Understanding face perception by means of prosopagnosia and neuroimaging

Bruno Rossion[1]

[1]*Institute of Research in Psychology and Institute of Neuroscience, University Louvain de Louvain, 10, Place Cardinal Mercier, 1348 Louvain-la-Neuve, Belgium*

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1. ABSTRACT

Understanding the human neuro-anatomy of face recognition is a long-standing goal of Cognitive Neuroscience. Studies of patients with face recognition impairment following brain damage (i.e., acquired prosopagnosia) have revealed the specificity of face recognition, the importance and nature of

holistic/configural perception of individual faces, and the distribution of this function in the ventral occipito-temporal (VOT) cortex, with a right hemispheric dominance. Yet, neuroimaging studies in this field have essentially focused on a single face-selective area of the VOT and underestimated the right hemisphere superiority. Findings in these studies have also been taken as supporting a hierarchical view of face perception, according to which a face is decomposed into parts in early face-selective areas, these parts being subsequently integrated into a whole representation in higher-order areas. This review takes a historical and current perspective on the study of acquired prosopagnosia and neuroimaging that challenges this latter view. It argues for a combination of these methods, an approach suggesting a coarse-to-fine emergence of the holistic face percept in a non-hierarchical network of cortical face-selective areas.

2. INTRODUCTION

The human face is a highly familiar, complex, multidimensional visual pattern, conveying a wide variety of information about an individual (identity, sex, age, mood, ethnical origin, etc.). Extraction and interpretation of this information require elaborate and refined perceptual skills that few other categories of objects call for, which makes the face a particularly well-suited stimulus for both the study of visual perception and the specific processes underlying the combination of component parts into a meaningful whole. Understanding *face perception* means understanding how, from sensory information, the human brain builds a visual representation – an internal image - of a face. Face perception includes the capacity to detect a face in a visual scene (*face detection*), to discriminate a particular face from other faces (*face individualization* or *individual face discrimination*), and to associate a percept with a stored representation of a particular face in memory (*face recognition*).

The goal of this review is to provide the reader with an overview of the neural basis of face perception in humans, with an emphasis on prosopagnosia following brain damage and on functional neuroimaging. I will first present the two main views about how faces are perceived at the functional level (section 3). Then, I will provide a functional account of acquired prosopagnosia, arguing that it is the inability to perceive a face holistically at a sufficiently detailed level of resolution to individualize it (section 4). In section 5, I will provide a review of what was known about the neuro-anatomy of human face perception before the first functional neuroimaging study in this field (1). With these three sections in hand, I will then suggest that the emergence of a full face percept in the human brain – a percept that is both holistic and fine-grained – requires the integrity of a large network of brain areas, from the occipital pole to the temporal pole, with a right hemispheric dominance. I will argue that this wide distribution of function is what makes face perception particularly fragile. Section 6 will provide an overview of functional neuroimaging – mainly functional magnetic resonance imaging (fMRI) - studies of face perception performed over the last two decades, with an emphasis on
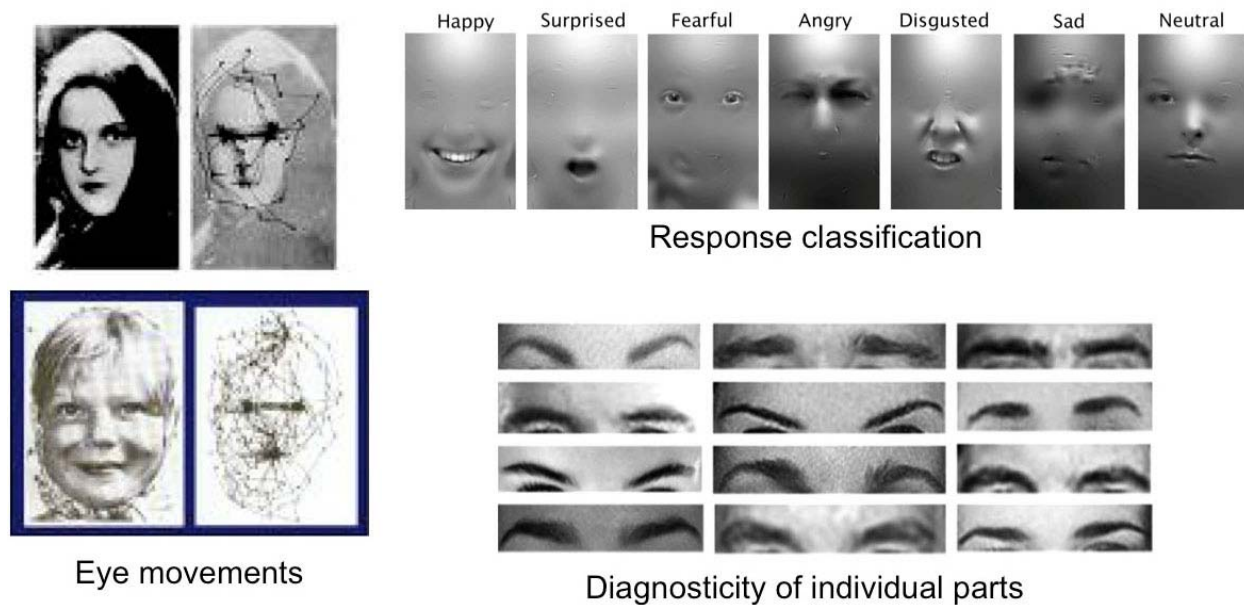
individual face perception and the hierarchical processing view that prevails in this area of research. Finally (section 7), I will challenge this conventional hierarchical view by providing evidence both from single-case studies of prosopagnosia and from neuroimaging studies of normal observers that rather support a non-hierarchical view of the neural dynamics of face perception in the human brain.

3. HOW IS A FACE PERCEIVED?

3.1. Cue saliency and the analytical view of face perception

The field of face perception took off in the mid-1970s, and the early experimental approach, known as *cue saliency*, was characterized by studies aiming at defining which of the parts/features ("cues") of faces were the most salient for various perceptual tasks (2, 3). These early studies revealed the dominance of the eye/eyebrow combination for individual face perception (4-6), an observation that has always been supported by subsequent observations (e.g., 7-9). The cue saliency approach is still active nowadays and takes three forms (Figure 1). The first approach consists in selectively revealing, masking or manipulating experimentally-defined pieces of information of the face (e.g., the eyes or the nose only) and measuring human observers' performance at a given task in these conditions (e.g., 8). The second approach consists in the analysis of eye gaze fixations on the face, following Yarbus (10); these fixations are often defined by drawing regions of interest around specific parts of faces (e.g., the right eye, the mouth, etc.; e.g., 11) although more recent approaches derive pixelwise statistical maps of fixations across the face (12, 13)

The third approach is called *response classification* or *classification images*, and it deserves a longer description because it is apparently more complex than the other two approaches and it has become more popular over recent years. This approach was introduced in the field of face perception by Haig (the "distributed aperture technique"; 14, 15) (for a general review on classification images, see 16). In his study, Haig divided 4 face pictures into square grids of 8 x 8 apertures, or more. These apertures were revealed or masked randomly at each trial. The number of apertures revealing facial features was randomly selected for each trial, and observers were asked to recognize the faces revealed through a subset of apertures on each of thousands of trials. Classification images were obtained by representing each aperture as a square having a brightness that was a linear function of the percentage correct at that aperture address. The results showed that very few apertures were needed to achieve a good performance, and identified a high proportion of correct responses across the eyes/eyebrows. Haig's original response classification approach with faces is objective in the sense that the experimenter does not define in advance the piece of information that is selectively revealed or masked: the diagnostic parts emerges from the pattern of responses of the observer and could potentially occupy any spatial location on the face. This is the same approach that has been reintroduced and popularized many years later in face perception research under the name of "*Bubbles*" (17) or more simply *response classification* (18).

