Beyond localisation

de Gelder, B.; Rouw, R.

Published in:
Acta Psychologica

DOI:
10.1016/S0001-6918(01)00024-5

Publication date:
2001

Citation for published version (APA):
de Gelder, B., & Rouw, R. (2001). Beyond localisation: a dynamic dual route account of face recognition. *Acta Psychologica*, *107*, 183-207. https://doi.org/10.1016/S0001-6918(01)00024-5

ELSEVIER

Acta Psychologica 107 (2001) 183–207

acta psychologica

www.elsevier.com/locate/actpsy

Beyond localisation: a dynamical dual route account of face recognition

Beatrice de Gelder [a,b,c,*], Romke Rouw [a]

[a] *Cognitive Neuroscience Laboratory, Tilburg University, P.O. Box 90153, 5000 LE Tilburg, The Netherlands*

[b] *Helmholtz Institute, Utrecht University, Utrecht, The Netherlands*

[c] *Laboratory of Neurophysiology, Université de Louvain-la-Neuve, Brussels, Belgium*

Received 25 July 2000; received in revised form 18 December 2000; accepted 20 December 2000

Abstract

After decades of research the notion that faces are special is still at the heart of heated debates. New techniques like brain imaging have advanced some of the arguments but empirical data from brain-damaged patients like paradoxical recognition effects have required more complex explanations aside from localisation of the face area in normal adults. In this paper we focus on configural face processes and discuss configural processes in prosopagnosics in the light of findings obtained in brain-imaging studies. In order to account for data like paradoxical face recognition effects we propose a dual route model of face recognition. The model is based on the distinction between two separate aspects of face recognition, detection and identification, considered as dynamical and interrelated. In this perspective the face detection system appears as the stronger candidate for face-specific processes. The face identification system on the other hand is part of the object recognition system but derives its specificity in part from interaction with the face-specific detection system. The fact that face detection appears intact in some patients provides us with a possible explanation for the interference of configural processes on feature-based identification. © 2001 Elsevier Science B.V. All rights reserved.

PsycINFO classification: 2300; 2323; 2520; 2800

---

[*] Corresponding author. Tel.: +31-13-466-2167; fax: +31-13-466-2370.
E-mail address: b.degelder@kub.nl (B. de Gelder).

PII: S0001-6918(01)00024-5

Keywords: Prosopagnosia; Face recognition; Object recognition; Face detection; Inversion effect; Paradoxical effects; Development

1. Introduction

In the debate about categorical specialisation of the visual cortex, faces occupy a prominent place. It is therefore not surprising that in recent studies using methods of brain imaging like PET of fMRI this question has attracted considerable attention. It is undoubtedly too early to ask what these new methods have contributed to a longstanding debate. Evidence in support of face specificity has traditionally come from a number of different sources like single-cell recordings and lesion studies. One of the oldest sources of evidence is prosopagnosia, the observation that focal brain damage can give rise to a disorder of visual recognition that appears to be specific for faces (Bodamer, 1947). The notion of the face specificity of prosopagnosia has repeatedly been challenged and the debate is reactivated with each new theory of object recognition and with every new research technique. Prosopagnosia is accompanied by normal vision and intact visual knowledge which excludes an explanation in terms of low-level visual problems (apperceptive agnosia, as defined by Lissauer, 1890). Besides prosopagnosia following brain damage in adulthood, other face recognition impairments have also been documented. Anomalous face recognition is found, for example, in developmental disorders like autism or Williams syndrome. These two disorders have a genetic aetiology and the face deficits accompanying them are part of more general visual and cognitive problems. Yet there also exists a specific face recognition disability with a developmental origin that is more comparable to acquired prosopagnosia, namely developmental prosopagnosia. It concerns face recognition problems that have their origin in anomalous perinatal development causing visual recognition problems exclusively in the domain of face recognition.

Over the last three years we have extensively studied prosopagnosic patients, acquired as well as developmental cases. Our goal was not to provide direct support for or against views on category specificity, but to map in greater detail visual processes involved in face recognition and to understand the interplay between the damaged and the spared components of visual cognition in prosopagnosia. In this paper we bring together recent behavioural findings obtained with prosopagnosic patients and results from neuroimaging studies of face and object recognition in normal viewers. The scope is limited to a central issue in these debates namely the role of configural (or whole-based) vs. part- or feature-based processes in *face recognition*. We will use the latter term to refer to the general ability to process faces while the notion of *face identification* will be reserved for the specific skill of recognising an individual face and that of *face detection* for the ability to detect the presence of a face-like pattern independently of identification. Face detection is thus not used here as a synonym for face categorisation.

We first summarise some recent brain-imaging studies that are relevant for the issue of configural processing. Next, we present a brief overview of some new data from neuropsychological studies. Finally, we return to the relationship between neuropsychology and brain imaging and propose different explanations for the neuropsychological findings.

2. The neuroanatomy of face perception: recent evidence from brain-imaging research

Progress in neuroanatomical localisation of cognitive functions like face recognition raises hope for a better understanding of the rather mixed pattern of lesions and behavioural deficits associated with prosopagnosia (Damasio, Damasio, & Van Hoesen, 1982; Farah, 1990; Spreeuwenberg & de Gelder, submitted). Following the initial findings of neuroanatomical face specificity obtained with PET (Sergent, Ohta, & Mc Donald, 1992) more recent fMRI studies have provided converging evidence for a dedicated face area in the fusiform gyrus, the so-called fusiform face area or FFA (e.g., Kanwisher, McDermott, & Chun, 1997). But it is fair to say that these new results have not inspired unanimity among the participants in the face specificity debate. On the one hand, the actual function of this face area for the ensemble of face recognition ability is currently rather unclear (Tovée, 1998). On the other hand, there is considerable disagreement as to what extent the observed neuroanatomical localisation indicates unambiguously that there is category specificity.

Let us first consider the issue about domain specificity. We will not review this debate fully here and limit ourselves to indicating some general orientations (for recent overviews, see the papers in Kanwisher & Moscovitch, 2000). Some authors believe that object representations in the temporal cortex cluster by semantic categories (e.g., fruits, musical instruments), whereas others believe that objects are clustered according to their visual properties. Some believe that all objects are dealt with in the same way, with the exception of a few privileged categories (e.g., faces) that are processed by specialised modules, whereas others believe that there are no exceptions to the existence of a generic mechanism of object recognition.

It seems fair to say that claims about face specificity represent a continuum. Faces are entirely or absolutely specific in case there exists a special purpose processor or module as has been argued in the behavioural and neuropsychological domain by Farah, Wilson, Drain, and Tanaka (1995). In the neuroanatomical domain Kanwisher and collaborators made a similar claim about face modularity based on brain-imaging studies indicating that the FFA is involved in face but not in object recognition (Kanwisher et al., 1997; see also Haxby et al., 1994; Puce, Allison, Gore, & McCarthy, 1995; Sergent et al., 1992).

Alternatively, it has been argued that neuroanatomical face specificity is only relative because there is evidence for a continuum between face and object recognition since recognition could be based on the perception of a topological maps or geometrically defined feature maps (Chao, Haxby, & Martin, 1999; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). A third alternative boils down to the notion that specificity is in the eye of the beholder. In other words, specificity is not based on stimulus characteristics but is a matter of the cognitive state of the viewer like his subjective experience with the stimulus domain and of task variables such that when these are equated, faces are no longer special (Gauthier et al., 2000).

The second major issue is that of the specific function implemented in the face area or of the functional significance of that area. The first brain-imaging studies assumed more or less implicitly that the area that appeared to activate to faces was ipso facto involved in face recognition in the sense of identification of an individual face. One should note though that subjects in brain-imaging experiments were not presented with tasks specifically suited to probe identity-based matching as is common in behavioural studies of face recognition. At this stage one might argue that the modular view presents the advantage of a direct connection with the neuropsychological phenomenon of prosopagnosia. The notion that there exists an area specifically tuned to faces suggests a way of combining neuropsychological observations and brain-imaging data. This leads to a straightforward prediction that in prosopagnosic patients the face area should not activate when a patient with profound face recognition impairments is presented with face stimuli. This was indeed found for patients RP (de Gelder & Kanwisher, 1999) and AV (de Gelder, Rossion, de Volder, Bodart, & Crommelinck, 1999) which did not show activation in the putative face area when passively viewing faces.

