Behavioral and Cognitive Neuroscience Reviews

http://bcn.sagepub.com

How Does the Brain Process Upright and Inverted Faces?

Bruno Rossion and Isabel Gauthier

Behav Cogn Neurosci Rev 2002; 1; 63
DOI: 10.1177/1534582302001001004

How Does the Brain Process Upright and Inverted Faces?

Bruno Rossion
Brown University and University of Louvain, Belgium
Isabel Gauthier
Vanderbilt University

The face inversion effect (FIE) is defined as the larger decrease in recognition performance for faces than for other mono-oriented objects when they are presented upside down. Behavioral studies suggest the FIE takes place at the perceptual encoding stage and is mainly due to the decrease in ability to extract relational information when discriminating individual faces. Recently, functional magnetic resonance imaging and scalp event-related potentials studies found that turning faces upside down slightly but significantly decreases the response of face-selective brain regions, including the so-called fusiform face area (FFA), and increases activity of other areas selective for nonface objects. Face inversion leads to a significantly delayed (sometimes larger) N170 component, an occipito-temporal scalp potential associated with the perceptual encoding of faces and objects. These modulations are in agreement with the perceptual locus of the FIE and reinforce the view that the FFA and N170 are sensitive to individual face discrimination.

Key Words: configuration, ERPs, face inversion effect, FFA, fMRI, modularity, N170, second-order relational information

For more than three decades, behavioral studies have revealed that picture-plane inversion dramatically impairs face recognition (e.g., Hochberg & Galper, 1967). A landmark article on this topic is that of Yin (1969) in which face recognition was found to be disproportionately affected by inversion, an observation called the face inversion effect (FIE). This suggested that faces may be "special," or processed in a qualitatively different manner than other objects by a dedicated module (e.g., Ellis, 1975; Kanwisher, 2000; Nachson, 1995). Yet another landmark article in the literature on face inversion is the last extensive review on the topic from Valentine (1988), who concluded that the effect of inversion provided little or no evidence of a unique process involved in face recognition.

In recent years, many other phenomena and techniques (including functional magnetic resonance imaging [fMRI] and event-related potentials [ERPs]) have allowed a more thorough examination of the modularity hypothesis for face recognition (e.g., see Kanwisher, 2000; Tarr & Gauthier, 2000; Tovée, 1998), lessening a considerable theoretical burden on the FIE, whose causes remain an active topic of investigation. Indeed, yet a third beacon in this literature is the study by Diamond and Carey (1986), demonstrating an inversion effect with dog pictures but only in dog experts. Since then, many authors have asked the fascinating question of how faces become special (rather than the semantic conundrum of asking whether they are special) by studying how putative face-specific effects can be obtained with nonface categories through extensive experience at discriminating visually similar objects (e.g., Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998; Rhodes, Brennan, & Carey, 1987; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, in press; Tanaka & Taylor, 1991). These results suggest that face-specific effects are a reflection of the different goals and recognition strategies associated with faces through experience and that under certain conditions, the same goals and strategies can be associated with nonface objects.

In the developmental literature, an analog of the FIE is the finding that newborns prefer to look at upright rather than inverted facelike configurations (e.g., Valenza, Simion, Mucchi Cassia, & Umilta, 1996). This is often cited as evidence for an innate basis to face process-

Behavioral and Cognitive Neuroscience Reviews
Volume 1 Number 1, March 2002 63-75

ing. However, a series of elegant experiments recently revealed that newborns prefer the "upright" version of any pattern with more elements located in the upper part of the configuration (Simion, Macchi Cassia, Turati, & Valenza, 2001). Therefore, any effect of inversion in infants could simply reflect this general principle. Similarly, the observation of an FIE in chimpanzees raised by humans for both chimpanzee and human faces, but not capucin monkey faces (Parr, Dove, & Hopkins, 1998), supports the view that it is not the face configuration per se that is a critical factor for the FIE.

Thus, the FIE does not appear to reflect processes unique to faces in the sense that they could only develop and/or be used to process objects with the geometry of faces. Rather, it probably reflects a combination of general constraints of the visual system and the extensive expertise we possess in face recognition. However, as Valentine (1988) noted, even if it is not unique to faces, the basis of the FIE remains interesting: In particular, it offers a window on the different processes available for face recognition and those that may have been tuned to the more familiar, upright orientation. The present review will focus on the perceptual mechanisms underlying the FIE (Section 1), its neural underpinnings (Section 2), and recent claims about what the FIE reveals regarding the processing stage represented by face-selective neural responses (Section 3).

1. WHAT CAUSES THE FIE?

The FIE has been obtained in old-new recognition paradigms (e.g., Carey, Diamond, & Woods, 1980; Philips & Rawles, 1979; Scapinello & Yarmey, 1970) and two alternative forced choice paradigms with or without delay (e.g., Carey & Diamond, 1977; Diamond & Carey, 1986; Freire, Lee, & Symons, 2000; Leder & Bruce, 2000; Scapinello & Yarmey, 1970; Tanaka & Farah, 1993; Valentine & Bruce, 1986; Yarmey, 1971; Yin, 1969). It is virtually the same for unfamiliar and familiar faces (Collishaw & Hole, 2000; Rock, 1974; Yarmey, 1971). It is observed when orientation is manipulated in separate blocks—or in between subjects' designs (e.g., Toyama, 1975; Valentine & Bruce, 1986)—as well as in randomized presentation of upright and inverted faces (e.g., Carey & Diamond, 1977; Diamond & Carey, 1986; Scapinello & Yarmey, 1970; Yarmey, 1971; Yin, 1969).

Valentine (1988, 1991) suggested that the source of the FIE is related to the encoding of faces in memory: Upright and inverted faces would not be perceived differentially, but memory encoding would not be as efficient for inverted faces as for upright faces. This view has been challenged by subsequent studies in which the FIE was obtained for simultaneous presentation of unfamiliar faces (e.g., Farah, Wilson, Drain, & Tanaka, 1998; Moscovitch, Behrmann, & Winocur, 1997; Phelps & Roberts, 1994; Searcy & Bartlett, 1996). Recently, Freire and colleagues (2000) compared the discrimination of pairs of upright or inverted faces in simultaneous or sequential presentation (1-second, 5-second, or 10-second delay). They found no effect of having a delay or of its length and obtained an FIE in all conditions in which faces differed only on the basis of metric. There is thus a growing consensus that the FIE occurs primarily during perceptual encoding rather than in the architecture of long-term memory. This is consistent with the fact that the first and perhaps only consistent effect of inversion in ERPs is obtained on a very early potential peaking around 170 ms after stimulus presentation (e.g., Rossion, Gauthier, et al., 2000).

Many recent studies investigated the difference in encoding processes between upright and inverted faces. At the time of Valentine's (1988) study, there was already some evidence that configural information was more important in the encoding of upright than inverted faces (Sergent, 1984; Young, Hellawell, & Hay, 1987). Many models for this configural information have been offered (see Bartlett & Searcy, 1993; Diamond & Carey, 1986; Leder & Bruce, 1998, 2000; Rhodes, Brake, & Atkinson, 1993; Tanaka & Gauthier, 1997). Covering all such proposals is beyond the purpose of this review (the reader is referred to discussions by Diamond & Carey, 1986; Farah et al., 1998; Gauthier & Tarr, in press; Rhodes et al., 1993; Searcy & Bartlett, 1996; Tanaka & Gauthier, 1997), but one distinction has become particularly important recently: This is the interpretation of configural information as either holistic or relational. The holistic interpretation suggests that configural effects, such as the better recognition of a face part presented in a whole face than in isolation (Tanaka & Farah, 1993), reflect the existence of Gestalt patterns or undifferentiated templates (Farah, Tanaka, & Drain, 1995; Tanaka & Farah, 1993). In its extreme version, this model claims that an object yielding these configural effects is represented as a whole and that its parts are not represented explicitly (Farah et al., 1998). The relational interpretation instead proposes that configural information is represented as the explicit and precise relative spatial relationships between the different object parts, for instance, the distance between the eyes (e.g., Diamond & Carey, 1986; Leder & Bruce, 2000; Rakover & Teucher, 1997).