Happy · Surprised · Fearful · Angry · Disgusted · Sad · Neutral

Response classification

Eye movements

Diagnosticity of individual parts

Figure 1. The cue saliency approach in face perception research: three different approaches under the framework of part-based analysis of faces. Left: Eye movements during exploration of faces (from 10) focus on specific parts of the face (right eye, left eye, mouth). Above, right: The approach of response classification, initiated by Haig (14), extracts objectively the local diagnostic information for various face categorization tasks (here the categorization of facial expressions using "Bubbles", adapted with permsision from 21). Below, right: Diagnosticity of individual parts: recognition of individual faces can be performed on the basis of local parts presented in isolation. Adapted with permission from (8).

Generally speaking, this cue saliency approach is associated with an *analytical view* of face perception, according to which the goal of the face perception system is to extract the most diagnostic piece of information from the face, and a face is processed part-by-part (Figure 2A). Studies performed under this framework are often considered as providing evidence for a part-based analysis and representation of faces (19-21) and are generally associated with the view that the whole face is no more than the sum of its parts (22).

3.2. Holistic/configural face perception

According to a fundamentally different tradition of research, the face is perceived as a whole unit or a Gestalt, along the lines of the Gestalist view of visual perception (23, 24; for recent reviews, see 25, 26). This view is based primarily on *phenomenology*. For instance, a visual stimulus can be perceived as face even though none of its parts is face-like and none would be perceived as a facial attribute if presented in isolation (e.g., binarized "Mooney" faces as in Figure 3; or Arcimboldo paintings, see 27).

One reason for which the human face is often considered as the quintessential whole, or Gestalt (28, 29), is because faces are perceived more easily than objects in such Mooney pictures (30). The most compelling illustration of this holistic/configural view of face perception is the composite face illusion, an illusion named after the composite face effect reported by Young and colleagues (31, 32). The illusion shows that the top half of a face cannot be perceived without being influenced by the identity of its bottom half 33, 34 for review). Or, to put it more exactly, even if this bottom half is not fixated, its alignment with the top half creates the perception of a whole new face (Figure 4).

Many behavioral studies have used such visual illusions to show that the processing of a facial "part" (e.g., eyes, nose, mouth, or half of a face) is affected by alterations to the identity or the position of one or several other parts of the face (31, 32, 35-41). Collectively, these studies support a holistic rather than a part-based perception of faces. Other studies that belong to this holistic/configural view of face perception have emphasized the role of relative distances between face parts, such as the interocular distance, or the distance between the eyes and the mouth (42-45)[1].

Tanaka and Farah (40) were perhaps the first authors to clearly articulate this holistic/configural view of face perception (see 34 for a recent comprehensive review). According to these authors, the face undergoes little or even no part decomposition: the parts of a face would not even have a distinct representation in the system. "Holistic/configural" refers to a *process* of the face as an integrated unit, not to a particular kind of information on the face. That is, both the local parts *and* their relative distances are included in this process, without giving a particular status to the latter cues (33, 34, 46; see also 47). Importantly, this holistic/configural process – defined as *the simultaneous integration of the multiple parts of a face into a single perceptual representation*' (33) - can be applied to a local region of the face only. Indeed, the face
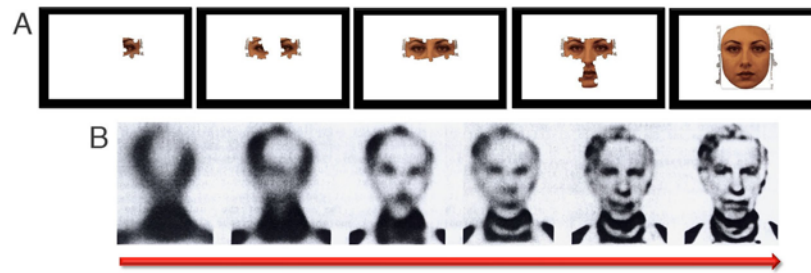
Figure 2. A. A. The analytical view of face perception, according to which a face is perceived part-by-part, these parts having to be integrated progressively, like the pieces of a puzzle, in order to obtain a representation of the whole face. B. The coarse-to-fine view of face perception, in which the initial face percept is already global but coarse. There is no decomposition in facial parts and the whole percept is progressively refined over time.
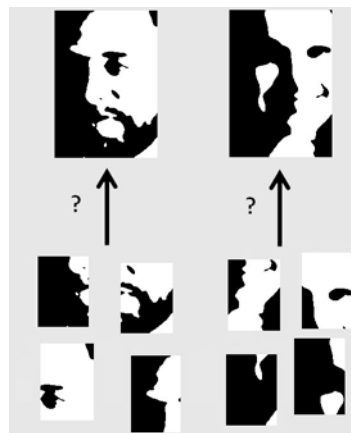
Figure 3. In a binarized picture of a face, the individual elements cannot be perceived as facelike. The representation of a face emerges from the whole stimulus. The perception of a face in such "Mooney" faces poses a great challenge for any hierarchical view of face perception that posits the extraction of face-selective parts being then associated to form a whole face (e.g. 248). Note that the isolated squares below may appear facelike *after* perception of the face that they form on the top of the figure. However, without the whole face stimulus, they would not be perceived as facelike.
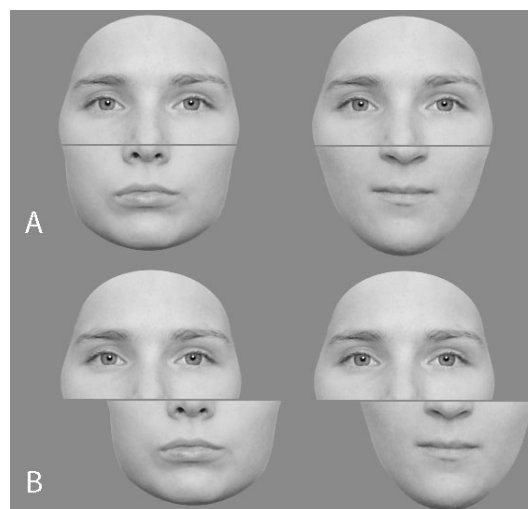
Figure 4. The composite face illusion (adapted from 34 with permission). A. The two identical top halves are perceived as being different because they are aligned with different bottom halves. Misaligning the bottom halves as in B, breaks the illusion. This powerful visual illusion indicates that the visual system automatically glues the two halves of a face into an integrated configuration ("holistic face perception").

could be partially occluded for instance. Or, a small part only, such as the eyes and eyebrows, could be available. Yet, the process can take place at different degrees of resolution (48) and can be applied to such a partial face stimulus (34).

