 2008a,b).

Overall, the pattern emerging across studies argues that expertise induces an N170 that has different properties of spatial localization from the N170 for faces. This suggests that the neural generators producing the N170 for objects of expertise are different from those producing the N170 for faces.

Interference between faces and objects-of-expertise on the N170

Another approach using the N170 has examined competition effects between faces and objects-of-expertise. Results show that, at traditional face-selective sensors, the amplitude of the N170 to faces is reduced more by simultaneous presentation of objects of expertise than by the same objects in novices (greebles: Rossion et al., 2004; cars: Rossion et al., 2007). Rossion et al. (2007) also found that the degree of reduction correlates with level of expertise, and showed the competition effects were unlikely to be attributable to attention differences between experts and novices (e.g. no group differences on P1 were observed).

How should these results be interpreted? It is possible that they could reflect the activation of "face-selective" neural generators by objects of expertise, and thus be consistent with the expertise hypothesis. However, there is an equally valid alternative explanation. The N170 to face stimuli almost certainly includes a component arising from non-face selective cortical regions—for example, faces activate the LOC (e.g. Yovel and Kanwisher, 2005), and this is an area very likely to contribute to the N170 (Rossion and Jacques, 2009). The interference effect could then arise from competition for resources between faces and objects-of-expertise within these object-general regions and, because expertise with objects has been shown to increase LOC activation (e.g. Op de Beeck et al., 2006), this competition between faces and objects will be larger in experts than in novices. Thus, these studies cannot answer the crucial question of whether claimed face-specific neural generators contributing to the face N170 are also used by objects-of-expertise.

Other arguments for the expertise hypothesis

We now describe, and discard, four other arguments sometimes made for the expertise hypothesis.

"Null effects don't count"

Gauthier and Bukach (2007) have argued that results failing to support the expertise hypothesis should be ignored because many of these rely on statistical null effects; that is, findings of no significant difference between objects in experts and novices.

This argument ignores the fact that many relevant studies find statistically significant effects in other parts of their design (e.g. significant effects for faces, or significant differences in the size of the effect for faces and objects-of-expertise; e.g. see Tables 9.2–9.4), arguing against poor experimental methods or a general lack of statistical power. It also ignores the fact that trends in the reverse-to-predicted direction are often obtained (e.g. see Tables 9.2–9.4), in contrast to the pattern that would be expected if statistical power was the problem. Finally, we believe it represents (p. 168) poor scientific practice—and a misunderstanding of the role of statistics—to ignore consistent evidence of null findings on a given task. This approach allows only for one theoretical outcome: "proof" of the hypothesis that happens to predict the "positive" statistical finding. For example, the logic of Gauthier and Bukach (2007) would never allow us conclude that women's height does *not* change between the ages of 20 and 30 years, regardless of how many studies showing null effects of age were conducted. Another useful example to consider is that of a pharmaceutical company that wishes to bring its new product to market: no scientist would consider it acceptable that this company could choose to count as valid only studies in which their product produced a significant improvement in health outcomes and ignore those in which it failed to produce any significant improvement or produced a significant worsening of health.

"Children show late emergence of holistic processing"

Early studies claimed that children needed 10 years of experience of faces to develop the hallmarks of adult holistic processing (Carey et al., 1980), which was taken as strong support for the expertise hypothesis (Diamond and Carey, 1986). However, this early evidence was rapidly refuted. All holistic effects for faces have been demonstrated in children as young as 4 years, and there are even good reasons to argue that holistic processing is at *full adult levels of strength* by 5 to 6 years (see Crookes and McKone, 2009). Thus, developmental results do not provide support for the expertise hypothesis.

The other-race effect

Some have argued in favor of the expertise hypothesis because face recognition is sensitive to experience. For example, holistic processing, and FFA activation can be affected by race of the face (Golby et al., 2001; Tanaka et al., 2004). However, such findings are not evidence that learning has taken place within a generic expertise

system. The effects are equally consistent with experience-based tuning within face-specific mechanisms.

Downward shift in preferred categorization level

The fact that expertise with objects causes a downward shift in entry level of categorization (i.e. faster reaction times for judgments at individual or subordinate levels as compared to basic or superordinate levels, Tanaka and Taylor, 1991) has been taken by some as support for the expertise hypothesis. However, this is based on out-of-date evidence. It has recently been shown that: (1) for objects, preference for the individual level can be obtained without expertise (towers: Anaki and Bentin, 2009), and (2) for faces, preference for the individual level for faces occurs only under certain circumstances (D'Lauro et al., 2008).