One interesting aspect of the relational interpretation is that configural effects need not involve the entire object: They can occur locally; for instance, the image of a half face may trigger configural processing because the relationships between the parts shown can be processed in terms of their relative relations (whereas in a holistic account, a half face may not be enough to invoke the appropriate template and default part-based mechanisms have to be used). In a relational account, there is only a fine line between stimuli evoking configural effects and those that do not: Whereas the relation between two eyes is configural information, the shape of these two eyes may not be[1] (in contrast, the holistic model sees both as local information that may not be sufficient to invoke a template and lead to configural effects). To test the relational hypothesis, Leder and Bruce (2000) created a set of eight faces, each containing a unique local feature as well as a unique relational feature (e.g., one face had a unique mouth within the set and the same eyes as another face but with a different spacing). Participants first learned the names of the full faces and then identified them in six conditions: the full faces, upright and inverted; portion of the images including only the unique local feature for each face, upright and inverted; and portion of the images showing only the unique relational feature for each face, upright and inverted. The FIE obtained in this experiment was equally large for the relational information as for the full faces (although full faces were better recognized), and there was no FIE at all for the local features (see also Leder & Bruce, 1998).

These findings lead to two important conclusions: First, the FIE for full faces seems to be entirely accounted for by the distinctive relational information present locally. This is clearly incompatible with a strong holistic template hypothesis (Farah et al., 1998). Second, the presence of unique local information does not necessarily reduce the FIE if relational information is available. This occurs even in conditions where overall accuracy with local features is as good as that for local plus relational features (Leder & Bruce, 2000, Experiment 2) and suggests a strong bias in favor of the use of relational information in face processing (perhaps even obligatory).

Clear demonstrations for the relational hypothesis are an important development in the past 10 years or so and perhaps one of the most significant contributions of the FIE to our understanding of face processing. In many prior studies setting out to measure configural effects, holistic and relational information are both disrupted and could both account for the findings (e.g., Bartlett & Searcy, 1993; Farah et al., 1998; Gauthier & Tarr, 1997; Kemp, McManus, & Pigott, 1990; Rhodes et al., 1993; Searcy & Bartlett, 1996; Sergent, 1984; Tanaka & Sengco, 1997; Young et al., 1987).

Evidence in favor of the relational hypothesis (Freire et al., 2000; Leder & Bruce, 1998, 2000; Leder, Candrian, Huber, & Bruce, 2001; Murray, Yong, & Rhodes, 2000) seems to indicate that relational information is represented explicitly (e.g., the shape of each eye and the precise distance between the eyes would be part of the representation of face). If this were the case, then we would also need to postulate that when part information is activated, that information for the relationships between parts is also activated. This is because configural effects are obtained even when subjects explicitly try to ignore the other parts (e.g., Gauthier & Tarr, 1997; Tanaka & Sengco, 1997; Young et al., 1987). An explicit representation of the parts, as well as that of the distance between them, with a very strong connection between the two kinds of information is a reasonable interpretation of the relational findings.

However, at least one alternative exists in which there is no qualitative difference between mechanisms used in processing upright versus inverted faces and faces versus objects or between novices and experts (e.g., Bruyer, Galvez, & Prairial, 1993; Gauthier & Tarr, 1997; Valentine & Bruce, 1988). Perrett and Oram (1993) suggested that configural sensitivity at the level of face-selective neurons could be derived from the combination of inputs selective for complex features. Some cells would be selective for the two eyes, some to one eye and a nose, and another to a nose and a mouth: The convergence of many such inputs on another cell would lead to selectivity for the entire face configuration. A recent neurally plausible model of object recognition makes use of a similar code, overrepresenting the object using a very large and overlapping set of features, leading to a redundant representation that can support selectivity for configural information (Riesenhuber & Poggio, 1999; see also Edelman, 1995). This kind of image-based representation has been invoked to explain how subjects trained to expertise with novel objects (called Greebles) started showing configural processing for new exemplars of upright Greebles but not for inverted Greebles (Gauthier & Tarr, 1997). Specifically, the acquisition of expertise could lead to the acquisition of new feature detectors, larger and more complex than those used by novices. For instance, new features created during learning (Schyns & Murphy, 1994; Schyns & Rodet, 1997) could combine parts that co-occurred on the objects.

More direct evidence that the apparently qualitative difference between novices and experts could be of a continuous sort comes from a recent study in which participants were tested behaviorally several times during the acquisition of Greeble expertise. In face recognition, the holistic template hypothesis finds support from the finding that judgments about all of the parts of face are dependent on configural changes of other parts (Tanaka & Sengco, 1997). Similarly, at the outset of an extensive training protocol, participants can also show configural effects for all Greeble parts (Gauthier & Tarr, 1997). Gauthier and Tarr (in press) recently proposed that such a complete interdependence between all parts may be obtained only because participants were tested when they were extremely practiced with a category. However, when configural processing is measured at several points during expertise acquisition, these effects appear at different points for different Greeble parts (Gauthier & Tarr, in press). In other words, there is a time in the training where some of the parts appear to be represented relationally, whereas other parts are not. It is possible that participants are accessing an object template only for some of the parts of the object, but a more plausible alternative is that we are merely witnessing an intermediate stage in which only some of the new features have been created (perhaps those that are most diagnostic). An interesting aspect of this continuous feature-tuning hypothesis is that local relational effects are not accounted for by the explicit representation of the relations between parts but rather by the creation of relatively large and complex image-based features: essentially a redundant set of small templates (making the relational information much less distinct from the holistic model)!

In summary, most if not all of the decrease in face discrimination performance caused by inversion can be accounted for by the disruption in inverted faces of the processing of the local spatial relationships between features (Freire et al., 2000; Leder & Bruce, 2000; Rhodes et al., 1993; Searcy & Bartlett, 1996). Whereas this seems to be a fatal blow to the holistic hypothesis, a set of overlapping holistic templates, each including more than single parts, may be able to account for the local relational effects as well as the pattern of acquisition of these effects in newly trained experts.

2. WHERE AND WHEN IN THE BRAIN DOES THE FIE OCCUR?

Recent work using fMRI and ERPs focused on determining the neural bases of the difference between faces and objects (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier, Tarr, Moylan, Anderson, et al., 2000; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Rossion, Gauthier, et al., 2000). Once we know where and when face selectivity occurs, what more can be added by studying the neural basis of the FIE? The behavioral work reviewed in Section 1 suggests that this manipulation should allow us to relatively precisely identify those neural responses important for configural processing. In addition, the comparison of upright to inverted faces offers a very good control on most low-level visual properties of the image (only the phase information is different), the impact of which is not completely understood in extrastriate areas involved in object processing.

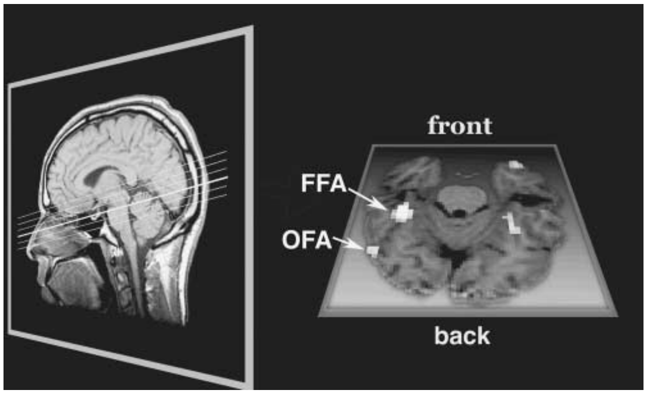

Figure 1: Transversal Slices Illustrating the Regions of the Inferior Occipital Gyrus (OFA, right lateralized) and Middle Lateral Fusiform Gyrus (FFA, bilateral) As Observed in a Localizer (faces-object) fMRI Study.

NOTE: FFA = fusiform face area; OFA = occipital face area; fMRI = functional magnetic resonance imaging.

Three bilateral regions of the visual cortex appear to form the core of the neural system involved in face processing in humans (see Figure 1): the inferior occipital (or posterior fusiform) gyrus, the lateral middle fusiform gyrus, and the superior temporal sulcus (STS) (see Haxby, Hoffman, & Gobbini, 2000, for a review). Given the complexity and richness of face processing, many more regions are probably involved, but these areas are the main ones that are more involved in face processing than that of other categories.

The fusiform face area. The most robust difference in activity between faces and objects has been described in the lateral middle fusiform gyrus, bilaterally but often stronger in the right hemisphere (e.g., Gauthier et al., 1999; Haxby et al., 1999; Kanwisher et al., 1997; McCarthy et al., 1997; Rossion, Dricot, et al., 2000; Sergent, Otha, & MacDonald, 1992). This is the region that has been dubbed the "fusiform face area" ("FFA") (Kanwisher et al., 1997). There remain, however, disagreements about whether this region represents in itself a module for face perception (Kanwisher, 2000; Kanwisher et al., 1997) or whether it is a part of a larger network involved in general object recognition, including faces (Haxby et al., 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999), that can be modified among other factors by task constraints and visual expertise (Gauthier, Anderson, Skudlarski, & Gore, 2000; Gauthier et al., 1999; Tarr & Gauthier, 2000).