This holistic view of face perception is almost impossible to reconcile with an analytical view of face perception according to which a face would be processed first part-by-part and *then* as a whole. This is because the "parts" of a Mooney face cannot even be categorized as face-like, for instance (Figure 3), and yet the Mooney stimulus is perceived as a face. However, as proposed by Sergent (48) in her seminal paper, the holistic view of face perception agrees very well with a coarse-to-fine processing of information, according to which the initial percept of a face is the whole face, at a very coarse scale. With such a coarse percept, the stimulus can be categorized as a generic face, no more ("it's a face"). The percept then evolves from a coarse whole face to an increasingly refined whole face, providing sufficient information to individualize it ("whole-to-whole", 48; Figure 2B; see also 49 as well as 50 for a general review on coarse-to-fine visual processing). Understanding how such a dynamic coarse-to-fine holistic process could be implemented in the human brain is particularly challenging. Hence, it is not surprising that neuroscientific and computational models of face perception have rather privileged the analytical view, associated with a hierarchical view.

4. HOW ARE FACES NOT (WELL) PERCEIVED? THE FUNCTIONAL ASPECTS OF ACQUIRED PROSOPAGNOSIA

Before the advent of functional neuroimaging, clinical reports of brain-damaged patients complaining of face recognition impairments provided the main source of information for understanding the human neuro-anatomy of face perception. The first cases were described in the 19th century (51, 52). Bodamer (53) later introduced the term prosopagnosia (from the Greek, "prosopon", *face* and "a-gnosia", *without knowledge*). Most patients with prosopagnosia[2] follow a (right) posterior cerebral artery infarct; other causes include trauma, carbon monoxide poisoning, temporal lobectomy, encephalitis, neoplasms, right temporal lobe atrophy, medial/anterior temporal lobe epilepsy, or even Alzheimer's disease (53-55). Acquired prosopagnosia can be defined as *the inability to recognize faces following brain damage, an impairment that cannot be accounted for by low-level (sensory) visual defects or intellectual deficiencies*. The major complaint of these patients is in recognizing previously seen (i.e., familiar) faces and in learning to recognize new faces.

4.1. Prosopagnosia as a face-specific impairment in holistic perception of individuality

What goes wrong with faces in prosopagnosia? How does a patient with prosopagnosia *see* faces? There are several views on this issue. First, it has been claimed that prosopagnosia is not specific to faces and concerns a general difficulty at discriminating visually similar items (56-58). The patient would complain mainly, or only, of face recognition problems, because faces are more visually similar to one another than other object categories, and because faces *have to* be individualized. Whether prosopagnosia is specific to faces or not, some authors have claimed that it is essentially a memory problem (56, 59), or that there are both perceptual and mnesic forms of prosopagnosia (60), or else that there are multiple forms of prosopagnosia (61, 62). A common view is that prosopagnosia concerns a general difficulty in holistic/configural perception (e.g., 63-68). Some authors also make further distinctions between holistic perception and the processing of relational features on faces (referred to as "configural processing", 69, see endnote 1). Based on in-depth single case studies carried out over the last decade, I will rather argue here that the core impairment in prosopagnosia following brain damage takes only one form: *a face-specific impairment in holistic perception of individuality*.

4.1.1. A face-specific impairment

Most patients with of prosopagnosia complain of difficulties in object recognition, and indeed have such clear difficulties. Some of these neuropsychological patients have been primarily studied for their object recognition impairment, with faces merely considered as one of the visual categories that they do not recognize anymore (e.g., HJA: 70; for studies on faces with this case, see e.g., 71, 72). Other patients with clear difficulties and complains at object recognition have been mainly, or even exclusively, studied with face stimuli; and these patients have been described primarily as cases of prosopagnosia (e.g., 58, 62, 63, 73). The most well known example of such a case is the patient LH, who was described eight years after his accident as having a major impairment at identifying drawings of single objects (74). Subsequently, despite important difficulties in basic level object recognition, LH was almost exclusively tested for his impairment in recognizing faces in several studies (e.g., 66, 75, 76). Unfortunately, this frequent comorbid presentation of impairment in object recognition has complicated the understanding of prosopagnosia, and of the nature of what makes faces a "special" kind of visual category.

Until recently, brain-damaged prosopagnosic patients who did not complain of object recognition problems were quite rare and insufficiently documented with respect to their ability (and speed) at recognizing nonface objects (e.g., 60, 77-84). Some years ago, we came across such a case, the patient PS. Her case is worth being reviewed specifically in the following section, because she has been studied extensively since 2000, and has proved to be a particularly inspiring case for understanding the issue of face-specificity of prosopagnosia and the neuro-functional aspects of face perception in general. Her case will also be referenced later in this paper, in particular in the last section.

4.1.1.1. PS, a case of pure prosopagnosia

Following a dramatic head injury in 1992, PS (female, born in 1951, first reported in 85) complains of a severe impairment in face recognition in real life, with no difficulties at recognizing other visual objects, whether they

are living or nonliving things. Despite extensive posterior brain damage (85, 86), PS has no impairment in language, motor behavior, verbal or visual memory, or intelligence. She has a small left paracentral scotoma, her visual acuity is below normal range but reasonably good, and her color perception is also in the lower normal range (86). She recovered so well from her accident that she went back to work in a kindergarten classroom the following year. PS is independent in all aspects of her life except driving (due to the scotoma), and she has kept a very rich social life. PS also claims that before her accident she was exceptionally good at face recognition, but that her impairment was now causing all sorts of problems in real life. Her case has now been reported in more than fifteen scientific papers that have documented the severity of her face recognition impairment. In short, PS is massively impaired at recognizing famous or personally familiar faces (85, 87; experiment 5). Her impairment with faces relative to controls can be observed in both accuracy rates and speed, even in the simplest simultaneous face matching task (85, 87, 88). Personally, I have also been able to observe PS' face recognition impairment in real life circumstances many times, and there are numerous anecdotes from her and her family about highly familiar people that she did not recognize when meeting them in unexpected contexts.

In contrast to her severe impairment in face recognition, PS never complains of object recognition difficulties. Her relatives, the clinicians or the experimenters never noticed any problem of object recognition in real life circumstances. One of the first tests that we asked her to do was to name loud, as accurately and rapidly as possible, the full list of the 260 coloured drawings of Snodgrass and Vanderwart (89). Although some of the drawings were not always easily recognizable ("old objects"), PS performed this task extremely well, making no mistakes and rapidly naming each object in turn (85).

4.1.1.2. Discriminating visually similar items is not the issue in prosopagnosia

Despite such observations, claiming that PS has a *pure* form of prosopagnosia requires more. Indeed, the most well known, or perhaps the only, alternative view to the face-specific account of prosopagnosia is the hypothesis that *prosopagnosia is a general impairment at recognizing items belonging to visually similar categories* (56-58). For instance, the patients of Damasio and colleagues (56) were unable to recognize their own car among other cars in a parking lot. Beyond anecdotal evidence, Gauthier *et al.* (58) reported increased error rates and response times in a delayed forced-choice matching task for two prosopagnosic patients when the similarity of the distractor to the target item increased. Unfortunately, this latter study has significant methodological limitations, the most serious being that the patients had large difficulties at basic level object recognition to start with. Moreover, the data of this paper does not support the authors' claim (see 90).