As the number of reports from brain imaging increases, one puzzling fact is that brain-imaging studies have not found a clear neural correlate of the inversion effect like for example a significant decrease of activation in the face area when inverted faces are presented. Or, more strongly and more in line with claims in the literature, a level of activation for the inverted faces that would be comparable to that found for objects. In fact, the FFA responds to both upright and inverted grey scale faces as well as to upright two-tone Mooney faces but not anymore if the stimulus is no longer recognised as a face (like in the case of an inverted Mooney face; Kanwisher, Tong, & Nakayama, 1998). Another result was that activation levels were quite similar whether the subject was shown a naturalistic human face, a schematic face or an animal face. To some authors the implication appeared to be that the face area is not responsible for face identification but only for what is then referred to as face detection (Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000). But other fMRI data clearly indicate that the face area is involved in face recognition of familiar faces (George et al., 1999). Note though that none of the available studies directly addressed the specific issue of detection vs. recognition by designing experiments in which early (detection) vs. late (identification) face processes could be separated.

As we shall argue below, the distinction between detection and identification may be more critical than previously envisaged. Present evidence does not plead unambiguously in favour of limiting the role of FFA to detection at the detriment of recognition or the other way round (Hoffman & Haxby, 2000). Differences in stimuli and in task used complicate comparisons of results across different studies. More importantly, a limitation of current fMRI methods concerns the lower limits on temporal resolution (see Savoy, 2001, for more information). Because of that, the present brain-imaging techniques are probably unable to settle this debate as it is not possible to pull apart the two processes by providing detailed information about their separate time course.

Limitations on interpretations of present fMRI data also come from another area which has provided evidence for face sensitivity in the past, namely that of single-cell studies in animals. Ultimately, findings from brain-imaging studies must connect with research measuring single-cell activity. Single-cell recordings have provided clear evidence that face-sensitive cells are not restricted to the face area identified in brain-imaging studies alone. Besides face cells in the FFA (Puce, Allison, & McCarthy, 1999) there are face-sensitive cells all over the fusiform gyrus (Rolls, 1992; Tanaka, 1993) as well as in pre-frontal cortex (Marinkovic, Trebon, Chauvel, & Halgren, 2000; O'Scalaide, Wilson, & Goldman-Rakic, 1997), in inferior occipital gyrus (Hoffman & Haxby, 2000) and in the amygdala (Leonard, Rolls, Wilson, & Baylis, 1985). This distribution is consistent with the earlier finding that after selective ablation of STS, monkeys were still able to recognise faces (Heywood & Cowey, 1992). The notion that face cells are distributed is important for functional separation of face detection and identification.

The relation between single-cell studies and techniques providing indirect measures of global neuronal activity like PET and fMRI is an intricate one that is not well understood at present (see also Grill-Spector & Malach, 2001; Op de Beeck, Wagemans, & Vogels, 2001). To put it bluntly, it would be too simplistic to assume that the category specificity of a cortical area shown by PET or fMRI is directly and exclusively related to the presence of a high density of face-sensitive cells in just that area. Stimulus presentation and task manipulation can have very different and separable effects on the activity of a population of cells as opposed to each cell taken individually. This duality adds to the fact that specialisation in visual cortex is relative rather than absolute since a cell will fire to a number of different stimuli (e.g., Desimone & Duncan, 1995). In line with this, studies of the neuronal substrates of cognitive functions in the visual cortex have reported considerable overlap among stimulus categories. On the other hand, attention raises the level of activation in the face area (Wojciulik, Kanwisher, & Driver, 1998). This raises the question of the role of attention in generating the clear-cut category specificity reported in some studies. Further research will need to clarify to what extent the positive effects obtained in studies manipulating attention are actually co-extensive with the deployment of attention and associated visual awareness.

Because of these limitations of method and of interpretation, it seems at present at least unlikely that we will any time soon be able to map neuropsychological data seamlessly onto results obtained in brain imaging studies and vice versa. Face recognition is functionally complex and likely to consist of a network of neuroanatomically and functionally autonomous sub-parts. Only a small part of the issues is currently addressed in studies using brain-imaging techniques. To advance further the dialogue between neuropsychology and findings from brain imaging we need a detailed understanding of the pattern of spared and damaged components of prosopagnosic face perception as well as more functionally oriented and more analytical brain-imaging studies that go beyond localisation. We would like to point out that unlike other processes where highly developed models exist (e.g., reading), there is at present no theoretical framework to guide researchers along this path. This is not because the complexity of the face-processing system has not previously been noted.

But the kind of complexity represented in the well-known models of Sergent et al. (1992) or Bruce and Young (1986) concerns predominantly the later stages of face recognition involved in person identification. In our own research we have focussed on the stages that precede the division into semantically segregated processing streams (expression, identity, name, etc.). Unfortunately, it is these early stages of face processing that have not yet received much attention from neuropsychologists.

3. Paradoxical performance after brain damage: recent neuropsychological findings

Many authors agree that understanding how the face configuration is processed is a crucial piece of the riddle of face specificity and the close link between face recognition and configural processing is a constant theme in face research. It is at the basis of the best known phenomenon in face research, the face inversion effect (Yin, 1969), traditionally defined as the fact that normal adults are better at matching upright than inverted faces (hereafter called the face *inversion inferiority* effect). The standard explanation of inversion inferiority is that identification relies on configural operations on canonically oriented faces and these operations become ineffective when faces are presented upside down. The inversion effect became *de facto* a diagnostic marker for intact face perception. Yin (1970) compared the performance of a group of patients with right hemisphere damage (who were not specifically prosopagnosic) with the performance of normal adults and found that the brain damaged group did not show an inversion effect and performed at the same level with upright and inverted faces. This confirmed the prediction popular at the time, that the right hemisphere is involved in processing the whole stimulus rather than attending to separate features (see Corballis, 1991, for a historical overview). In the late 1980s Levine and Calvanio (1989) proposed that prosopagnosia was due to a loss of a general ability for configural processes. They tested this idea on patient LH and found confirmation for their view because LH's performance on the kind of configuration tasks that they used was indeed rather poor. But a later study of the same patient provided evidence that LH's configural processing was normal (Etcoff, Freeman, & Cave, 1991). Unfortunately, neither the first nor the second study directly addressed the critical issue because neither study tested configural processes with face stimuli. Instead, only line drawings, abstract figures and Kanizsa-type visual illusions were used. But these only allow one to conclude that the patient does not suffer from general perceptual deficits like the ones that are characteristic for apperceptive and integrative agnosia (Riddoch & Humphreys, 1987) but say very little about intact configuration in face processing.

In older studies of prosopagnosic patients, information about face-processing disability is often limited to results of tests of familiar faces. Inferences about intact vs. damaged processes are typically based on comparisons between faces and other visual objects as illustrated by the typology of agnosic disorders defended in the early 1990s by Farah (1991). While cross-patient and cross-domain comparisons remain informative, it is also possible to investigate directly the critical requirements of face processing. Here we would like to draw attention to four major lines of evidence that have emerged in recent reports of prosopagnosic patients, which specifically focussed on the issue of configuration. One is that of a paradoxical pattern of inversion superiority and context superiority which has now been found for a small number of prosopagnosics. The second is that these paradoxical patterns are in some cases also observed in object matching tasks are to be matched. The third is that in cases where we found evidence of a paradoxical or abnormal processing of the face configuration we nevertheless found normal processing of the face configuration when the patients were presented with simple face detection tasks. Finally, for one patient (RP) showing paradoxical inversion effects, longer exposure duration actually decreased detection accuracy. We briefly review these findings and point out some implications for brain-imaging results.