Four published fMRI studies compared the processing of upright and inverted faces (Aguirre, Singh, & D'Esposito, 1999; Gauthier et al., 1999; Haxby et al., 1999; Kanwisher, Tong, & Nakayama, 1998). Three of these studies found a small but significant decrease for face inversion in the FFA (bilateral: Gauthier et al., 1999;

Haxby et al., 1999; only right hemisphere tested: Kanwisher et al., 1998). There was a small but nonsignificant decrease observed in the FFA for inverted faces in the fourth study (Aguirre et al., 1999). However, in contrast to the other fMRI experiments, this study reported a very small difference between upright faces and objects in the FFA and no significant increase for objects (cars) as compared to faces in the region normally selective for faces, suggesting an overall lack of statistical power. On the basis of the other studies, face inversion appears to reduce the level of activation in the FFA.

What is the effect of object inversion in the same region? Whereas objects were not tested in Kanwisher et al. (1998), Haxby et al. (1999) reported no difference for upright and inverted houses, Aguirre et al. (1999) found no differences between upright and inverted cars, and Gauthier et al. (1999) found only a small difference for upright and inverted novel objects (Greebles) before any familiarization with these objects. However, as participants acquired expertise with Greebles, the difference in activity for upright versus inverted Greebles (even unfamiliar ones) showed a significant increase in the right FFA (Gauthier et al., 1999). In recent analyses correlating behavioral changes during expertise training and the neural changes in this region, Gauthier and Tarr (in press) found that an increase in holistic processing[2] during training was significantly correlated with activity in the right FFA for upright Greebles (but not for inverted Greebles or upright or inverted faces).

In line with behavioral effects (Yin, 1969), the FFA shows a larger inversion effect for faces than nonface objects. In addition, when studied with either behavioral (Diamond & Carey, 1986) or fMRI (Gauthier et al., 1999) methods, the FIE appears to be a general phenomenon related to the participants' expertise (and associated changes in processing strategies).

The other face-sensitive regions. Posterior to the FFA, a region of the inferior occipital gyrus (infOG) (termed OFA for occipital face area) also responds more to faces than objects, generally with a larger response in the right hemisphere (Gauthier et al., 1999; Halgren et al., 1998; Haxby et al., 1999; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Rossion, Dricot, et al., 2000; Sergent et al., 1992). Haxby et al. (2000) suggested that this region is involved in the early perception of facial features and may provide input to the FFA and the face-selective areas in the STS. However, there is no current fMRI or anatomical data supporting the view that there is a processing stage at which facial features are extracted before they would be later combined to form whole representation of faces. Rather, several studies suggest that encoding faces as a whole is dominant over encoding individual facial features (e.g., Farah et al., 1998; Hillger & Koenig, 1991; Tanaka & Farah, 1993). Moreover, the early N170 component sensitive to faces peaks earlier for whole faces than for isolated face features (e.g., Bentin et al., 1996; Taylor, Itier, Allison, & Edmonds, 2001). In regard to the FIE and the OFA, Haxby et al. (1999) found larger activity for inverted than for upright faces and objects in this region. In anatomically defined regions of the infOG and lateral occipital gyrus, which would include the area typically defined functionally as the OFA, significant inversion effects for both faces and Greebles have been found (Gauthier, 1998). Within these regions, some voxels showed a significant preference for upright over inverted Greebles, but this effect was not obtained for faces. In addition, within these two areas, other voxels preferred inverted faces and Greebles over their upright versions.[3] Interestingly, in the infOG, the activity for inverted minus upright Greebles showed a significant increase between the first and later five testing sessions. This effect of familiarity in the occipital lobe, occurring much more rapidly than the expertise effects in the FFA in the same study, suggest different sources for the inversion effects obtained in different areas of extrastriate cortex. Familiarity effects can arise early, perhaps as soon as participants develop a canonical orientation for an object category, whereas expertise effects are slower and correlated with behavioral changes during the acquisition of expertise (Gauthier & Tarr, in press). Other face-sensitive regions, such as the posterior part of the STS (Haxby et al., 1999; Hoffman & Haxby, 2000; Kanwisher et al., 1997) or a fusiform area more anterior than the FFA, also show significant decreases of activation for face inversion (Gauthier et al., 1999; Haxby et al., 1999) with a nonsignificant decrease for object inversion.

Regions showing a preference for objects over faces. Given that our expertise with faces is fairly limited to the upright orientation, it is not so surprising that face-selective areas respond less to inverted than upright faces. Along the same lines, one may expect that areas that generally respond more to nonface objects than faces should prefer inverted faces. These "object-selective" areas include a medial area, joining part of the ventral occipital lobe to the parahippocampal gyrus (Epstein & Kanwisher, 1998; Haxby et al., 1999; Ishai et al., 1999). There is also an area lateral to the FFA in the inferior temporal gyrus that generally responds more to objects than to faces (e.g., it responded more to chairs than faces) (Ishai et al., 1999), but we will focus on the object-selective region because there is no study of the FIE in the lateral area. Part of the medial object-selective area (Haxby et al., 1999; Ishai et al., 1999) includes the region termed *parahippocampal place area* (*PPA*) because it is particularly sensitive to scenes depicting locations (Epstein & Kanwisher, 1998). The PPA is far more active for images of scenes than for any other object, but it responds significantly more to objects than faces (Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998). This region also responds more to houses and buildings than other objects (Aguirre, Zarahn, & D'Esposito, 1998), presumably because of their importance in spatial navigation. A summary from Kanwisher's studies gives percent signal changes (PSC) relative to a fixation baseline of approximately 0.0, 0.45, 1.0, and 1.8 for upright faces, nonface objects, houses, and unfamiliar outdoor scenes, respectively (Kanwisher, Downing, Epstein, & Kourtzi, 2001). The object-selective area that overlaps significantly with the PPA may therefore be relatively larger when it is defined by the direct comparison of houses to faces (e.g., Haxby et al., 1999) than if it was defined by a comparison of objects minus faces and, in that case, may be more appropriately called house selective than object selective.

Two fMRI studies of stimulus inversion found a significant increase of activation in this medial area for inverted faces, as compared to upright faces (Aguirre et al., 1999; Haxby et al., 1999). More precisely, Haxby et al. (1999) described this "face inversion superiority" in three regions more active for houses than faces, two that are medial to the FFA/OFA (posterior fusiform gyrus and the medial fusiform gyrus/parahippocampal gyrus) as well as one in the posterior superior occipital cortex. The inversion superiority for faces in this medial house-selective area was the largest effect of inversion obtained for either faces or houses in either face- or object-selective regions.

Therefore, inverted faces recruit the face-sensitive areas less than upright faces and object- (or house-) selective areas more than upright faces. On the basis of fMRI findings, inverted faces have been argued to be processed more like upright faces than objects because face-selective areas still show face selectivity with inverted images (Kanwisher et al., 1998). On the other hand, inverted faces can also be argued to be processed more like objects than upright faces because they recruit object-selective areas more than upright faces do (Haxby et al., 1999).

These two claims are not inconsistent, especially when put in the perspective of the acquisition of expertise. An interesting question is whether any difference between upright and inverted faces in a given brain area is entirely attributable to changes for upright faces as expertise is acquired for upright faces or whether the processing of inverted faces also changes in the process. The changes in the activity for the trained (upright) orientation of an object category (e.g., upright birds in bird experts) have been found mainly in the right hemisphere face-selective areas (OFA/FFA) (Gauthier, Anderson, et al., 2000; Gauthier et al., 1999).[4] In addition, inverted faces are not processed just like any other objects in the FFA: They elicit more activity than nonface objects in this region (e.g., Kanwisher et al., 2001). This is consistent with the fact that training with upright objects transfers to some extent, although not completely, to inverted objects. For instance, Greeble experts perform better with inverted Greebles than novices do (Gauthier et al., 1998, 1999). If the FFA is engaged for relational and or holistic processing, these processes may also be engaged, albeit unsuccessfully, for inverted faces.