Given her normal basic-level object recognition, PS was an ideal case to test the visual similarity account of prosopagnosia stringently. Contrary to this hypothesis, PS

was able to discriminate exemplars of nonvisual categories as accurately and rapidly as age-matched controls (e.g., cars, birds, boats, houses, in 85, 88; see also 87). This observation is even more remarkable considering that the patient has a small scotoma and a lower visual acuity than normal controls (86). Hence, in principle, her performance should be compared to brain-damaged controls matched in terms of visual acuity and visual field (for videos of PS recognizing visually similar shapes such as fruits and vegetables, or arbitrary shapes in a video memory game, see http://face-categorization-lab.webnode.com/).

Most importantly, we subsequently tested PS in a series of delayed forced-choice matching tasks in which the similarity of the distractor to a target was parametrically manipulated. Whether she was tested with single geon shapes, nonface artificial objects from living or nonliving categories, or photographs of a well-known category (cars), PS did not show increasingly less accuracy or correct RTs with increasing levels of visual similarity relative to controls (90; Figure 5a). In contrast, when performing the same task on *faces*, a task that was easier for normal controls, PS was impaired relative to controls even when the target and distractor faces differed maximally (Figure 5b; 90).

4.1.1.3. Generalization

These observations were replicated recently with two other prosopagnosic patients with right unilateral damage, GG (91) and LR (92; a case reported previously by Bukach *et al.*, (93)). These two patients presented with normal object recognition and showed preserved fine-grained discrimination of nonface objects (but not faces). These observations show that the account of prosopagnosia as concerning the general recognition of visually similar items is incorrect (see also 94). Rather, in rare cases, the impairment in visual recognition can be limited to faces and is not particularly increased when similarity between members of a visual category is increased. Interestingly, these three patients all presented with distinct patterns of brain damage, an issue that will be discussed in section 5.

4.1.2. An impairment in visual perception

Following the classical distinction of the visual agnosias by Lissauer (95), both *aperceptive* and *associative* forms of prosopagnosia have been defined (60, 96). While patients with aperceptive prosopagnosia would be unable to build a proper percept of a face, patients with associative prosopagnosia would be unable to match a correctly perceived representation to stored representations in memory. However, this distinction between a perceptual and a mnesic form of acquired prosopagnosia is not clear-cut: when properly tested (i.e., measuring response times in addition to accuracy rates), even so-called pure associative cases of prosopagnosia appear to have deficits at deriving a full perceptual representation of an individual face. Hence, they usually perform below normal range at matching different pictures of unfamiliar faces. Or, when they perform within normal range, they use extremely slow and painstaking strategies (66, 73, 93, 97, 98). Thus, while it is well acknowledged that low-level sensory deficits cannot explain prosopagnosia (99, 100), prosopagnosia can be
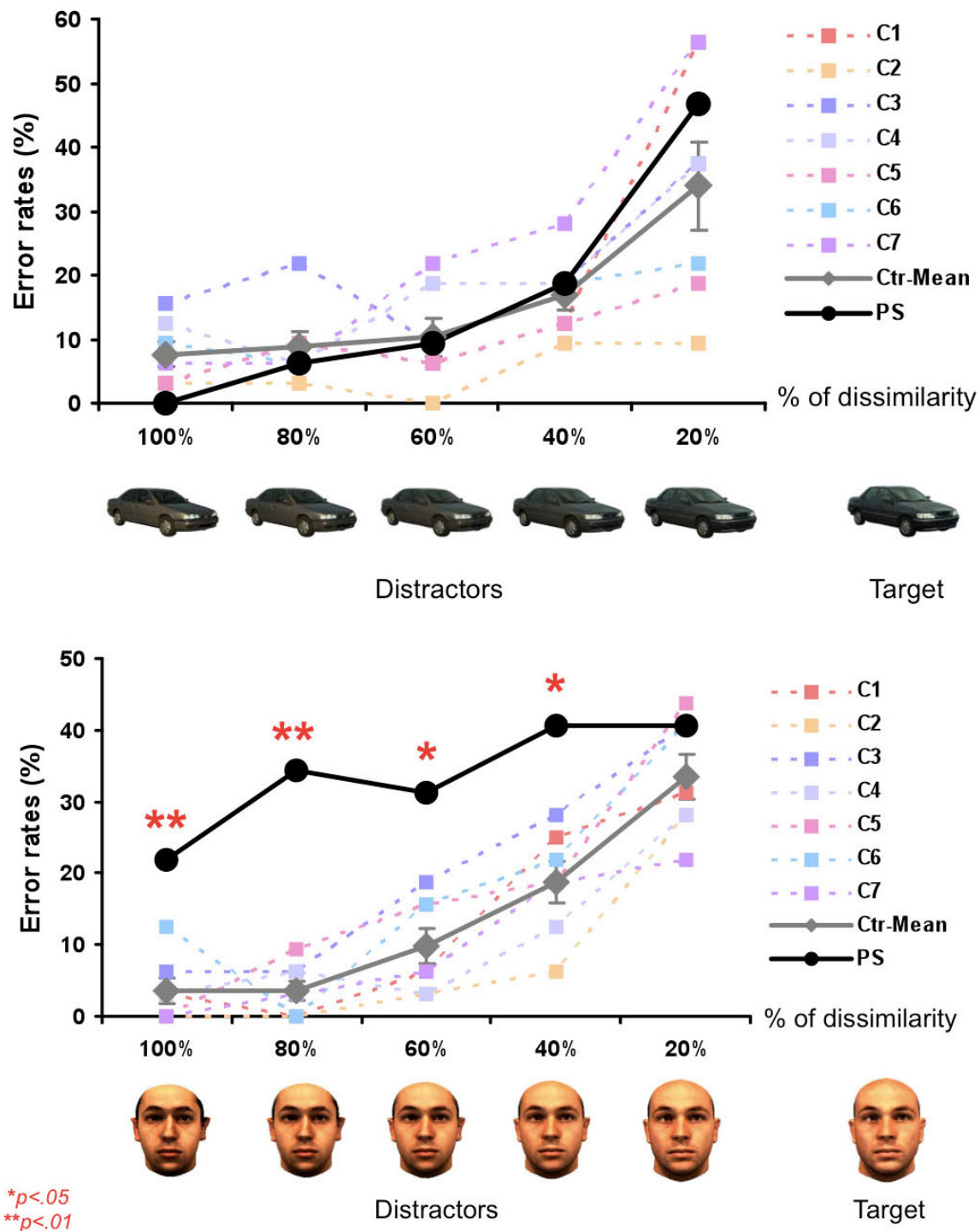
Figure 5. Percentage of error rates at a delayed forced-choice matching task performed by the prosopagnosic patient PS and seven age-matched control participants (adapted with permission from 90). Top: with nonface objects, error rates increase progressively as the similarity between a target and its distractor increases parametrically. Performance of the patient is undistinguishable from the control participants, at all levels of similarity tested. With faces (below), the patient is impaired even at the easiest level of discrimination. Note that on average, discriminating car pictures leads to more errors than discriminating faces in normal controls, while the opposite is observed for the patient. The same pattern is observed in correct RTs (90) and for other patients with prosopagnosia (91, 94). These observations rule out a simple account of acquired prosopagnosia in terms of a general defect at discriminating visually similar items.

defined as a deficit of face *perception*. While patients with prosopagnosia can usually classify a visual stimulus as a face ('face detection', see 101) they cannot build a full percept of an individual face, an impairment that is inevitably associated with the inability to recognize faces[3].