Summary

Taken together, results reviewed in this section argue compellingly against the expertise hypothesis. The relevant findings are: (1) on the gold standard measures of face-type holistic processing, expertise does not induce holistic processing for other objects; (2) evidence of expertise effects on other behavioral tasks sometimes presented as measures of "holistic processing" can be explained on the basis of things other than face-type holistic processing; (3) in fMRI, expertise-related changes in BOLD are usually greater in object general areas than in the FFA; (4) where expertise effects are found in the FFA these are open to an attentional explanation or a confound of neighboring face and body areas; (5) neuropsychological cases show a double dissociation between faces and objects-of-expertise; (6) the expertise-related changes in the N170 for objects produce patterns that are typically not face-like in terms of spatial distribution; (7) interference from (p. 169) objects-of-expertise on the face N170 could potentially arise from competition within object-general areas; and (8) other arguments that have been made in favor of the expertise hypothesis are either based on out-of-date evidence (childhood development, downwards categorization shift) or are theoretically invalid (null effects, other-race effects). We also note that the expertise hypothesis provides no explanation of the evidence of an evolved and innate face representation: if processing mechanisms claimed to be special to faces were instead general to objects-of-expertise, then it is impossible to explain why infants are born with the ability to individuate faces but are not born experts with, say, cars.

Should faces and objects be different in all possible ways?

It is important to note that, theoretically, the idea that "faces are special" does not predict that faces should be different from objects in *all* possible ways. For one thing, many stages of the total processing stream will of course be shared by faces and objects: these stages include early visual processing (e.g. no-one would propose that area V1 processes only face stimuli and not object stimuli, or vice versa), and general cognitive processes such as working memory, control of spatial attention, and general decision-making strategies. It is also unsurprising that certain basic properties that improve perceptual efficiency will be shared by both face and object modules: for example, both faces and objects show the property that recently repeated stimuli are processed faster with fewer neural resources than previously unseen items. Our point here is that a finding that object processing is similar to face processing in some way is not evidence against the idea that "faces are special" unless the underlying process was originally a serious candidate for face-specificity.

Summary and conclusions

This chapter addressed whether there are unique visual mechanisms for processing identity-related information in faces compared to other objects. We reviewed literature on an evolved face representation, including studies of newborns, face-deprived monkeys and twins; on holistic/configural behavioral processing in object novices and object experts; and on neural processing in object novices and object experts including single-unit recording, fMRI, ERPs, TMS, and neuropsychological studies. Results clearly favored the view that faces are special. Evidence argued that neither individual-level categorization (within-class discrimination hypothesis) nor individual-level categorization with extensive expertise (expertise hypothesis) leads to face-like processing for objects. Instead, results showed that holistic/configural processing is limited to faces, argued that there are dissociable cortical regions dedicated to processing faces per se, and showed that there exists an evolved representation of the structure of an upright face that is able to support individual level discrimination of faces apparently from birth.

Very recent studies support our conclusions. Key theoretical findings are that (a) twin studies have demonstrated heritability of behavioural face recognition ability independent of object recognition and general cognitive abilities (e.g., IQ); results include heritability of holistic processing for upright faces (composite effect, face inversion) but no heritability of recognition of inverted or split faces (Wilmer et al., 2010; Zhu et al., 2010; for summary and discussion see McKone and Palermo, 2010); and (b) a whole-brain analysis showed object-expertise was associated with increased activation across extensive regions of visual cortex (even V1), that expertise effects were much stronger outside the FFA than inside it, and provided evidence that expertise effects reflect top-down attentional modulation (Harel et al., 2010). Key methodological findings supporting our views about appropriateness of tasks are: (a) the Gauthier 'congruency effect' is nearly as large for inverted faces as for upright faces at typical presentation times (Richler et al., (p. 170) 2011), in contrast to the substantial inversion effects on the traditional tasks (e.g. composite illusion as assessed by naming or standard same-different version); and (b) ERPs have confirmed the standard same-different composite effect arises from perceptual integration, not later decisional processes (Kuefner, Jacques, Prieto, and Rossion, 2010).

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Notes:

- (1) Researchers differ as to whether holistic, configural, and second-order relational processing are independent aspects of the "special" processing style used for faces (D. Maurer et al., 2002), or not (McKone and Yovel, 2009; Tanaka and Sengco, 1997; Yovel and Duchaine, 2006). For present purposes, it is not necessary to distinguish between them, and we use the term "holistic" throughout.
- (2) Using higher-resolution fMRI, Grill-Spector et al. (2006) claimed the FFA was not uniformly face selective, reporting it contained many finer-scale voxels highly selective for non-face objects (e.g. sculptures). However, this claim relied on invalid data analysis (Baker et al., 2007; Simmons et al., 2007).

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