Insofar as the house-selective area is concerned, it is not as clear that inverted faces are not processed in this region just like other objects. In Haxby et al. (1999), inverted faces elicited at most 0.5 PSC relative to fixation during delayed matching (less than during passive viewing). Unfortunately, in that study, there was no comparison with nonface objects other than houses, which, in other studies, elicit about twice as much activity in the PPA as other objects not associated with places (e.g., houses: 1.0 PSC; objects: 0.3 PSC to 0.6 PSC) (Kanwisher et al., 2001). These comparisons across studies could be misleading, but they suggest that inverted faces are processed like objects in object-selective areas but not in face-selective areas. In contrast, upright faces more clearly elicit less activity than objects in this region (Kanwisher et al., 2001). Based on the current fMRI evidence, our expertise with upright faces appears to both increase the role of the OFA/FFA and decrease that of medial areas (including the PPA) for the processing of upright faces. Some of this expertise with upright faces appears to generalize to the processing of inverted faces in the FFA, but there is little evidence that it influences the processing of inverted faces in the PPA relative to what it would be in face-recognition novices. One caveat is that effects of inversion may not be entirely captured in fMRI. Indeed, neurophysiological studies indicate robust effects of face inversion at a temporal scale that would not be detectable by fMRI: This is reviewed next.

ERP studies of face (and object) inversion. The most salient scalp ERP response to the presentation of faces is a dipolar component with a negative deflection peaking around 170 ms at bilateral occipito-temporal sites, termed the *N170* (following Bentin et al., 1996), and a corresponding positivity at centro-frontal sites (termed the *vertex positive potential* or *VPP*, following Jeffreys, 1989) (see Figure 2).

The neural source(s) of the N170 is unclear, as is its relationship to the face-sensitive regions identified in fMRI. Establishing a direct relationship between the N170 component and the activation of specific face-selective areas identified in fMRI is not at all straightforward, even in the context of recent findings that the

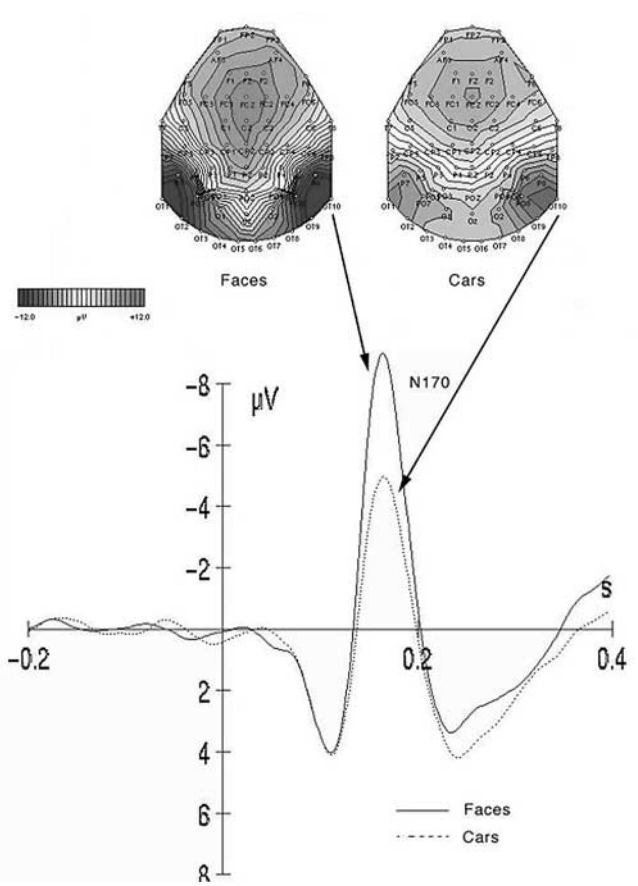

Figure 2: The N170 ERP Component Recorded to Pictures of Faces and Objects.

NOTE: ERP = event-related potentials. The top of the figure shows 2D topography (average between 150 ms to 170 ms after onset of stimulation) showing the bilateral negative component (N170) at occipito-temporal sites for both faces and cars, as well as the corresponding positivity (vertex positive potential) at central and frontal sites. The bottom of the figure shows waveforms from a right occipito-temporal site (2 cm below PO8 or T6) for both faces and cars between –200 ms and 400 ms following stimulus onset (grand-average data on 24 participants, average reference) (unpublished data from B. Rossion).

neurophysiological basis of the blood oxygen level–dependent fMRI signal and of the local field potentials recorded in visual cortex is likely to be identical (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). First, the fMRI signal is measured over several seconds, whereas the N170 reflects transient changes of electrical potential on the order of a few tenths of milliseconds. Moreover, scalp ERPs are thought to originate from the excitatory/inhibitory depolarizations in the dendrites of cortical pyramidal cells with an open-field spatial organization (dendritic trees oriented on one side of the brain structure). Accordingly, ERPs reflect essentially postsynaptic activity (as also suggested for fMRI) (Logothetis et al., 2001) but only of a subset of brain structures (mainly cortical). Muddling the correspondence even more, probably at least more than a dozen visual areas show activity between 100 ms and 200 ms following the presentation of a visual complex stimulus, such as a face, with several showing differential activation to faces and objects (individual neurons responding to faces in the infero-temporal cortex becomes activated at around 100 ms to 120 ms following stimulus presentation) (e.g., Rolls, 1992). Therefore, the N170 is likely to reflect the combination of several generators with different orientations active around this latency. Intracranial recordings made directly on the surface of the brain of epileptic patients also support this view. Several local electrophysiological components responsive to faces and objects such as the N200, which show a larger response to faces (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Allison, Puce, Spencer, & McCarthy, 1999) at some locations but may be larger to objects at other locations (Allison et al., 1999), are recorded on a multitude of sites along the ventral and lateral parts of occipito-temporal cortex (Allison et al., 1999). Most of these local components are likely to contribute to the far-field N170 scalp potential. For this reason, functional links between the scalp ERPs such as the N170 and the activity of face-sensitive regions in fMRI may be the most meaningful approach.

Temporally, the N170 is the first (and the only consistent) difference between faces and other object categories, with larger amplitude for faces than nonface objects (Bentin et al., 1996; Bötzel, Schulze, & Stodieck, 1995; Eimer, 1998, 2000a, 2000c; Rebai, Poiroux, Bernard, & Lalonde, 2001; Rossion et al., in press; Rossion, Gauthier, et al., 2000; Taylor, McCarthy, Saliba, & Degiovanni, 1999) (see Figure 2). The N170 is bilateral, sometimes with a slight right hemisphere advantage (Bentin et al., 1996), but the N170 amplitude difference between faces and objects is generally as large at right and left scalp locations. Although some ERP studies (generally using passive viewing of the stimuli compared) described small negative deflections for objects (e.g., Bentin et al., 1996), clear identifiable N170 potentials can be recorded for nonface categories including cars, chairs, glasses, houses, dogs, birds, flowers, butterflies, or hands (e.g., see Eimer, 2000c; Rossion, Gauthier, et al., 2000; Tanaka & Curran, 2001) and even novel objects such as Greebles (Rossion et al., in press) or 2D ink-blob shapes (Curran, Tanaka, & Weiskopf, 2001). Recording of the magnetic field on the scalp using magnetoencephalography (MEG) reveals an “M170” component with similar response properties as the N170 (e.g., Linkenkaer-Hansen et al., 1998; Liu, Higuchi, Marantz, & Kanwisher, 2000).

Whereas several authors (e.g., Bentin et al., 1996; Eimer, 1998) emphasize the difference in amplitude of the N170 for faces versus nonface objects, Rossion,

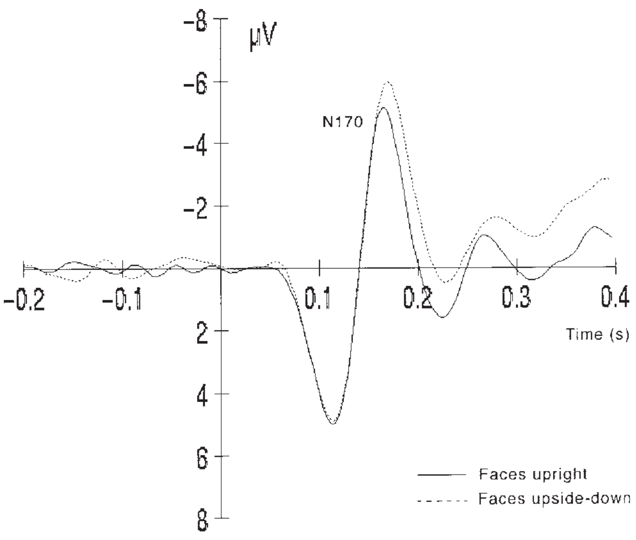

Figure 3: Effect of Face Inversion on the N170 Component.
NOTE: T6 electrode; 15 participants' grand-average waveforms; common average reference (unpublished data from B. Rossion).