4.2. Prosopagnosia as an impairment in holistic perception of individual faces

As mentioned above, a common view is that a number of patients with prosopagnosia have difficulties in a form of holistic/configural perception (63-68, 82). This is indicated by several markers: their reduced or abolished face inversion effect (87) composite face effect (91, 102) or other effects measuring the interactivity of processing between facial parts (63-68, 82). When they are involved in a face individualization task, it is as if these patients need to focus on each facial part in turn, in order to extract diagnostic information. Moreover, when focusing on a single part, their performance is unaffected by the whole face. Unfortunately, vastly different paradigms have been used to test this hypothesis, usually with patients who present with non face-specific impairments, making it difficult to understand the true nature of their impairment with faces (102). In order to understand the nature of the core deficit in acquired prosopagnosia, it seems important to identify and test patients with prosopagnosia who have preserved object recognition, such as PS. Let me illustrate this point by describing several observations made initially on this patient PS.

First, PS relies heavily on the mouth to individualize faces, as indicated by her response classification images (section 4) in an individual face recognition task (103; Figure 6). This stands in contrast to normal observers, who rely much more on the region of the eyes in the same task (103). Other patients with prosopagnosia, such as GG, LR and others, also appear to rely and fixate more on the mouth than on the eyes when they have to individualize faces (91, 93, 104). To account for this behavior, we proposed that difficulties in processing information around the eye region is not due to local information contained in this region. Rather, we suggested that this difficulty results from an impaired ability to integrate *simultaneously* the numerous pieces of information provided by this region of a face (e.g., pupils, eyelids, iris, eyebrows, distance between eyes, distance from nose and forehead) into a single representation. That is, there is impairment in holistic/configural face perception, which results in a reduced diagnosticity of the eye region for these patients. Consequently, there is a relative increase of diagnosticity of a more isolated part in the face, the mouth region (103-105; see also 106, 107).

Second, the pattern of eye gaze fixations during a personally familiar face recognition task revealed a striking contrast between the patient PS and an age- and gender-matched control who was also familiar with these faces (children of the kindergarten). In the familiar face recognition task, the normal observer focused on the center of the face, slightly below the eyes, i.e. outside of any specific part of the face (Figure 6A from 105). This fixation location is typical of normal observers when they are involved in face recognition tasks (13, 108). Most importantly, taking into account in resolution and sensitivity from the fovea toward the periphery, the central point below the eyes is the optimal fixation to recognize faces for an ideal observer that does not fixates local regions with maximal information but *integrates information optimally across the whole face* (13; Figure 6B). In this context, it is particularly informative that the prosopagnosic patient PS avoided this fixation location completely and rather focused exactly on each of the three main facial face parts (mouth, left eye, right eye; Figure 6A), as an observer using local information only would do. I consider this figure as one of the clearest representations of the contrast between a holistic/configural (typical observer) and an analytical (PS) way of perceiving individual faces.

The third observation was inspired by this pattern of eye gaze fixations, which prompted the application of gaze-contingency to face perception (109; see also 110). With gaze-contingency, one can selectively manipulate the field of view online, that is, when the patient is engaged in an individual face matching task. Relative to normal observers, reducing the field of view to one part of the face (i.e., the fixated part), did not affect much PS' performance in that task as compared to when the face was presented in full view: the patient behaved as if she was processing the face part-by-part even when the full face was available (Figure 7). In contrast, selectively masking online the fixated facial part promotes holistic/configural perception: one has to use the information that is outside of the fixated part to perform the task[4]. In these conditions, PS' performance relative to control observers dropped dramatically (Figure 7): despite no visual field defect in the periphery she was almost unable to use information outside of fixation. Strikingly, this better performance for the local window as compared to the mask condition relative to normal observers has also been found both with the patient GG (111) and LR (92).

Taken together, these observations go a long way towards clarifying the nature of prosopagnosia following brain damage: these patients have lost their ability to see the whole of an individual face at once. They have a reduced perceptual field – *the area of vision where one can extract diagnostic information* (33, 46) – and, as a result, they have to process an individual face piece-by-piece, analytically.