3.1. Inversion superiority

A puzzling finding of the last decade is that more is at stake than that prosopagnosic patients are no longer able to process faces like normals do, which is presumably by configuration-based processes. Rather, difficulties with processing the face can manifest themselves behaviourally in quite different ways. In some cases the patients' performance no longer shows face selectivity. But in other, less frequent cases, the patient continues to process faces in a special way even if this is no longer an efficient one. This generates a surprising pattern of performance whereby the patient can match upside down faces much better than normal, upright ones. Such a pathological pattern has been referred to as 'an inverted inversion' effect (Farah et al., 1995) or a 'paradoxical inversion' effect (de Gelder et al., 1998; de Gelder & Rouw, 2000a,b,c; Rouw & de Gelder, in press). For the sake of clarity we refer to this paradoxical pattern as the *inversion superiority* effect and we contrast it with the normal pattern, which is that of inversion *inferiority*. A situation similar to that observed for patient LH (Farah et al., 1995) was found in a study of another patient (AD) (de Gelder et al., 1998). Like LH this patient presented clear positive symptoms of inversion superiority as she was near chance matching upright faces. The difference between poor performance with upright stimuli vs. good performance with their inverted counterparts was even stronger than originally reported by Farah and collaborators. But in our experiment face matching required recognition across a difference in viewpoint and therefore taxed more specifically face recognition.

To highlight this phenomenon we adopt a distinction between prosopagnosia accompanied by *negative* symptoms and its alternative, prosopagnosia accompanied by *positive* symptoms, a distinction that proved useful to discriminate between two types of schizophrenia. In schizophrenia, the notion of negative symptoms refers to the absence of the normal pattern of reactivity and a low degree of reactivity to emotional stimuli, a situation often characterised as affective flattening (see Frith, 1992, for further discussion). In contrast, the clinical condition can also manifest itself through the so-called positive symptoms like, for example, auditory hallucinations. One can make a similar distinction between prosopagnosic patients with negative and with positive symptoms. A patient with negative symptoms has simply lost face recognition and is no longer able to apply the appropriate perceptual processes to face stimuli and treats faces as any other kind of object. Inversion superiority is an example of positive symptoms because the patient persists in treating faces in a special way. Note that in clinical tests positive and negative patients show the same behavioural deficit of being unable to recognise faces. Many cases of prosopagnosia reported in the literature seem to fit a pattern of *negative* symptoms or complete loss of face recognition. This may be either because the deficit is indeed limited to negative symptoms or because the critical tests with inverted faces have not been performed, as is the case for older studies.

What is the contribution of learning and experience to configural processing? It has often been noted that faces are different from almost any other visual object category because humans are natural experts at telling faces apart. Arguments for the special status of faces and/or mechanisms involved in face perception are typically based on comparisons with other object categories, but such comparisons may be inherently flawed if faces are over-learned. A different kind of comparison, which does not suffer from that asymmetry, is that of patients with very different degrees of face experience.Therefore, as a means of better understanding the role of experience and learning we studied a case of acquired prosopagnosia (patient RP, similar to patients AD and LH) and a patient (AV) with a face deficit that had a purely developmental origin and never learned to recognise faces. AV did not show the paradoxical effect of inversion superiority (see Fig. 1). Nor did he perform like normal subjects because he showed little evidence of a face inversion inferiority effect. The contrast between these two patients certainly fits the notion that residual configuration in RP is related to experience with faces before his accident. By the same token the fact that a developmental patient (AV) is not sensitive to the canonical face orientation indicates that he does not process the face configuration.

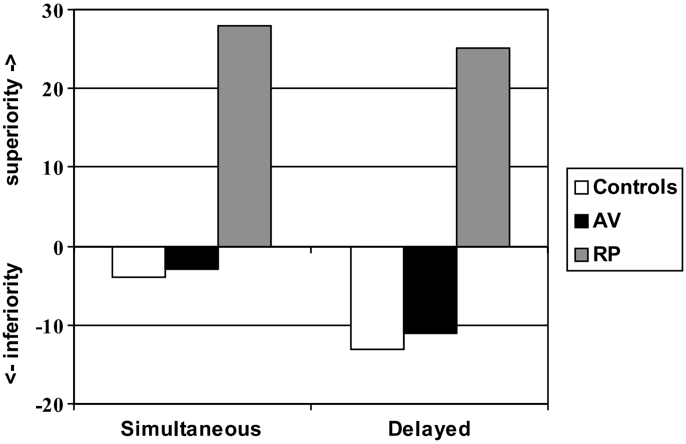

Fig. 1. Orientation effect (subtracting percentage correct upright presentation condition from percentage correct in inverted presentation condition) for matching whole faces in a two-alternative forced choice task in either simultaneous or delayed matching showing inversion superiority with RP and inversion inferiority for controls, but no effect for AV (adapted from de Gelder & Rouw, 2000c).

Note that we refer to experience (age-dependent) rather than expertise (processes bound to a particular stimulus class). To summarise so far, inversion superiority indicates that notwithstanding complete loss of face recognition, processing of the face configuration continues to drive face recognition. Telling from the excellent performance obtained in matching faces presented upside down, these patients can access feature-based processes when the stimuli are not in their canonical orientation.

In subsequent studies we collected direct evidence that patients with an inversion superiority effect cannot overcome configural processing and efficiently use feature strategies as long as the stimuli are normally oriented. A variant of the face context effect (Homa, Haver, & Schwartz, 1976; see also Suzuki & Cavanagh, 1995) was used for this purpose. The notion is that an isolated facial part can be matched more efficiently to the corresponding whole face presented upright than to an upside-down version or one with scrambled parts. LH was at chance when matching a face part previously shown in the context of normal face but his performance is good when the part was previously shown in an inverted or scrambled face context (de Gelder & Rouw, 2000a). This result indicates inhibition rather than facilitation of the face context on matching parts. A very similar pattern of a paradoxical inhibition from the face configuration was found for patient RP (de Gelder & Rouw, 2000c; Rouw & de Gelder, in press). This provided direct evidence that some patients cannot use feature strategies as long as the stimulus is a normal face. Such conclusion is consistent with the double dissociation between object and face recognition, which is illustrated very well by the case of patient CK. This patient suffered from loss of feature-based processes and corresponding loss of ability for object recognition with preserved face recognition (Moscovitch, Winocur, & Behrmann, 1997).

3.2. Paradoxical effects in object recognition

In the studies mentioned above we also used an object task in order to explore a possible contrast in the inversion effect for faces vs. objects and we designed it to be as similar as possible to the face recognition task. Subjects were given a two-alternative forced choice task and required to find the match between target and distractors across a difference in viewpoint. A surprising aspect of our results with patients AD, LH and RP was that they showed inversion superiority for objects also. This result indicates that configural processing is also important for object recognition and to that extent it challenges the accepted division often made in neuropsychology between object-specific feature-based recognition and face-specific whole-stimulus-based recognition. But inversion superiority for objects is consistent with studies showing that the overall stimulus configuration is not only important for faces but also for objects (Jolicoeur, 1985; Tarr & Pinker, 1989). In line with those studies, we found that under some testing conditions normal subjects show an inversion effect with objects (de Gelder & Rouw, 2000b).

At this stage one might argue that similarity between a disorder in face recognition and in object recognition is consistent with a variety of non-modular accounts of face recognition, an explanation defended convincingly in neuropsychology by Damasio and collaborators (Damasio et al., 1982) and supported by recent studies using brain imaging (see above). While we are not opposed to views that make face identification part of the object identification system we will argue below that this is in fact not the complete story.

3.3. Face detection and prosopagnosia

We mentioned already the uncertainty about the functional significance of the middle fusiform gyrus and the debate on whether this activation indicated face identification or simply detection of a face-like pattern. We refer to the process whereby the presence of a face is detected only schematically so that no recognition is initiated, as face detection (Purcell & Stewart, 1988a,b). In the discussion below the distinction between detection and categorisation will be sharpened further. An intriguing and so far unexplored question is whether developmental prosopagnosics with profound recognition deficits nevertheless automatically detect and code visual input as a face even when not processing the stimulus in ways required for identification. Moreover, the issue of preserved face detection is also relevant for acquired prosopagnosics showing residual configural processes. Indeed, an intriguing question is whether these patients would also be faster in a pure detection task not requiring face identification.