Gauthier, et al. (2000) recently suggested that a better candidate for a face-selective effect in scalp recording may be the N170 delay for upside-down pictures that is obtained only with faces. Face inversion significantly delays the peak latency of the N170 (Bentin et al., 1996; Eimer, 2000a; Linkenkaer-Hansen et al., 1998; Rebai et al., 2001; Rossion, Delvenne, et al., 1999; Rossion et al., in press; Rossion, Gauthier, et al., 2000; Sagiv & Bentin, 2001; Taylor et al., 2001) and most often also increases its amplitude (Linkenkaer-Hansen et al., 1998; Rossion, Delvenne, et al., 1999; Rossion, Gauthier, et al., 2000; Sagiv & Bentin, 2001) (see Figure 3). These effects are also observed on the VPP, the positive counterpart of the N170 (e.g., Jeffreys, 1993; Rossion, Delvenne, et al., 1999). The delay of the N170 is small (around 10 ms) but very robust and consistent across studies and paradigms. It is also observed on the face-sensitive intracranial N200, which shows a similar delay (11 ms) in both hemispheres for face inversion (McCarthy, Puce, Belger, & Allison, 1999).

These findings on an early visual component confirm the perceptual origin of the FIE suggested by behavioral and fMRI studies. The N170 appears to be the only component (with its positive counterpart, the VPP) delayed by face inversion.[5] The delay for inversion has not been observed for other categories of objects tested (e.g., chairs, cars, shoes, houses) (see Rossion, Gauthier, et al., 2000). The exception is a study of Greeble expertise (Rossion et al., in press). Whereas Greeble novices showed identical N170 potentials for upright and inverted Greebles, the N170 delay for inverted Greebles was significant for experts only on the left hemisphere (although there was no interaction between the effect of expertise and lateralization). This delay with inversion may be related to the disruption of relational and holistic information that experts learn to rely on (as Greeble experts demonstrate configural processing for upright but not inverted exemplars) (Gauthier & Tarr, 1997).

There is other indirect evidence that the N170 delay to face inversion is related to the disruption of relational information processing (Eimer, 2000a; Rossion, Delvenne, et al., 1999; Rossion, Gauthier, et al., 2000): The N170 is delayed to faces with displaced features (Eimer & McCarthy, 1999; George, Evans, Fiori, Davidoff, & Renault, 1996) or removed or masked features (Eimer, 1998, 2000c; Jemel, George, Chaby, Fiori, & Renault, 1999), as well as to the presentation of isolated face features (Bentin et al., 1996; Cauquil, Edmonds, & Taylor, 2000; Taylor et al., 2001).

The physiological mechanisms underlying this latency delay for faces presented upside down are currently unclear. Response latency delays of face-selective cells to inverted faces have been reported in earlier studies (Perrett et al., 1988), but these authors have suggested recently that the response of face cells to different stimulus orientations actually begins at approximately the same latency (Perrett, Oram, & Ashbridge, 1998). However, a slower accumulative rate of activity at the level of the whole cell population may underlie the population potential response delay and thus a peak delay on cortical surface or scalp ERPs (see Perrett et al., 1998).

In addition to the delay with inversion, several ERP studies also described an enhancement of the N170 to inverted faces as compared to upright faces (Rossion, Delvenne, et al., 1999; Rossion et al., in press; Rossion, Gauthier, et al., 2000; Sagiv & Bentin, 2001). This may appear surprising because relational information is not as useful for inverted faces as for upright faces: How could this decrease in efficiency of processing increase the N170 amplitude? Moreover, intracranial face N200s are not increased by face inversion but rather show a slight amplitude reduction, in addition to the delay with inversion (McCarthy et al., 1999), more consistent with what is observed at the level of the FFA in fMRI. Single-cell recordings of face-selective neurons in the macaque STS also usually show comparable amplitude to upright and inverted faces (Perrett et al., 1988, 1998). However, the difference between scalp and intracranial recordings may be explained by the fact that the scalp N170 is likely to reflect the activation of several local cortical potentials, some of which are also larger for objects than faces (Allison et al., 1999), and their sources may be in the object-selective areas both medial and lateral to the OFA and FFA (Aguirre et al., 1999; Haxby et al., 1999). In short, even if inverted faces decrease the level of activation of face-sensitive cortical areas, the increase in the number of other sources more active for inverted than upright faces may be reflected in a higher amplitude at the scalp. This interpretation is speculative because amplitude differences of scalp ERPs can be related to increases of the source of the activity but also to the addition of other sources, or to changes in dipole orientation. Nevertheless, it has the advantage of bringing together findings from ERP, intracranial recordings, and fMRI.

Finally, a recent study using upright and inverted faces presented to normal and pathological populations (Grice et al., 2001) has shown that an increase of N170 amplitude to inverted faces could be accompanied by a decrease of gamma-band (around 40 Hz) electroencephalogram (EEG) bursts at the same latency. Because increases of gamma-band EEG have been related to the integration of perceptual features ("binding") (see Singer & Gray, 1995; Tallon-Baudry & Bertrand, 1999), a reduced gamma activity to inverted faces is consistent with the idea that the processing of relational information is impaired on inverted faces. This result may also support the proposal that the increase of N170 voltage amplitude to inverted faces is not related to an increase of face activity but to the contributions of other populations of cells, perhaps discharging at different frequency rates.

3. THE FIE AND THE PROCESSING STAGE OF FACE-SELECTIVE EFFECTS

Kanwisher et al. (2001) suggested that the primary function of the FFA may be to detect faces rather than recognize or discriminate them at the individual level. This hypothesis was based on three findings. First is the fact that familiarity for faces does not influence the activity of this region (Epstein et al., 1999). However, using fMRI, Gauthier, Tarr, Moylan, Skudlarski, and colleagues (2000) found that repetition of the same facial identity over a block reduces the activity in the FFA as compared to the presentation of different facial identities. They argued that whereas FFA activity may not be involved in holding long-term memories of faces, it may be responsible for the processing necessary to perceive facial identity. Second, the response in the FFA to line drawings of faces is only moderately reduced compared to gray scale images (Halgren et al., 1998; Ishai et al., 1999), whereas this is a manipulation that greatly influences face recognition (but see Gauthier & Epstein, 2001, for evidence that the right FFA responds more to low-pass than high-pass images of faces). Third, the FFA only shows a small effect of inversion for gray scale faces (Aguirre et al., 1999; Gauthier et al., 1999; Haxby et al., 1999; Kanwisher et al., 1998). Kanwisher et al. (1998) obtained a larger effect of inversion for two-tone "mooney" faces, which are difficult to recognize as faces when upside down. This reinforced their position that the FFA activity seems to reflect whether subjects see a face rather than whose face it is.

Implicit in this argument is that manipulations with a large effect on face discrimination should likewise have a large effect on activity in the FFA if this area is responsible for discriminating faces. However, it is unclear how large an effect described in terms of PSC between two conditions needs to be to account for a large behavioral effect. Kanwisher and colleagues (2001) reported a difference of approximately 1 PSC to 1.5 PSC for faces compared to nonface objects in the FFA (a large effect) and a difference of about 0.5 PSC between upright and inverted gray scale faces (a small effect). In comparison, the effect of expertise in the right FFA for bird and car experts may be only 0.4 PSC, but it shows a very strong correlation (*r* more than .75) with an independent behavioral measure of relative expertise for birds and cars (Gauthier, Anderson, et al., 2000). Therefore, a small effect can account for a very large behavioral effect in individual discrimination (the difference induced by 20 years of experience with a category!). Perhaps more important than the size of the FIE are two important facts: (a) The FFA can be shown to be involved in individual discrimination for both faces and nonface objects (Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997, Gauthier, Tarr, Moylan, Skudlarski, et al., 2000; Hoffman & Haxby, 2000), and (b) lesions in the territory of face-selective areas can lead to a severe deficit in face discrimination, whereas "face detection" remains intact when tested in prosopagnosia (e.g., Bodamer, 1947 [translation by Ellis & Florence, 1990]; Bruyer et al., 1983).

In parallel with the proposal that the FFA may be involved in face detection, the face-selective N170 component has also been argued to be implicated in a similar stage of processing (e.g., Bentin & Deouell, 2000; Bentin, Deouell, & Soroker, 1999; Liu et al., 2000; Sagiv & Bentin, 2001), based on the same arguments: the absence of N170 modulation by face familiarity (Bentin & Deouell, 2000; Eimer, 2000b; Rossion, Campanella, et al., 1999), line drawings versus gray scale face images (Liu et al., 2000), as well as the absence of N170 amplitude reduction for inverted faces (Bentin et al., 1996). These observations have led to the suggestion that the mechanism associated with the N170 acts on basic physiognomic features and precedes within-category identification (Sagiv & Bentin, 2001), being an electrophysiological manifestation of the structural encoding stage proposed by Bruce and Young (1986) (see also Eimer, 1998, 2000c). However, it must be stressed that the "structural encoding stage" in terms of Bruce and Young's cognitive architecture is not at all considered as a face detection stage but rather as a level "*which capture those aspects of the structure of a face essential to distinguish it from other faces* [italics added]" (p. 307) and thus supposedly reflects within-category discrimination!