Can these studies help us understanding which of the two views of face perception outlined in section 3 is correct? According to the analytical view, the prosopagnosic patient would be able to process a face part-by-part, but would be unable to assemble these parts in a whole representation, at the end of the process. In contrast, in a coarse-to-fine dynamic scheme, a prosopagnosic patient is unable to refine an initially holistic, but coarse, representation: fine-grained information can only be added locally, exactly where the patient fixates. Interestingly, contrary to the coarse-to-fine holistic view, the analytical view cannot explain why some patients with prosopagnosia – those who also happen to have intact object recognition
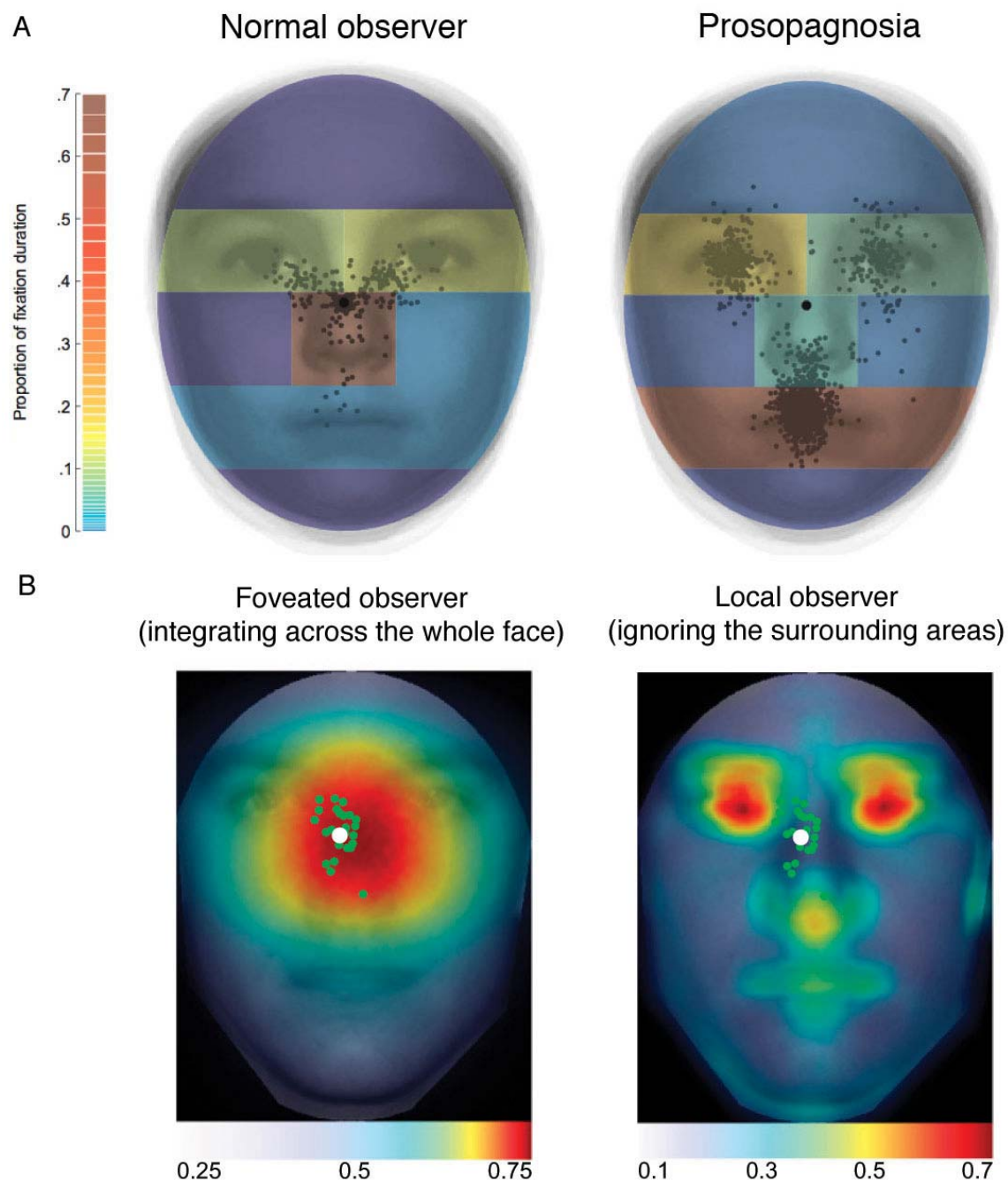
Figure 6. A. Distribution of gaze fixations during a personally familiar face recognition task for a normal observer (left) and for a well-known case of acquired prosopagnosia (PS, 85; Figure adapted with permission from 105). During face recognition, the normal observer fixates on the center of the face, slightly below the eyes, rather than on any of the specific parts of the face. This fixation location is biased towards the superior half of the face, and has been proposed as the center of mass for face recognition (105). In contrast, a patient with pure prosopagnosia (PS) who is impaired at holistic face perception fixates exactly on each part of the face, with a large proportion of fixations on the mouth (here 60%), but also exactly on each eyeball (see also 111 for a similar observation and display on the prosopagnosic patient GG). B. Images taken from (13 fig.5) and adapted with permission, showing mean fixations in a face identification task (white = group; green = individuals). The color scale indicates the predictions of fixations from two models: 1. The foveated ideal observer (FIO) on the left, taking into account the information of the whole face, weighted by the loss of spatial resolution away from the fovea; and 2. The regional ideal observer (ROI), which integrates information perfectly within the extracted region while ignoring the surrounding area. (see 13). Contrary to normal observers, patients with acquired prosopagnosia behave as "regional" observers.
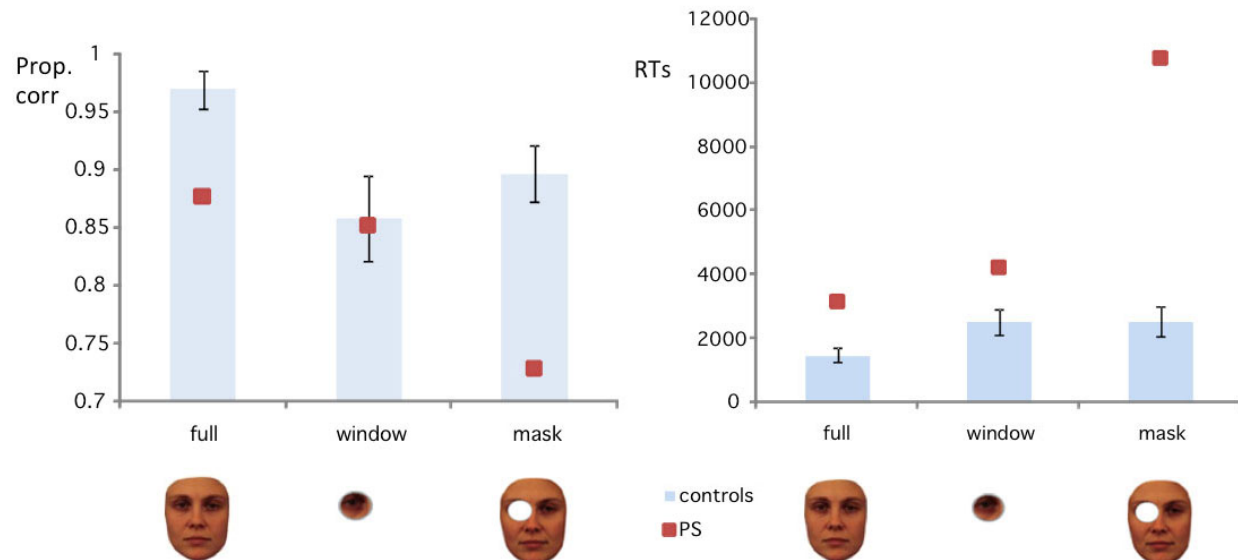
Figure 7. Performance of the patient PS and age-matched controls at a delayed matching task in which a target and a distractor were either full faces, or a gaze-contingent window revealing only the part at fixation ("window" condition) or a gaze-contingent mask of the fixated part. The task was easy enough for the patient (i.e., at a satisfying performance level) for full faces, allowing testing of the effect of the gaze-contingent mask and window. Contrary to normal observers, PS performed much worse in the mask than in the window condition, as if she was unable to discriminate individual faces when the fixated part was not available (adapted with permission from 109). The exact same pattern was found if the patient and controls were moved away from the display, showing that it is the relative size of the window/mask to the face and not the absolute size that matters. Although their overall performance varies, patients GG and LR show the same pattern of performance across the three conditions (92, 111). Videos of PS performing the task in these two conditions are available at *http://face-categorization-lab.webnode.com/pictures/*.

like PS – can still process a generic face holistically. More precisely, while patients who suffer from general forms of visual agnosia or integrative visual agnosia may have troubles even at this level (112), detecting a face in a generic Mooney or Arcimboldo pattern is not a problem for patients like PS: a coarse representation is entirely sufficient (91, 101).

For these reasons, I would like to argue that the study of patients with prosopagnosia favors a coarse-to-fine rather than an analytical view of face perception in the human brain. That is, the patient is able to derive an initial holistic percept at a coarse level of resolution but is unable to refine this percept as a unit (i.e., simultaneously across the whole face): the necessary refinement for individualization can only be done locally, part-by-part (Figure 8).

Thus, by studying the negative side of an expert process, i.e. patients who have lost their expertise at face recognition, we can infer that extracting detailed, independent face-like parts may not be how the *normal* brain processes faces, and that such a process does not lie at the heart of our visual expertise with faces.

According to this framework, the cause of (pure) prosopagnosia is neither a defect of holistic visual perception, nor a defect of fine-grained analysis of visual stimuli. Some of these patients may still perceive a generic face holistically, such as a Mooney face, and they also show normal global-to-local interference effects, for

instance, using Navon hierarchical stimuli (94, 101, 113). The same patients may still be able to extract local details to discriminate highly similar nonface items. Rather, the cause of their prosopagnosia lies in the combination: they cannot see a face holistically at a sufficiently fine-grained level of resolution, and this "holistic fine-grained process" is necessary for faces only.