To avoid triggering identification we designed a task that only required face detection. Stimuli were presented either with speeded presentation (50 and 200 ms) followed by backward masking or under unlimited viewing. Interestingly, the acquired as well as the developmental prosopagnosic patient were very good at such a speeded detection. Patient RP who showed a strong preference for inverted faces in previous recognition tasks here displayed a normal pattern of fast detection of a normally oriented face. However, when the face stimulus was shown till a response was given performance was at chance. In contrast, a drop in performance as a function of longer exposure time was observed neither for normal subjects nor for our developmental patient AV. We conjecture that with long presentation times face identification abilities are activated and interfere with detection performance. This explains why the negative effect of long presentation on detection performance was only found with RP and not with AV. Thus, the two patients are similar in the detection task but show a different pattern of impairments in the recognition tasks.

To summarise, two main themes emerge from the data above. One is that face deficits can either consist in a straightforward loss of configural processing whereby faces are dealt with by the object route or can cause residual configural effects leading to paradoxical patterns and positive symptoms. The other theme is that severe impairment in face identification whether as a positive (as for example in RP) or as a negative symptom (as for example in AV) can go together with entirely normal performance on face detection. In order to better understand these data we propose a new framework of face recognition based on the notion that faces are processed along two separate routes, one dedicated to the detection of face-like patterns and the other to identification of individual faces (de Gelder & Rouw, 2000c). Here we expand this suggestion in the light of some recent brain-imaging results and ask whether this is a useful framework for explaining the neuropsychological patterns we observed.

4. The face configuration in single route hierarchical models

A common assumption present in otherwise very different theories of face recognition is that of hierarchical and sequential processes. The basic notion is that visual stimuli are processed in a feed-forward sweep from posterior to anterior areas (Lamme, 2001). Within this processing stream two separate stages are discerned and hierarchically ordered, going from the early general to the more specific, later stages of object and face recognition. Disagreements concern the later stages: Is the face system part of the object system, to be viewed as a specialisation within the object system or does it have a larger degree of autonomy? Since this issue is crucial for understanding the configuration deficits and the patients' residual processing resources we look at it in more detail.

4.1. The face configuration in hierarchical models of face modularity

Hierarchical models of face modularity are based on the notion that after some initial processing, a general categorisation mechanism assigns input to one or another object category like for example, faces, cars, birds or living vs. non-living entity. Once a face is correctly categorised by this generic mechanism, further processing takes place in a special-purpose recognition system. On this account face categorisation necessarily precedes face identification and the specialised face processor takes over only after the stimulus is correctly assigned to the face category (Farah et al., 1995; Rhodes, Brake, & Atkinson, 1993; Tanaka & Farah, 1993). From the perspective of a hierarchical model, the distinction between general object recognition processes vs. face-specific identification processes runs parallel to the distinction between feature- vs. configuration-based processes (Biederman & Kalocsai, 1997; Bruce & Humphreys, 1994; Sergent et al., 1992). Well-known face models like those of Sergent et al. (1992) or Bruce and Young (1986) refer to the first stage of face-specific processes as the stage of 'structural encoding'. Although structurally encoding stands for a representation already sufficiently elaborate to be used in a memory search for a matching representation.

Since cognitive models of face recognition have primarily been developed to understand face identification, comparatively little attention was paid to the earlier stages. In the eighties Carey as well as Rhodes and collaborators have articulated two different views on categorisation. Rhodes argued for the distinction between first-order features (parts) and second-order features (relation between parts, Rhodes, 1988). Presumably, initial stimulus categorisation consists of a process of checking the stimulus features and assigning a stimulus category on that basis. Configuration processing only enters with face-specific processing and identification. The second proposal is somewhat different as it contrasts first- and second-order relational information (Diamond & Carey, 1986). First-order relational information refers to the relation between the different parts of a stimulus. The notion of second-order relational information refers to distinctive variations of a shared configuration are meant which are important for individual face recognition. For the present discussion, the similarities between these two models are more important than the differences. For example, whether categorisation proceeds by a feature check or is also sensitive to the fact that the object parts appear in the canonical relation is at present a moot point as these processes are still ill understood. The important similarity between the two views is that categorisation itself is not considered to be part of a dedicated processor. In other words, if the overall stimulus configuration plays a role in categorisation (as assumed by Diamond and Carey), it does so no more or no less in case the stimulus is a house or a chair than when it is a face.

The important point to note is that in a two-stage perspective the ability to use the face configuration is strictly linked to face identification. As a consequence, in arguments about configural deficits in prosopagnosia only configuration in relation to individual recognition is discussed. It is worth reminding in this context that the original evidence for configuration effects like the inversion effect or the composite effect were obtained in experiments using familiar faces (Yin, 1969; Young, Hellawell, & Hay, 1986).

Can one find an explanation for paradoxical configuration effects within the framework of hierarchical face modularity? Our data seem to be incompatible with two main assumptions of this type of model. First, contrary to what is assumed by the hierarchical model, we have seen that patients cannot fall back on the strategies that are characteristic of the general, pre-categorical stages of visual object processing. Secondly, the observation that there is a continued impact of the configural face operations challenges the tight link between face recognition and configural operations characteristic of the second stage of the sequential model.

Let us envisage a more conservative proposal. One might argue that focal brain damage is the equivalent of adding visual noise to the internal representations of the face recognition system. However, this suggestion leaves unexplained the critical finding that some prosopagnosic patients like LH and RP are unable to use alternative feature processes in order to achieve some reasonable level of performance. On a non-modular view of face recognition it is even harder to understand that faces cannot be matched on a feature-processing basis.

4.2. Configural face recognition in non-modular perspective

The difficulty of pinning down the perceptual impairments of prosopagnosics (Bruce & Humphreys, 1994) encourages alternative, non-modular explanations of face recognition which neither assume a preliminary category decision nor a separate face mechanism. Instead, all visual stimuli are presumably processed by a single recognition system and any differentiation into stimulus categories follows from differences in typical cognitive factors, task variables or perceiver-related factors rather than from perceptual complexity or visual specialisation. One such view argues that face specificity is an artefact of expertise and of recognition at the subordinate level, and that this would constitute the central difficulty for prosopagnosic patients (Damasio, 1990; Diamond & Carey, 1986; Gauthier, Behrmann, & Tarr, 1999).

An advantage of a general purpose or a single-system approach, whether based in cognitive factors like viewers' expertise or in object-form topology (Ishai et al., 1999) is that since faces are not special one does not need to postulate a critical moment at which a category decision takes place and the face-specific processing stage is launched. This perspective is consistent with data showing that the strong sensitivity of face recognition to canonical orientation is a product of our expertise with faces based on continuous exposure (Diamond & Carey, 1986). Indeed, the developmental literature has provided evidence for the claim that configural processing as measured by the inversion effect increases with age (Carey & Diamond, 1977; Carey & Diamond, 1994 but see Rouw & de Gelder, submitted). One should note though that in all the studies to date that have contrasted faces and objects, stronger inversion effects were obtained for faces than for objects.

Can a single system theory based on the role of task demands and viewers' expertise (e.g., Gauthier et al., 1999) provide the explanation of residual configuration we are looking for moreover? In other words, can it explain the fact that loss of face expertise leaves the patients with a strong residual configural ability which interferes negatively with feature-based operations? Given the tight link which those expertise-based theories make between configural processes and face (or expert object) recognition, it appears difficult to explain that the former is preserved when the latter two are so clearly lost. In other words, the dissociation between face identification and configural processing shown in our data illustrating loss of face identification and preserved configural processing is hard to understand from that perspective.