How can we reconcile these apparent contradictions? The N170 is the first component that differentiates between faces and objects and for which differences among other object categories are also observed (Rossion, Gauthier, et al., 2000), thus consistent with the idea that basic- or entry-level categorization occurs at about this time. Accordingly, this component is sensitive to the level of categorization required by the task (Tanaka, Luu, Weisbrod, & Kiefer, 1999). However, faces also appear to be individualized at this stage. For instance, the N170 is reduced in amplitude for repeated facial identities (Campanella et al., 2000; Guillaume & Tiberghien, 2001).[6] The fact that faces would be categorized at the basic and individual level at approximately the same latency may seem surprising if one assumes that faces must be categorized as faces before they are processed at the individual level. However, whereas this two-step categorization process may be a good approximation for most cases of object recognition (Jolicoeur, Gluck, & Kosslyn, 1984), faces are categorized as quickly at the basic level than at the subordinate or individual level (Tanaka, in press). This is thought to reflect a shift in entry level due to our expertise with faces, and it is also observed in real-world experts (e.g., bird experts recognize a bird as a robin as fast as they recognize it as a bird) (Tanaka & Taylor, 1991) and in subjects trained to expertise with novel objects (Gauthier & Tarr, 1997). As a matter of fact, expertise effects can also be measured directly on the N170: This potential is larger for nonface objects of expertise such as birds and dogs in experts with these categories (Tanaka & Curran, 2001). Such expertise effects on the N170 also suggest that this component reflects a stage of individuation between exemplars rather than category detection because it is in individuation that these experts seem particularly skilled.

The fMRI and ERP evidence suggests that the FIE is observed in the FFA as well as on the N170 component because these are markers of a processing stage at which objects are individuated. Any account of the origins of the FIE (apart from an innate explanation, for which evidence is lacking) is likely to include an analysis of these relational and/or holistic processes that are acquired selectively for upright faces through our experience with them in this orientation. The kind of expertise with objects that also leads to a behavioral and neural inversion effect is one where observers acquire exquisite skills in discriminating visually similar objects of a category (Diamond & Carey, 1986; Gauthier et al., 1999; Gauthier & Tarr, 1997, in press; Rossion et al., in press; Tanaka & Curran, 2001). Therefore, although expertise may also influence processing at the basic level (e.g., Purcell & Stewart, 1988), subordinate-level recognition appears more central to the inversion effect.

CONCLUSIONS

The dramatic decrease of performance for face inversion as compared to object inversion observed more than 30 years ago (Yin, 1969) continues to be an interesting and stimulating topic in cognitive neuroscience. Regarding the FIE, behavioral, fMRI, and neurophysiological data are highly consistent with each other. Our review of the literature on the inversion effect led us to conclude that this effect (a) has a perceptual basis, (b) is caused to a large extent by the disruption of the expert use of local relational information between parts of an object when processing inverted faces, and (c) occurs at a stage where faces are individuated (likely simultaneously with their categorization at the entry level).

We suggest that expertise is a suitable framework for understanding the manner in which the brain processes upright and inverted faces. A full account, however, must specify the relationship of expertise effects to those that occur in development. Autism may be an interesting model in this respect, as adult individuals with autism have been suggested to lack normal expertise with faces and indeed show little evidence of specialization for faces in the FFA (Schultz et al., 2000). This population also shows an abnormally small effect of inversion for faces (e.g., Hobson, Ouston, & Lee, 1988) and an absence of reduced gamma-band activity around 200 ms when faces are presented upside down (Grice et al., 2001). Recent results in adolescents who received limited visual input for as little as 2 months from birth due to cataracts that were later removed suggest that permanent deficits in the configural processing of upright faces can result from early deprivation (Le Grand, Mondloch, Maurer, & Brent, 2001). Although there is still much to learn about the development of face recognition, these kinds of results are consistent with experimental studies of expertise in adults in suggesting that the FIE and associated face-selective effects need to be studied within a dynamic framework.

NOTES

1. Most authors are careful to note that changing the shape of features may also modify their relative position to other parts. However, many studies successfully abolish inversion effects using faces that differ only in feature shape, color, or brightness (Freire, Lee, & Symons, 2000; Leder & Bruce, 1998; Searcy & Bartlett, 1996).

2. The effect correlated with fusiform face area activity was actually called "holistic-inclusive." As participants become experts with Greebles, they no longer can restrict a part judgment to half of a Greeble image (Is the bottom of these two Greebles the same?): Part judgments seem to obligatorily include all parts present in the image. Thus, when the part to be ignored is inconsistent with the judgment, experts show more interference than novices. This consistency effect is

not properly speaking "configural" because it was independent of whether the two parts were in the original or a new configuration. It may reflect a different facet of expert processing than the relational effects described by Leder and Bruce (1998).

3. These analyses were performed independently on the positive and negative voxels, comparing their density in a region of interest (ROI) to the mean density in all ROIs. It is thus possible to find within the same ROI a significant preference for upright and for inverted stimuli, as long as those are expressed in different voxels.

4. Gauthier, Anderson, Skudlarski, and Gore (2000) found that bird and car experts also engaged a bilateral area in the parahippocampal gyrus for their category of expertise relative to the other category. This was not observed with experts for novel objects (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999) and could result from the associated semantic knowledge in real-world experts.

5. A magnetoencephalography study reported a slight but significant delay with face inversion already at the level of the preceding P1 (Linkenkaer-Hansen et al., 1998). It is thus possible that such effects occur earlier as they are usually measured at the N170 peak latency, but most probably originate before 170 ms, in between the P1 (around 100 ms) and the N170.

6. Note that some event-related potential studies reported effects of face repetition much earlier than 100 ms (e.g., Braeutigam, Bailey, & Swithenby, 2001; Seeck et al., 1997), but they are likely to be related to the mere repetition of the same complex images and thus of low-level visual properties, rather than of the same facial identities. When different images of the same facial identities are repeated, earlier effects of repetitions are found peaking at around 150 ms following stimulus onset (Campanella et al., 2000; Munte et al., 1998).

REFERENCES

Aguirre, G. K., Singh, R., & D'Esposito, M. (1999). Stimulus inversion and the responses of face and object-sensitive cortical areas. *Neuroreport*, *10*, 189-194.

Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: Evidence and implications. *Neuron*, *21*, 373-383.

Allison, T., McCarthy, G., Nobre, A., Puce, A., & Belger, A. (1994). Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. *Cerebral Cortex*, *5*, 544-554.

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception: Potentials generated in occipitotemporal cortex by face and nonface stimuli. *Cerebral Cortex*, *9*, 415-430.

Bartlett, J. C., & Searcy, J. (1993). Inversion and configuration of faces. *Cognitive Psychology*, *25*, 281-316.

Bentin, S., Allison, T., Puce, A., Perez, A., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*, 551-565.

Bentin, S., & Deouell, L. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology*, *17*, 35-54.

Bentin, S., Deouell, L. Y., & Soroker, N. (1999). Selective visual streaming in face recognition: Evidence from developmental prosopagnosia. *Neuroreport*, *10*, 823-827.

Bodamer, J. (1947). Die-Prosop-agnosie. *Archives of Psychiatry Nervenkrankh*, *179*, 6-54. English translation by par Ellis, H. D., & Florence, M. (1990). *Cognitive Neuropsychology*, *7*, 81-105.

Bötzel, K., Schulze, S., & Stodieck, R. G. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research*, *104*, 135-143.

Braeutigam, S., Bailey, A. J., & Swithenby, S. J. (2001). Task-dependent early latency (30-60 ms) visual processing of human faces and other objects. *Neuroreport*, *12*(7), 1531-1536.

Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology*, *77*, 305-327.

Bruyer, R., Galvez, C., & Prairial, C. (1993). Effect of disorientation on visual analysis, familiarity decision and semantic decision on faces. *British Journal of Psychology*, *84*, 433-441.

Bruyer, R., Laterre, C., Seron, X., Feyereisen, P., Stryptien, E., Pierrard, E., & Rectem, D. (1983). A case of prosopagnosia with some preserved covert remembrance of familiar faces. *Brain and Cognition*, *2*, 257-284.