According to this view the extraction of a detailed holistic face representation in the normal brain is accomplished because of a template-based matching between the incoming input – which can be degraded or masked – and an internal face representation. This internal face representation, the "schema", exists at multiple spatial scales, but is always of a whole integrated face. The input initially fits with the schema at a very coarse level, and the resulting percept ("a" face) is dynamically refined into an individual face. Therefore, in this framework, the ultimate cause of prosopagnosia should not be defined in terms of perception or memory. The ultimate cause is that the balance of the system is disturbed due to brain damage: the internal holistic face representation, the template, becomes noisy so that the incoming input cannot be registered with the template sufficiently well to individualize the face. Because this holistic template is necessary to build an integrated, i.e. holistic, percept of an individual face, the failure to register with the template reduces the perceptual field and forces a part-by-part analysis to individualize the face (Figure 7). This alternative part-by-part analysis is not achieved by face-selective processes.

Typical observer

Prosopagnosia
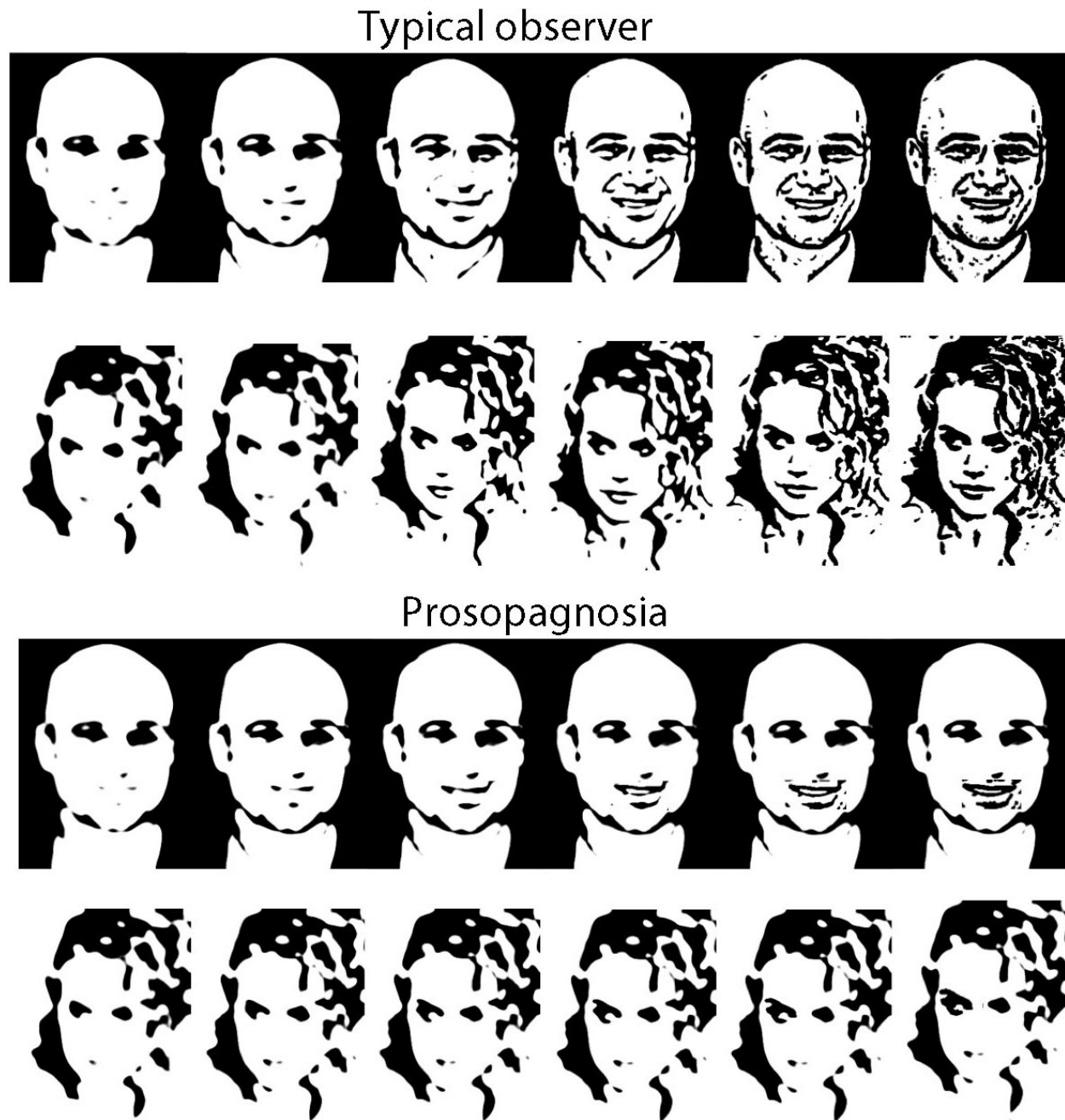
Figure 8. Schematic representation of the hypothetical perception of a face by a typical observer, for whom the initial global face percept is refined simultaneously across the whole face, in order to be able to recognize the individual face (here Andre Agassi and Nicole Kidman). The patient with pure prosopagnosia can see the whole coarse face initially, and is thus able to perform face detection. He/she is also able to extract fine-grained information, but has to do it part-by-part, at fixation (here the mouth for Agassi's face, and the right eye for Kidman's face). This figure was made by Thomas Busigny.

Interestingly, this is a view that the German neurologist Lissauer (95), who introduced the distinction between aperceptive and associative visual agnosia, already considered at the end of his famous report: "I consider purely associative visual agnosia to be a contradiction in terms. It is necessary at this point to limit the strict division which has been made so far between aperceptive and associative functions. We have defined apperception as that function which enables us to give information about the differences between sensory impressions. When simple stimuli are concerned it is easy to think of apperception as independent of the associative processes necessary for recognition. However, this way of thinking poses problems where complex stimuli are concerned … Detailed

differentiation of complex stimuli and their overall comprehension is much facilitated by the linkage of the content of what has been perceived with various associative notions. I touched on this in the discussion of form perception when I cited the example of the minimal yet so obvious difference shown by the pictorial representations of two human figures, who differ only in their facial expressions. Of course the relevant details have first to be perceived before the associative ideas can ensue. These associations are necessary to bring to the percept the full illumination of the conscious mind, thus completing their apperception. Only then it is possible to give a precise description of the percept." (1890; text in bold by the author of the present paper). To put it briefly, if an internal representation ("association") is noisy or missing, one cannot use it as a template to which the incoming face input can be applied. As a result, the face cannot be perceived as a detailed integrated whole.

I would like to make one last point in this section. Although I have argued that the core impairment in acquired prosopagnosia is identical in all patients, the degree of severity of the face perception impairment can vary substantially between patients. Moreover, there is a large amount of variability in terms of *associated* functional impairments between patients with prosopagnosia (e.g., 61, 62, 106, 114). Hence, although the core functional impairment could be identical, the study of single cases rather than of group of such patients should be recommended. Or, at the very least, when several patients are reported, the data of each patient should be reported separately. Moreover, in order to isolate and understand better what is the core deficit in acquired prosopagnosia, it seems important to identify cases of prosopagnosia with preserved object recognition.

With this framework about (dis)function in hand, let us now move to the neural basis of face perception, starting with the study of prosopagnosia.

5. THE HUMAN NEURO-ANATOMY OF FACE PERCEPTION BEFORE FUNCTIONAL NEUROIMAGING

In this section, I will describe the knowledge about the neural basis of face perception in humans from lesion studies, before the advent of functional neuroimaging in this field (i.e., before 1992).