Further evidence against face experience as the only explanation of configural processes is provided by the abnormal object configuration effect shown by the acquired prosopagnosics. Obviously, a face-specific account of configural processes has difficulty explaining residual configural processes in object recognition (de Gelder et al., 1998). In order to explain the inversion superiority effects one might argue that faces are over-learned (Diamond & Carey, 1986) but it is difficult to make this claim for recognition of object categories like houses or shoes. The alternative theoretical account sounds equally implausible. As the patient had no particular expertise with these two categories of objects, the finding of a paradoxical object effect indicates that expertise is not a decisive factor in obtaining a paradoxical inversion effect. The extension of configural effects to objects also pleads against the assumptions of the sequential model discussed in the previous section. If configural processing is specifically linked to fluent face recognition, then a disorder in configural face operations should not spill over into object processing.

Special expertise does not appear to be relevant here but what does seem to matter is face experience and learning ability. The absence of configural face processes in developmental prosopagnosia is compatible with learning-based explanations of configural face processes since developmental prosopagnosics did not learn to recognise individual faces. One might even conjecture that the existence of a learning curve of configural effects in young children (Carey, Diamond, & Woods, 1980) leads to detailed predictions about the impact of a brain damage occurring in childhood. The strength of the paradoxical effects should be a function of the amount of previous face experience. For example, all other things being equal, paradoxical inversion superiority should be weaker in a patient whose brain injury occurred before his face expertise and his configural face skills reached adult level (Rouw & de Gelder, in press).

5. Perception of configuration based on face detection only

There are indications for a different notion of face configuration which is not linked to the ability of face identification but has its roots in a separate autonomous system of face detection. Evidence for detection-based as opposed to identification-based configuration can be found in single-cell studies, in developmental research and in cognitive psychology. As used here face detection is not an instance of *object categorisation*, at least not when this term refers to the stage of initial stimulus classification as is common in many theories of face recognition. As understood for example by Carey and Diamond or by Rhodes, visual object categorisation takes place at the juncture of the early (features) and the later stages (objects) of vision and before a face stimulus enters the specialised face processor. In other words, face detection as used here is not a process resulting from a category decision. Nor is face detection dependent on top-down effects on categorisation from structural object descriptions stored in memory. But categorisation is used by neurophysiologists to refer to the fact that cells have stimulus-specific responses, like for example shape selectivity or face selectivity of IT cells. This latter meaning of categorisation corresponds closely to our use of detection. To avoid misunderstandings with the more cognitive notion of categorisation we prefer to use the term detection.

Central to the notion of face detection is the claim that face-like patterns are apprehended as gestalts prior to and independent of feature synthesis. We mentioned already evidence about face selective cells from animal studies (Ashbridge, Perrett, Oram, & Jellema, 2000) and human electro-physiology (Puce et al., 1999). These findings can be linked with results from developmental research where there is also evidence for a primitive face detection mechanism that is neither dependent on face identification nor on learning. Goren, Sarty, and Wu (1975) showed that new-borns are sensitive to a face-like pattern and selectively track a normal as opposed to a scrambled face. The exact age at which infants can discriminate face patterns has been debated and it has been proposed that neonates (12.5–201 h) can already recognize their mother's face (Bushnell, Sai, & Mullin, 1989) and infants between 17 and 22 weeks can discriminate different faces (Fagan, 1972). More recent studies support the view that knowledge of the layout of the human face is present in the first months (de Schonen & Bry, 1987; de Schonen, Gil de Diaz, & Mathivet, 1986). Valenza, Simion, Cassia, and Umiltá (1996) found evidence for a primitive face detection system in a study that exploited the existence of naso-temporal asymmetry in infants suggesting a sub-cortical mechanism. Studies comparing different age groups have clearly shown that identification continues to develop until puberty and that identification skills only reach adult level around 10–11 years of age (Ellis & Flin, 1990; Feinman & Entwistle, 1976).

At present it is unclear how the detection and the recognition system are related to each other in early infancy, whether they co-exist as separate systems at least for some time during development or whether, once the recognition system starts to develop it takes over and integrates the detection system. As argued, for example, by Morton and Johnson (1991) this detection system may evolve into the face recognition system driven by increasing face experience. On the other hand, the primitive detection system could remain functional even in adults and it could even retain a separate functional and neuroanatomical basis. One conjecture thus is that in case focal brain damage dramatically impairs the face identification system, the primitive detection system might be available as a fallback system and continue to drive face-specific processes in patients with face identification deficits. In other words, in the latter case there would still be face-specific processes in prosopagnosic patients but face identification would be lost. Undoubtedly, provided the two face systems co-exist, it is very difficult to pull them apart in normal adults. As with any recognition system that is highly automated, the presence of an appropriate stimulus will automatically trigger the full recognition system and thus make it difficult to get a window on face representations at pre-recognition stages. A similar situation is known from debates on the pre-lexical stage of speech processing (Cutler & Norris, 1988). In fluent speakers speech input automatically triggers lexico-semantic processing and this complicates the task of demonstrating that certain brain areas are specifically involved in speech segmentation as opposed to general auditory processing but are not involved in speech recognition.

6. A dual route account: detection-based vs. identification-based configuration

This brings us to the proposal that two different notions of configuration may be needed to render the complexity of human face recognition ability. One is largely independent of accumulated face experience while the other is shaped in the course of face learning and is connected to the different visual and mnemonic structures that implemented face experience (see Fig. 2). One of these, the face detection system is highly specialised for detecting the presence of a face stimulus but is not sensitive to face identity (or to any semantic aspect like gender or age, familiarity, etc.). The other, the face identification system, overlaps partly with the object identification system. These two systems could be neuroanatomically and functionally independent at least to some extent and at the relevant level of description. Recent evidence for two separate face areas (FA and IOG) is consistent with the present proposal (Hoffman & Haxby, 2000).

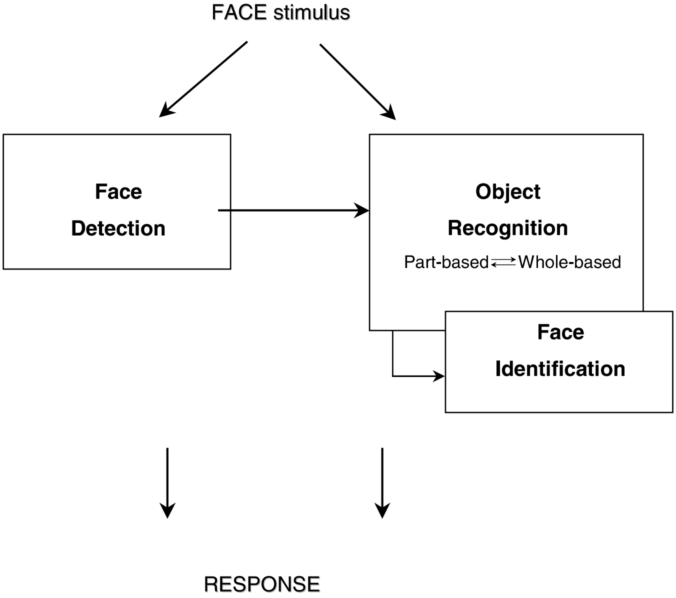

Fig. 2. Dual route account of face recognition with separate detection and identification systems and with both part-based and whole-based processes involved in face and object identification.

The major contrast between detection and recognition can be highlighted by contrasting speed of processing, relation to attention resources, degree of elaboration of the representations, domain specificity, degree of localisation, complexity and relative independence of experience (see Table 1). Detection is fast, it triggers exogenous attention, it only requires coarse-grained representations/processes, it re-

Table 1
An overview of some properties of the two separate face recognition routes: Face detection vs. face identification

	Face detection	Face identificaton
1	Fast	Slower
2	Based on exogenous attention	Under the influence of endogenous attention and perceptual strategies
3	Based on coarse-grained representations/ processes	Requires fine-grained representations
4	Requires limited stimulus exposure	Depends on extensive learning between ages 0 and 12 y
5	Category specific/unique	Shares resources with object recognition system
6	Neuronal basis is distributed across a variety of brain areas that contain face-sensitive cells	In FFA and overlapping with object recognition areas
7	Ontogenetically primitive	Ontogenetically complex as assembled from more primitive components

quires limited stimulus exposure/learning, and it is (relatively) category-specific. Its neuronal basis consists of a distributed network of face cells across a variety of brain areas that contain face-sensitive cells and it is ontogenetically primitive. In contrast, face identification is slower. Identification is under the influence of endogenous attention and of perceptual strategies. It requires fine-grained representations, depends on extensive exposure/learning from infancy through childhood, shares resources with the object recognition system, is probably based in the face area but overlapping with object recognition areas. It is ontogenetically complex and consists of different components or sub-processes. We return to this last point below.