Campanella, S., Hanoteau, C., Depy, D., Rossion, B., Bruyer, R., Crommelinck, M., & Guerit, J. M. (2000). Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology*, *37*, 796-806.

Carey, S., & Diamond, R. (1977). From piecemeal to configurational representation of faces. *Science*, *195*, 312-314.

Carey, S., Diamond, R., & Woods, B. (1980). The development of race recognition: A maturational component. *Developmental Psychology*, *16*, 257-269.

Cauquil, A. S., Edmonds, G. E., & Taylor, M. J. (2000). Is the face-sensitive N170 the only ERP not affected by selective attention? *Neuroreport*, *11*(10), 2167-2171.

Collishaw, S. M., & Hole, J. C. (2000). Featural and configurational processes in the recognition of faces of different familiarity. *Perception*, *29*(8), 893-909.

Curran, T., Tanaka, J. W., & Weiskopf, D. M. (2001, June). *Differentiating object categorization and recognition processes: A high density ERP study.* Poster session presented at the 7th Human Brain Mapping Conference, Brighton, UK.

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, *115*, 107-117.

Edelman, S. (1995). Representation, similarity, and the chorus of prototypes. *Minds and Machines*, *5*, 45-68.

Eimer, M. (1998). Does the face-specific N170 component reflect the activity of a specialized eye processor? *Neuroreport*, *9*, 2945-2948.

Eimer, M. (2000a). Effects of face inversion on the structural encoding and recognition of faces—Evidence from event-related brain potentials. *Cognitive Brain Research*, *10*, 145-158.

Eimer, M. (2000b). Event-related brain potentials distinguish processing stages involved in face perception and face recognition. *Clinical Neurophysiology*, *111*, 694-705.

Eimer, M. (2000c). The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*, *11*(10), 2319-2324.

Eimer, M., & McCarthy, R. A. (1999). Prosopagnosia and structural encoding of faces: Evidence from event-related potentials. *Neuroreport*, *10*(2), 255-259.

Ellis, H. D. (1975). Recognizing faces. *British Journal of Psychology*, *66*, 409-426.

Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: Recognition, navigation or encoding? *Neuron*, *23*, 115-125.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*, 598-601.

Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 628-634.

Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is "special" about face perception? *Psychological Review*, *105*, 482-498.

Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception*, *29*, 159-170.

Gauthier, I. (1998). *Dissecting face recognition: The role of categorization level and expertise in visual object recognition.* Unpublished doctoral dissertation, Yale University, New Haven, CT.

Gauthier, I., Anderson, A., Skudlarski, P., & Gore, J. C. (2000). Expertise for cars and birds recruits middle fusiform face-selective areas. *Nature Neuroscience*, *3*, 191-197.

Gauthier, I., Anderson, A. W., Tarr, M. J., Skudlarski, P., & Gore, J. C. (1997). Levels of categorization in visual recognition studied with functional MRI. *Current Biology*, *7*(9), 645-651.

Gauthier, I., & Epstein, R. (2001, June). *The role of spatial frequencies in face-selective areas: Task-dependent effects.* Paper presented at Human Brain Mapping, Brighton, UK.

Gauthier, I., & Tarr, M. J. (1997). Becoming a "Greeble" expert: Exploring the face recognition mechanism. *Vision Research*, *37*, 1673-1682.

Gauthier, I., & Tarr, M. J. (in press). Unraveling mechanisms for expert object recognition: Bridging brain activity and behavior.

Journal of Experimental Psychology: Human Perception and Performance.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform area increases with expertise in recognizing novel objects. *Nature Neuroscience*, *6*, 568-573.

Gauthier, I., Tarr, M. J., Moylan, J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (2000). Does visual subordinate-level categorization engage the functionally-defined fusiform face area? *Cognitive Neuropsychology*, *17*, 143-163.

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, *12*(3), 495-504.

Gauthier, I., Williams, P., Tarr, M. J., & Tanaka, J. (1998). Training "Greeble" experts: A framework for studying expert object recognition processes. *Vision Research*, *38*, 2401-2428.

George, N., Evans, J., Fiori, N., Davidoff, J., & Renault, B. (1996). Brain events related to normal and moderately scrambled faces. *Cognitive Brain Research*, *4*(2), 65-76.

Grice, S. J., Spratling, M. W., Karmilnoff-Smith, A., Halit, H., Csibra, G., deHaan, M., & Johnson, M. H. (2001). Disordered visual processing and oscillatory brain activity in autism and Williams Syndrome. *Neuroreport*, *12*, 2697-2700.

Guillaume, F., & Tiberghien, G. (2001). An event-related potential study of contextual modifications in a face recognition task. *Neuroreport*, *12*, 1209-1216.

Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R.B.H., Marinkovic, K., & Rosen, B. (1998). Location of human face-selective cortex with respect to retinotopic areas. *Human Brain Mapping*, *7*, 29-37.

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, *293*(5539), 2425-2430.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223-233.

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*, 189-199.

Hillger, L. A., & Koenig, O. (1991). Separable mechanisms in face processing: Evidence from hemispheric specialization. *Journal of Cognitive Neuroscience*, *3*, 42-58.

Hobson, R. P., Ouston, J., & Lee, A. (1988). What's in a face? The case of autism. *British Journal of Psychology*, *79*, 441-453.

Hochberg, J., & Galper, R. R. (1967). Recognition of faces: An explanatory study. *Psychological Science*, *9*, 619-620.

Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, *3*, 80-84.

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 9379-9384.

Jeffreys, D. A. (1989). A face-responsive potential recorded from the human scalp. *Experimental Brain Research*, *78*, 193-202.

Jeffreys, D. A. (1993). The influence of stimulus orientation on the vertex positive scalp potential evoked by faces. *Experimental Brain Research*, *96*, 163-172.

Jemel, B., George, N., Chaby, L., Fiori, N., & Renault, B. (1999). Differential processing of part-to-whole and part-to-part face priming: An ERP study. *Neuroreport*, *10*, 1069-1075.

Jolicoeur, P., Gluck, M. A., & Kosslyn, S. M. (1984). Pictures and names: Making the connection. *Cognitive Psychology*, *16*, 243-275.

Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, *3*, 759-763.

Kanwisher, N., Downing, P., Epstein, R., & Kourtzi, Z. (2001). Functional neuroimaging of human visual recognition. In R. Cabeza & A. Kingstone (Eds.), *The handbook on functional neuroimaging* (pp. 109-152). Cambridge, MA: MIT Press.

Kanwisher, N., McDermott, J., & Chun, M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *1711*, 4302-4311.

Kanwisher, N., Tong, F., & Nakayama, K. (1998). The effect of face inversion on the human fusiform face area. *Cognition*, *68*, B1-B11.

Kemp, R., McManus, C., & Pigott, T. (1990). Sensitivity to the displacement of facial features in negative and inverted images. *Perception*, *19*, 531-543.

Leder, H., & Bruce, V. (1998). Local and relational aspects of face distinctiveness. *Quarterly Journal of Experimental Psychology A*, *51*, 449-473.

Leder, H., & Bruce, V. (2000). When inverted faces are recognized: The role of configural information in face recognition. *Quarterly Journal of Experimental Psychology A*, *53*, 513-536.

Leder, H., Candrian, G., Huber, O., & Bruce, V. (2001). Configural features in the context of upright and inverted faces. *Perception*, *30*, 73-83.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Neuroperception—Early visual experience and face processing. *Nature*, *410*(6831), 890-890.

Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience*, *4*, 533-539.

Linkenkaer-Hansen, K., Palva, J. M., Sams, M., Hietanen, J. K., Aronen, H. J., & Ilmoniemi, R. J. (1998). Face-selective processing in human extrastriate cortex around 120 ms after stimulus onset revealed by magneto- and electroencephalography. *Neuroscience Letters*, *253*, 147-150.

Liu, J., Higuchi, M., Marantz, A., & Kanwisher, N. (2000). The selectivity of the occipitotemporal M170 for faces. *Neuroreport*, *11*, 337-341.

Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, *412*, 150-157.

McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception: Response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex*, *9*, 431-444.

McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *9*, 605-610.

Moscovitch, M., Behrmann, M., & Winocur, G. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, *9*, 555-604.

Munte, T. F., Brack, M., Grootheer, O., Wieringa, B. M., Matzke, M., & Johannes, S. (1998). Brain potentials reveal the timing of face identity and expression judgments. *Neuroscience Research*, *30*, 25-34.