The model we propose is a dynamical one and in this sense it is different from typical flow diagram and box models characteristic of cognitive neuropsychology in the past two decades. Output from the detection system can lead directly to a fast category-specific response (like for example in speeded face detection) and at the same time it can (but does not have to) feed in the object identification system. A plausible conjecture is that the much debated domain specificity of the face identification system is at least partly a consequence of input it receives from the face detection system. This means that the object identification system operates de facto as face identification system when receiving a face input from the face detection system. On this picture specialisation would be a dynamic rather than a local, static property. A fast hierarchically organised and feed-forward processing provides the system with basic information and is responsible for face detection. This is complemented by lateral and slower activity in infero-temporal cortex, which is responsible for more cognitive and decisional aspects of face processing like typically, involved in face identification. This general picture in which a fast feed-forward-processing stream is contrasted with slower context sensitive and more cognitive and memory-based processes is consistent with what is presently known about vision in the brain (e.g., Lamme, 2001). But detailed information about the time course of these two processing sweeps for the specific case of face recognition is at present still very limited. Electro-physiology of face detection vs. identification could provide critical support for this model. An ERP study by Bentin and Deouell (2000) provided evidence for structural face encoding prior to identification. The authors argue that the N170 reflects face perception without recognition, an interpretation based on the finding that the N170 is not yet sensitive to face familiarity (unlike the later N400). Developmental aspects of the time course of face processes are currently investigated (see Johnson & de Haan, 2000).

Before sketching how these two different notions of configuration might contribute to understanding the patterns of face deficits we elaborate further the notion of configuration at stake in face identification in the light of the debate over part- vs. whole-based identification.

7. Whole- and part-based processing in object and face identification

The notion that the face identification system may show a considerable functional overlap with the object recognition system implies that there is a substantial overlap in the processes involved in the two cases. If so, the traditional picture of holistic face processes vs. part-based object processes is not adequate. Both kinds of processes may be equally critical for processing the two stimulus categories and more so than previously envisaged, for example by Farah (1991). The older notion of face-specific holistic processing was based on neuropsychological evidence indicating that whole stimulus encoding is more lateralised to the right hemisphere (RH) and feature-based encoding more to the left hemisphere. Comfortable as this picture was for a while, it has been noted that prosopagnosia is in fact mostly accompanied by bilateral lesions (Damasio et al., 1982; Hécaen & Albert, 1979; Meadows, 1974). Only few cases of unilateral right-sided lesions have been observed (De Renzi, 1986; Ettlin et al., 1992; Michel, Poncet, & Signoret, 1989; see Farah, 1990, for an overview). On the other hand, there is considerable evidence suggesting that the right and left hemisphere are *both* involved in face processing but in different ways. Some lateralisation studies reported a left hemisphere advantage when presenting famous faces (Marzi & Berlucchi, 1977; Umiltá, Brizzolara, Tabossi, & Fairweather, 1978) or presenting novel faces frequently in the same experiment (Bradshaw & Sherlock, 1982; Hellige, Jonsson, & Michimata, 1988). Laeng and Rouw (2000) also found that both hemispheres are involved in face matching tasks, but in different ways. The left hemisphere was better for recognising familiar face from the optimal (22.5°) viewpoint, while the right hemisphere was better with non-optimal views as well as with unfamiliar face matching.

Hemispheric specialisation might be related to a difference in manner of stimulus processing. For example, the RH depends more on cells with a large receptive field, while the LH depends more on cells with a small receptive field, supporting an advantage of configural processing for the RH over the LH (see Kosslyn, 1994). Faces presented in the usual upright orientation to the left visual field are identified more rapidly and more accurately than when they are presented to the right visual field (Hillger & Koenig, 1991; Leehey, Carey, Diamond, & Cahn, 1978; Levine, Banich, & Koch-Weser, 1988; Rhodes, 1993). Stimulus inversion disrupts configural coding of faces (e.g., de Gelder & Rouw, 2000b; Rhodes et al., 1993; Tanaka & Farah, 1993) and eliminates or reduces the RH advantage for faces (Hillger & Koenig, 1991; Leehey et al., 1978). In contrast, the LH has the lead with feature-based processing, as indicated by a LH superiority when feature-by-feature processing of faces is induced by task manipulation (Hillger & Koenig, 1991).

Until recently it was difficult to bridge the gap between the well-known behavioural data in favour of lateral differences and recent brain imaging studies. Activation of the left posterior hippocampus was found with familiar (Kapur, Friston, Young, Frith, & Frackowiak, 1995) as well as repeatedly shown faces (Heit, Smith, & Halgren, 1998). Some researchers reported bilateral face-specific activity in regions of the middle fusiform gyrus (Gauthier, Skudlarski, Gore, & Anderson, 2000; Halgren et al., 1999; Haxby et al., 1994; Ishai et al., 1999) and differences between faces and objects mainly in the RH fusiform gyrus (Kanwisher et al., 1997; McCarthy, Puce, Gore, & Allison, 1997). But the fact that none of these studies found evidence for LH/RH specialisation along the lines of the behavioural results may be due to different task demands between the behavioural and the brain-imaging studies. None of the latter used a task requiring individual face recognition typically required in many of the behavioural experiments mentioned above.

In a recent PET study we looked at the respective contribution of feature and whole-based processes to face and object identification (Rossion et al., 2000). In the critical face condition subjects were given a delayed matching task using whole faces. In some blocks they were presented with the stimuli without further instructions than to match the faces for identity. But in other blocks they were told at the beginning of each block which face part would be the one that contained the critical difference. We observed a double dissociation between the whole and the parts condition corresponding to selective increase in activation of the left FFA for processing parts differences and of the right FFA for processing the stimulus as a whole. In other words, we found that the left FFA is specialised for faces but in a different way than the right FFA. Our data thus suggest a complex interaction *inside* the face identification mechanism between these two types of operations traditionally associated with face and object recognition, respectively.

8. Detection vs. identification and part-based vs. whole-based identification

Where does all this leave us with respect to understanding the peculiar deficits of some prosopagnosics? We now have two possible explanations and they may hold jointly or separately depending on the patients' lesions. First, we consider the implications of the brain-imaging study just summarised. The finding of a specialised left vs. right FFA has interesting implications for understanding the positive symptoms of prosopagnosia and also suggests a clarification of the longstanding debate in the literature as to whether prosopagnosia requires bilateral lesions. If both hemispheres are involved but each has a specific contribution then a workable hypothesis is that brain damage may lead to a different picture depending on whether the right, the left or both face areas are involved. It might be the case that a lesion limited to the left face area will lead to a different pattern of functional loss than one to the RH face area. In the latter case whole-based processing will be impaired while in the former the deficit will be more noticeable in feature-based face processes. A further prediction is that all other things being equal, patients with right FFA lesions will not show paradoxical recognition effects because of loss of whole-based face recognition.

Only a few cases of prosopagnosia have been studied in such detail as to test these predictions. Patients AD and LH have bilateral lesions and are therefore of no use in testing this prediction. As concerns patients RP and AV, they are also not informative because the latter is a developmental case and the former does not show any brain damage, as is common in patients with closed-head injury. A recent study by Gauthier et al. (1999) is more useful as their patients SM and CR did have lesions including the FFA. The authors did test for an inversion effect and report that patients have neither inversion inferiority (normal) nor inversion superiority (paradoxical). This result is thus in line with our prediction as both patients have exclusively RH lesions.

How does the notion of separate detection and identification routes help us to understand the paradoxical neuropsychological data and how do this represent a departure from current models? An important point to note is that on this dual route account loss of face recognition ability is not an all-or-nothing affair and an explanation assuming simply that the face module is defect (Farah et al., 1995) is not satisfactory. First, the face recognition system now consists of two separate qualitatively different parts and these can dissociate but also interact in a pathological way. Let us consider the possibility of a dissociation. If face recognition in the sense of face identification is lost, patients could still have residual *face-specific* processes in detection and our observations show that this is indeed sometimes the case.

Next, we can address the findings of pathological interaction. Although the two prosopagnosic patients perform similarly well on face detection, in the identification tasks one of them shows no evidence of configural processes while the other has inversion and context superiority. Note again that the paradoxical inversion and context superiority effects observed in patients LH, AD and RP are difficult to reconcile with the hierarchical and single route account discussed before. These models assume that in the typical case of a problem with face identification, prosopagnosics can fall back on more general and/or earlier and posterior stages of feature operations and discriminate faces as if they were objects instead of processing the face as a configuration. An explanation of the positive symptoms of functional loss which we observed in RP, LH and AD. The notion is that with the face detection system intact, configural face input is delivered to the identification system. This amplifies the face specificity of the object identification system and tends to overrule intact object recognition processes. As a consequence of the detection-based amplification, the face stimulus is not available for feature analysis available within the object recognition system.

9. Concluding remarks

We reviewed brain-imaging studies of face recognition, presented some recent neuropsychological data and proposed a framework for understanding face recognition and its impairments. We have so far tested a sizeable number of patients but of course our interpretations must await further confirmation. At present our results are compatible with the view that loss of individual face recognition can go hand in hand with specialised face detection and preserved (but inefficient) processing of the face configuration. We argued that hierarchical, single route theories, either modular face-specific ones or general object ones, have difficulty accounting for the complex pattern of spared and damaged face recognition abilities of prosopagnosics. We proposed a dual route account of configural face processes which departs from more familiar models on two major counts. The distinction between a face detection system and a specialised recognition system is the first one. The other is a distinction within the recognition system between whole-based and parts-based processes. The exact pattern of spared and damaged abilities will depend on the patients' lesion. Further research is needed to understand the different patterns of face recognition deficits that result from the interaction between these routes and their components.

Acknowledgements

We thank one of the Editors (J.W.) and two anonymous reviewers for helpful comments on the manuscript.

References

Ashbridge, E., Perrett, D. I., Oram, M. W., & Jellema, T. (2000). Effect of image orientation and size on object recognition: Responses of single units in the macaque monkey temporal cortex. *Cognitive Neuropsychology*, *17*(1/2/3), 13–34.

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

Biederman, I., & Kalocsai, P. (1997). Neurocomputational bases of object and face recognition. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *352*, 1203–1219.

Bodamer, J. (1947). Die prosop-Agnosie. *Archiv für Psychiatrie und Nervenkrankheiten*, *179*, 6–53.

Bradshaw, J. L., & Sherlock, D. (1982). Bugs and faces in the two visual fields: the analytic/holistic processing dichotomy and task sequencing. *Cortex*, *18*(2), 211–225.

Bruce, V. & Humphreys, G. W. (Eds.). (1994). *Object and face recognition*. Hove, UK: Erlbaum.

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

Bushnell, I. W. R., Sai, F., & Mullin, J. T. (1989). Neonatal recognition of the mothers face. *British Journal of Developmental Psychology*, *7*, 3–15.

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

Carey, S., & Diamond, R. (1994). Are faces perceived as configurations more by adults than by children? *Visual Cognition*, *1*, 253–274.

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

Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.

Corballis, M. (1991). *The lopsided ape: evolution of the generative mind*. New York: Oxford University Press.

Cutler, A., & Norris, D. (1988). The role of strong syllables in segmentation for lexical access. *Journal of Experimental Psychology: Human Perception and Performance*, *14*, 113–121.

Damasio, A. R. (1990). Category-related recognition defects as a clue to the neural substrates of knowledge. *Trends in Neuroscience*, *13*, 95–98.

Damasio, A. R., Damasio, H., & Van Hoesen, G. W. (1982). Prosopagnosia: anatomical basis and behavioural mechanisms. *Neurology*, *32*, 331–341.

de Gelder, B., Bachoud-Levi, A. C., & Degos, J. D. (1998). Inversion superiority in visual agnosia may be common to a variety of orientation polarised objects besides faces. *Vision Research*, *38*, 2855–2861.

de Gelder, B., & Kanwisher, N. (1999). Absence of a fusiform face area in a prosopagnosic patient. *NeuroImage*, *9*(6), S604.

de Gelder, B., Rossion, B., de Volder, A., Bodart, J. M., & Crommelinck, M. (1999). Prosopagnosia: a deficit of face-specific featural procedures? *Society for Neuroscience*, *1*, 354.

de Gelder, B., & Rouw, R. (2000a). Configural processing of faces in prosopagnosia. *Cognitive Neuropsychology*, *17*, 89–102.

de Gelder, B., & Rouw, R. (2000b). Paradoxical configuration effects for faces and objects in prosopagnosia. *Neuropsychologia*, *38*, 1271–1279.

de Gelder, B., & Rouw, R. (2000c). de Configural face processes in acquired and developmental prosopagnosia: evidence for two separate face systems? *NeuroReport*, *11*(14), 3145–3150.

De Renzi, E. (1986). Prosopagnosia in two patients with CT-scan evidence of damage confined to the right hemisphere. *Neuropsychologia*, *24*, 385–389.

de Schonen, S., & Bry, I. (1987). Interhemispheric communication of visual learning: a developmental study in 3–6 month old infants. *Neuropsychologia*, *25*, 601–612.

de Schonen, S., Gil de Diaz, M., & Mathivet, E. (1986). Hemispheric asymmetry in face processing in infancy. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. Young (Eds.). *Aspects of face processing* (pp. 199–208). Dordrecht: Martinus Nijhoff.

Desimone, R., & Duncan, J. (1995). Neural correlates of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.

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

Ellis, H. D., & Flin, R. H. (1990). Encoding and storage effects in 7-year-olds' memory for faces. *British Journal of Developmental Psychology*, *8*, 77–92.

Etcoff, N. L., Freeman, R., & Cave, K. R. (1991). Can we lose memories of faces? Content-specificity and awareness in a prosopagnosic. *Journal of Cognitive Neuroscience*, *3*, 25–41.

Ettlin, T. M., Beckson, M., Benson, D. F., Langfitt, J. T., Amos, E. C., & Pineda, G. S. (1992). Prosopagnosia: a bihemispheric disorder. *Cortex*, *28*, 129–134.

Fagan, F. J. (1972). Infants' recognition memory for faces. *Journal of Experimental Child Psychology*, *14*, 452–476.

Farah, M. J. (1990). *Visual agnosia: disorders of object recognition and what they tell us about normal vision.* Cambridge: MIT Press.

Farah, M. J. (1991). Patterns of co-occurrence among the associative agnosias: implications for visual object representation. *Cognitive Neuropsychology*, *8*, 1–19.

Farah, M. J., Wilson, K., Drain, H., & Tanaka, J. (1995). The inverted face inversion effect in prosopagnosia: evidence for mandatory face-specific perceptual mechanisms. *Vision Research*, *35*(14), 2089–2093.

Feinman, S., & Entwistle, D. R. (1976). Children's ability to recognise other children's faces. *Child Development*, *47*, 566–580.

Frith, C. D. (1992). *The cognitive neuropsychology of schizophrenia.* Erlbaum.

Gauthier, I., Behrmann, M., & Tarr, M. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience*, *11*, 349–370.

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.

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*(1/2/3), 143–163.

George, N., Dolan, R. J., Fink, G. R., Baylis, G. C., Russell, C., & Driver, J. (1999). Contrast polarity and face recognition in the human fusiform gyrus. *Nature Neuroscience*, *2*(6), 574–580.

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

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*, 293–321.

Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B. H., Marinkovic, K., & Rosen, B. (1999). Location of human face-selective cortex with respect to retinotopic areas. *Human Brain Mapping*, *7*, 29–37.

Haxby, J. V., Horwitz, B., Ungerleider, L. G., Maisog, J. M., Pietrini, P., & Grady, C. L. (1994). The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *Journal of Neuroscience*, *14*, 6336–6353.