Murray, J. E., Yong, E., & Rhodes, G. (2000). Revisiting the perception of upside-down faces. *Psychological Science*, *11*, 492-496.

Nachson, I. (1995). On the modularity of face recognition: The riddle of domain specificity. *Journal of Clinical and Experimental Neuropsychology*, *17*, 256-275.

Parr, L. A., Dove, T., & Hopkins, W. D. (1998). Why faces may be special: Evidence of the inversion effect in chimpanzees. *Journal of Cognitive Neuroscience*, *10*, 615-622.

Perrett, D. I., Mistlin, A. J., Chitty, A. J., Smith, P.A.J., Potter, D. D., Broennimann, R., & Harries, M. (1988). Specialized face processing and hemispheric asymmetry in man and monkey: Evidence from single unit and reaction times studies. *Behavioral Brain Research*, *29*, 245-258.

Perrett, D. I., & Oram, M. (1993). Neurophysiology of shape processing. *Image and Vision Computing*, *11*, 317-333.

Perrett, D. I., Oram, M. W., & Ashbridge, E. (1998). Evidence accumulation in cell populations responsive to faces: An account of generalisation of recognition without mental transformations. *Cognition*, *67*, 111-145.

Phelps, M. T., & Roberts, W. A. (1994). Memory for pictures of upright and inverted primate faces in humans, squirrel-monkeys, and pigeons. *Journal of Comparative Psychology*, *108*, 114-125.

Philips, R. J., & Rawles, R. E. (1979). Recognition of upright and inverted faces: A correlational study. *Perception*, *43*, 39-56.

Purcell, D. G., & Stewart, A. L. (1988). The face-detection effect: Configuration enhances detection. *Perception & Psychophysics*, *43*, 355-366.

Rakover, S. S., & Teucher, B. (1997). Facial inversion effects: Parts and whole relationship. *Perception and Psychophysics*, *59*, 752-761.

Rebai, M., Poiroux, S., Bernard, C., & Lalonde, R. (2001). Event-related potentials for category-specific information during passive viewing of faces and objects. *International Journal of Neuroscience*, *106*, 209-226.

Rhodes, G., Brake, S., & Atkinson, A. P. (1993). What's lost in inverted faces? *Cognition*, *47*(1), 25-57.

Rhodes, G., Brennan, S., & Carey, S. (1987). Identification and ratings of caricatures: Implications for mental representations of faces. *Cognitive Psychology*, *19*, 473-497.

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, *2*, 1019-1025.

Rock, I. (1974). The perception of disoriented figures. *Scientific American*, *230*, 78-85.

Rolls, E. T. (1992). Neurophysiological mechanisms underlying face processing within and beyond the temporal cortical visual areas. *Philosophical Transcripts of the Royal Society of London. Series B: Biological Sciences*, *335*, 11-21.

Rossion, B., Campanella, S., Gomez, C., Delinte, A., Debatisse, D., Liard, L., Dubois, S., Bruyer, R., Crommelinck, M., & Guérit, J.-M. (1999). Task modulation of brain activity related to familiar and unfamiliar face processing: An ERP study. *Clinical Neurophysiology*, *110*, 449-462.

Rossion, B., Delvenne, J. F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., & Guérit, J.-M. (1999). Spatio-temporal localization of the face inversion effect: An event-related potentials study. *Biological Psychology*, *50*, 173-189.

Rossion, B., Dricot, L., De Volder, A., Bodart, J.-M., Crommelinck, M., de Gelder, B., & Zoontjes, R. (2000). Hemispheric asymmetries for whole-based and parts-based face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *12*, 793-802.

Rossion, B., Gauthier, I., Goffaux, V., Tarr, M. J., & Crommelinck, M. (in press). Expertise training with novel objects leads to left lateralized face-like electrophysiological responses. *Psychological Science*.

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P. A., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is enhanced and delayed to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *Neuroreport*, *11*, 69-74.

Sagiv, N., & Bentin, S. (2001). Structural encoding of human and schematic faces: Holistic and part-based processes. *Journal of Cognitive Neuroscience*, *13*(7), 937-951.

Scapinello, K. F., & Yarmey, A. D. (1970). The role of familiarity and orientation in immediate and delayed recognition of pictorial stimuli. *Psychonomic Science*, *21*, 329-331.

Schultz, R. T., Gauthier, I., Klin, A., Fulbright, R. K., Anderson, A. W., Volkmar, F., Skudlarski, P., Lacadie, C., Cohen, D. J., & Gore, J. C. (2000). Abnormal ventral temporal cortical activity during face discrimination among individuals with autism and Asperger syndrome. *Archives of General Psychiatry*, *57*, 331-340.

Schyns, P. G., & Murphy, G. L. (1994). The ontogeny of part representation in object concepts. In D. Medin (Ed.), *The psychology of learning and motivation* (Vol. 331, pp. 305-354). San Diego, CA: Academic Press.

Schyns, P. G., & Rodet, L. (1997). Categorization creates functional features. *Journal of Experimental Psychology: Learning and Memory*, *23*, 681-696.

Searcy, J. H., & Bartlett, J. C. (1996). Inversion and processing of component and spatial-relational information in faces. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 904-915.

Seeck, M., Michel, C. M., Mainwaring, N., Cosgrove, R., Blume, H., Ives, J., Landis, T., & Schomer, D. L. (1997). Evidence for rapid face recognition from human scalp and intracranial electrodes. *Neuroreport*, *8*, 2749-2754.

Sergent, J. (1984). An investigation into component and configural processes underlying face perception. *British Journal of Psychology*, *75*, 221-242.

Sergent, J., Otha, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain*, *115*, 15-36.

Simion, F., Macchi Cassia, V., Turati, C., & Valenza, E. (2001, April). *The origins of face perception: Specific vs. non-specific mechanisms.* Paper presented at the Society for Research in Child Development, Minneapolis, MN.

Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience*, *18*, 555-586.

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences*, *3*, 151-162.

Tanaka, J. W. (in press). The entry point of face recognition: Evidence for face expertise. *Journal of Experimental Psychology: General*.

Tanaka, J. W., & Curran, T. (2001). A neural basis for expert object recognition. *Psychological Science*, *12*, 43-47.

Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology*, *46A*, 225-245.

Tanaka, J. W., & Gauthier, I. (1997). Expertise in object and face recognition. In R. L. Goldstone, P. G. Schyns, & D. L. Medin (Eds.), *The psychology of learning and motivation* (Vol. 36, pp. 83-125). San Diego, CA: Academic Press.

Tanaka, J. W., Luu, P., Weisbrod, M., & Kiefer, M. (1999). Tracking the time course of object categorization using event-related potentials. *Neuroreport*, *10*, 829-835.

Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory and Cognition*, *25*, 583-592.

Tanaka, J. W., & Taylor, M. (1991). Object categories and expertise: Is the basic level in the eye of the beholder? *Cognitive Psychology*, *23*, 457-482.

Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience*, *3*, 764-769.

Taylor, M. J., Itier, R. J., Allison, T., & Edmonds, G. (2001). Direction of gaze effects on early face processing: Eyes-only versus full faces. *Cognitive Brain Research*, *10*, 333-340.

Taylor, M. J., McCarthy, G., Saliba, E., & Degiovanni, E. (1999). ERP evidence of developmental changes in processing of faces. *Clinical Neurophysiology*, *110*, 910-915.

Tovée, M. J. (1998). Face processing: Getting by with a little help from its friends. *Current Biology*, *8*, R17-R320.

Toyama, J. S. (1975). *The effect of orientation on the recognition of faces: A reply to Yin.* Unpublished doctoral thesis, University of Waterloo, Canada.

Valentine, T. (1988). Upside-down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology*, *79*, 471-491.

Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. *Quarterly Journal of Experimental Psychology*, *43A*(2), 161-204.

Valentine, T., & Bruce, V. (1986). Recognizing familiar faces: The role of distinctiveness and familiarity. *Canadian Journal of Psychology*, *40*, 300-305.

Valentine, T., & Bruce, V. (1988). Mental rotation of faces. *Memory and Cognition*, *16*, 556-566.

Valenza, E., Simion, F., Mucchi Cassia, V., & Umilta, C. (1996). Face preference at birth. *Journal of Experimental Psychology; Human Perception and Performance*, *22*, 892-903.

Yarmey, A. D. (1971). Recognition memory for familiar "public" faces: Effects of orientation and delay. *Psychonomic Science*, *24*(6), 286-288.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*, 41-145.

Young, A. W., Hellawell, D., & Hay, D. (1987). Configural information in face processing. *Perception*, *10*, 747-759.