Hécaen, H., & Albert, M. L. (1979). *Human neuropsychology*. New York: Wiley.

Heit, G., Smith, M. E., & Halgren, E. (1998). Neuronal encoding of individual words and faces by the human hippocampus and amygdala. *Nature*, *333*, 773–775.

Hellige, J. B., Jonsson, J. E., & Michimata, C. (1988). Processing from LVF, RVF and bilateral presentations: examinations of metacontrol and interhemispheric interaction. *Brain and Cognition*, *7*(1), 39–53.

Heywood, C. A., & Cowey, A. (1992). The role of face-cell area in the discrimination and recognition of faces by monkeys. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *335*, 31–38.

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

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*(1), 80–84.

Homa, D. B., Haver, B., & Schwartz, T. (1976). Perceptibility of schematic face stimuli: Evidence for a perceptual gestalt. *Memory and Cognition*, *4*, 176–285.

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 National Academy Science USA*, *96*, 9379–9384.

Johnson, M. H. & de Haan, M. (2000). Developing cortical specialization for visual-cognitive function: The case of face recognition. In R. S. Siegler & J. L. McClelland (Eds.). *Mechanisms of cognitive development* (in press). Hillsdale, NJ: Lawrence Erlbaum Associates.

Jolicoeur, P. (1985). The time to name disoriented natural objects. *Memory and Cognition*, *13*, 289–303.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 402–4311.

Kanwisher, N., & Moscovitch, M. (2000). The cognitive neuroscience of face processing: an introduction. *Cognitive Neuropsychology*, *17*(1–3), 1–12.

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

Kapur, N., Friston, K. J., Young, A., Frith, C. D., & Frackowiak, R. S. J. (1995). Activation of human hippocampal formation during memory for faces: A PET study. *Cortex*, *31*, 99–108.

Kosslyn, S. M. (1994). *Image and brain*. Cambridge: MIT Press.

Laeng, B. & Rouw, R. (2000). Canonical views of faces and the cerebral hemispheres. *Lateralization*, in press.

Lamme, V. A. F. (2001). Blindsight: the role of feedforward and feedback corticocortical connections. *Acta Psychologica*.

Leehey, S. C., Carey, S., Diamond, R., & Cahn, A. (1978). Upright and inverted faces: The right hemisphere knows the difference. *Cortex*, *14*, 414–419.

Leonard, C. M., Rolls, E. T., Wilson, F. A., & Baylis, G. C. (1985). Neurons in the amygdala of the monkey with responses selective for faces. *Behavioural Brain Research*, *15*(2), 159–176.

Levine, D. N., & Calvanio, R. (1989). Prosopagnosia: a defect in visual configural processing. *Brain and Cognition*, *10*, 149–170.

Levine, S. C., Banich, M. T., & Koch-Weser, M. P. (1988). Face recognition: a general or specific right hemisphere capacity? *Brain and Cognition*, *8*, 303–325.

Lissauer, H. (1890). Ein fall von Seelenblindheit nebst einem Beitrage zur Theorie derselben. [A case of psychic blindness and a contribution of theory thereof]. *Archiv für die Psychiatrie und Nervenkrankheiten*, *21*, 222–270.

Marinkovic, K., Trebon, P., Chauvel, P., & Halgren, E. (2000). Localised face processing by the human pre-frontal cortex: Face-selective intra-cerebral potentials and post-lesion deficits. *Cognitive Neuropsychology*, *17*(1/2/3), 187–199.

Marzi, A., & Berlucchi, G. (1977). Right visual field superiority for accuracy of recognition of famous faces in normals. *Neuropsychologia*, *15*, 751–756.

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.

Meadows, J. C. (1974). The anatomical basis of prosopagnosia. *Journal of Neurology, Neurosurgery and Psychiatry*, *37*, 489–501.

Michel, F., Poncet, M., & Signoret, J. L. (1989). Les lésions responsables de la prosopagnosie sont-elles toujours bilatérales [Are lesions responsible for prosopagnosia always bi-lateral]? *Revue Neurologique*, *145*, 764–770.

Morton, J., & Johnson, M. H. (1991). Conspec and conlearn: A two-process theory of infant face recognition. *Psychological Review*, *98*(2), 164–181.

Moscovitch, M., Winocur, G., & Behrmann, M. (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.

O'Scalaide, S. P., Wilson, F. A., & Goldman-Rakic, P. S. (1997). A real segregation of face-processing neurons in pre-frontal cortex. *Science*, *278*, 1135–1138.

Op de Beeck, H., Wagemans, J., & Vogels, R. (2001). Can neuroimaging really tell us what the human brain is doing? The relevance of indirect measures of population activity. *Acta Psychologica*, *107*, 323–351.

Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology*, *74*, 1192–1199.

Puce, A., Allison, T., & McCarthy, G. (1999). Electrophysiological studies of human face perception: Effects of top-down processing on face-specific potentials. *Cerebral Cortex*, *9*, 445–458.

Purcell, D. G., & Stewart, A. L. (1988a). The face-detection effect: Configuration enhances detection. *Perception and Psychophysics*, *43*(4), 355–366.

Purcell, D. G., & Stewart, A. L. (1988b). The face-detection effect. *Bulletin of the Psychonomic Society*, *24*, 118–120.

Rhodes, G. (1988). Looking at faces: First-order and second-order features as determinants of facia appearance. *Perception*, *17*, 43–63.

Rhodes, G. (1993). Configural coding, expertise, and the right hemisphere advantage for face recognition. *Brain and Cognition*, *22*, 19–41.

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

Riddoch, J. M., & Humphreys, G. W. (1987). A case of integrative visual agnosia. *Brain*, *110*, 1431–1462.

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

Rossion, B., de Gelder, B., Dricot, L., Zoontjes, R., Volder, A., de De J.M, , & Crommelinck, M. (2000). Hemispheric asymmetries in wholes and parts face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *12*(5), 793–803.

Rouw, R. & de Gelder, B. (in press). Impaired face recognition does not preclude intact whole face perception. *Visual Cognition.*

Rouw, R. & de Gelder, B. (submitted). Configural processing is age-independent, but face-specific configural processes develop with age.

Savoy, R. (2001). History and future directions of human brain mapping and functional neuroimaging. *Acta Psychologica.*

Sergent, J., Ohta, S., & Mc Donald, B. (1992). Functional neuroanatomy of face and object processing: a positron emission tomography study. *Brain*, *115*, 15–36.

Spreeuwenberg, M. & de Gelder, B. (submitted). What to learn from lesion studies of face processing of the nineties?

Suzuki, S., & Cavanagh, P. (1995). Facial organisation blocks accesses to low-level features: an object inferiority effect. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(4), 901–913.

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

Tanaka, K. (1993). Neuronal mechanisms of object recognition. *Science*, *262*, 685–688.

Tarr, M. J., & Pinker, S. (1989). Mental rotation and orientation-dependence in shape recognition. *Cognitive Psychology*, *21*, 233–282.

Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., & Kanwisher, N. (2000). Response properties of the human fusiform face area. *Cognitive Neuropsychology*, *17*, 257–279.

Tovée, M. J. (1998). Is face processing special? *Neuron*, *21*, 1239–1242.

Umiltá, C., Brizzolara, D., Tabossi, P., & Fairweather, H. (1978). Factors affecting face recognition in the cerebral hemispheres: familiarity and naming. In J. Requin (Ed.). *Attention and performance VII* (pp. 363–374). Hillsdale, NJ: Erlbaum.

Valenza, E., Simion, F., Cassia, V. M., & Umiltá, C. (1996). Face preference at birth. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 892–903.

Wojciulik, E., Kanwisher, N., & Driver, J. (1998). Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *Journal of Neurophysiology*, *79*, 1574–1578.

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

Yin, R. K. (1970). Face recognition by brain-injured patients: a dissociable ability? *Neuropsychologia*, *8*, 395–402.

Young, A. W., Hellawell, D., & Hay, D. C. (1986). Configurational information in face perception. *Perception*, *16*, 747–759.