5.1. The neural basis of prosopagnosia
5.1.1. Right hemisphere dominance
Despite the relative rarity of this disorder[5], a number of detailed anatomo-clinical studies of patients with prosopagnosia were reported before the advent of functional neuroimaging (e.g., 56, 59, 115, 116). Among the most important contributions of these studies of prosopagnosia is the now well-established dominance of the right hemisphere in face perception. The first systematic evidence for this association can be traced back to Hecaen and Angerlergues (117)'s insightful observation that a majority of cases of prosopagnosia presented with *left* visual defects, in particular in the *superior* visual field

(left quadrantanopsia; 117; see also 116, 118). This clinical observation suggested a prevalence of right inferior lesions of the occipital lobe as a cause of prosopagnosia; these lesions extending posteriorly to the primary visual cortex and optic radiations in a number of cases, thus causing these associated visual field defects. While the necessity of a right hemispheric lesion to cause prosopagnosia was never questioned, the notion that the right unilateral lesion *alone* could cause prosopagnosia was challenged until the mid-eighties (56). However, the bilateral view of prosopagnosia advocated by Damasio and colleagues has been contradicted by numerous cases reported since then with a unilateral right hemispheric lesion (e.g., 60, 62, 68, 119: cases 1 & 2; for more recent cases, see e.g., 120: case 2; 84, 121, 122; 3 cases in 63, 91). Most of these cases follow right posterior cerebral artery infarct. Furthermore, functional neuroimaging examination (PET and fMRI) performed in some of these cases has indicated a normal metabolism in the left hemisphere (62). Thus, although bilateral lesions may possibly lead to more severe impairments in face recognition than unilateral damage (106), and although an additional posterior left hemisphere lesion appears to be necessary to cause prosopagnosia in some patients (123, 124), the view that right unilateral posterior brain damage can often be sufficient to cause prosopagnosia is currently largely accepted.

Comparatively, they are only five cases of prosopagnosia with unilateral left hemispheric damage, four of them being left-handed (107, 125-127[6]). These latter cases might be accounted for by an atypical pattern of hemispheric specialization of function, perhaps related to a shift in lateralization of their language functions (128, 129; see 130 for a discussion of this issue). Thus, overall, the current evidence indicates that a right hemisphere posterior lesion is *sufficient* to cause prosopagnosia, and is *necessary* in right-handed people.

5.1.2. A distributed pattern of brain damage
The lesions causing prosopagnosia are generally located in the right ventral occipito-temporal cortex. Classically, lesions of the fusiform, lingual and parahippocampal gyrus have been associated with prosopagnosia (56, 62, 106; Figure 9). This large region includes the collateral sulcus (separating the parahippocampal and the fusiform gyri, Figure 9), the occipitotemporal sulcus (separating the fusiform gyrus from the lateral occipito-temporal gyrus), as well as the midfusiform sulcus (separating the lateral and medial fusiform gyrus, see 131).

More recently, Bouvier and Engel (118) considered the lesion overlap in many cases of prosopagnosia and rather identified the lateral part of the right ventral occipital cortex as the primary region involved. Interestingly, this is also the location of the main lesion of the patient PS (Figures 10, 11). Transcranial magnetic stimulation (TMS) over this part of the cortex also appears to impair discrimination of individual faces (132, 133). More recently, Jonas and colleagues (134) reported a case of transient prosopagnosia following intracerebral electrical stimulation in the patient's lateral
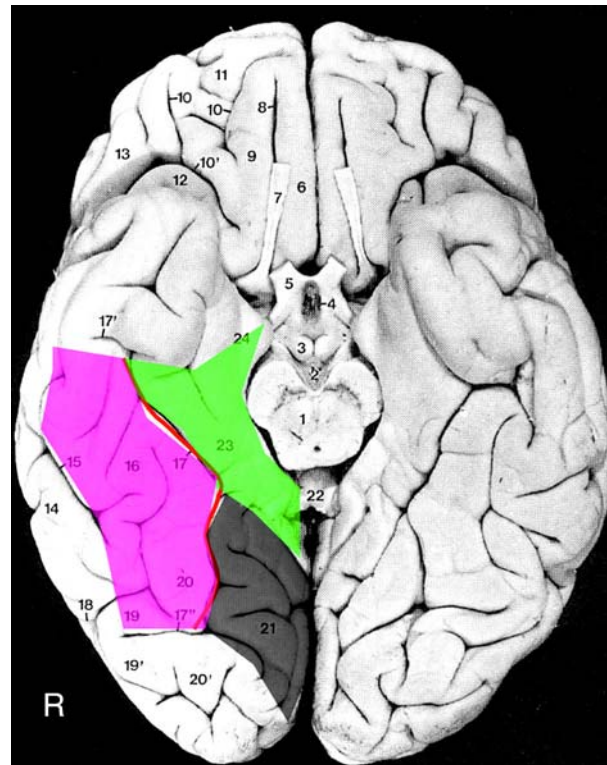
Figure 9. A view of the ventral surface of the human brain, showing in the right hemisphere the three regions where lesions have been classically associated with acquired prosopagnosia (56, 116): the lingual gyrus (dark grey), the parahippocampal gyrus (green) and the fusiform gyrus (magenta), separated by the collateral sulcus (red line). These regions concern a large part of the ventral cortical surface. The cortical tissue involved is particularly large because it concerns also the collateral sulcus, the occipitotemporal sulcus and the midfusifrom sulcus.
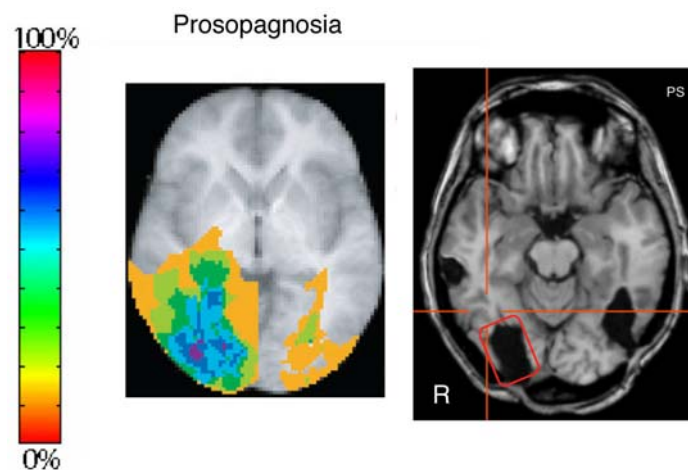
Figure 10. Left: Overlap of the lesions causing prosopagnosia in a series of 8 cases (118). Right: transversal slice showing the lesions of the patient PS, with the main lesion in the right inferior occipital cortex, corresponding to the region with maximal overlap as identified by Bouvier and Engel (118, adapted with permission). PS also has brain damage in the left middle fusiform gyrus and a small lesion in the right middle temporal gyrus (see 86 for details).

right occipital cortex (Figure 12). This observation provides more direct evidence for a critical role of this area in face perception[7]. This observation also indicates that prosopagnosia can follow the disruption of a focal region.

Nevertheless, overall, it is the variability in terms of distribution of brain lesions causing prosopagnosia that is particularly striking, with the lesions across patients covering almost all the ventral surface of the cortex, from
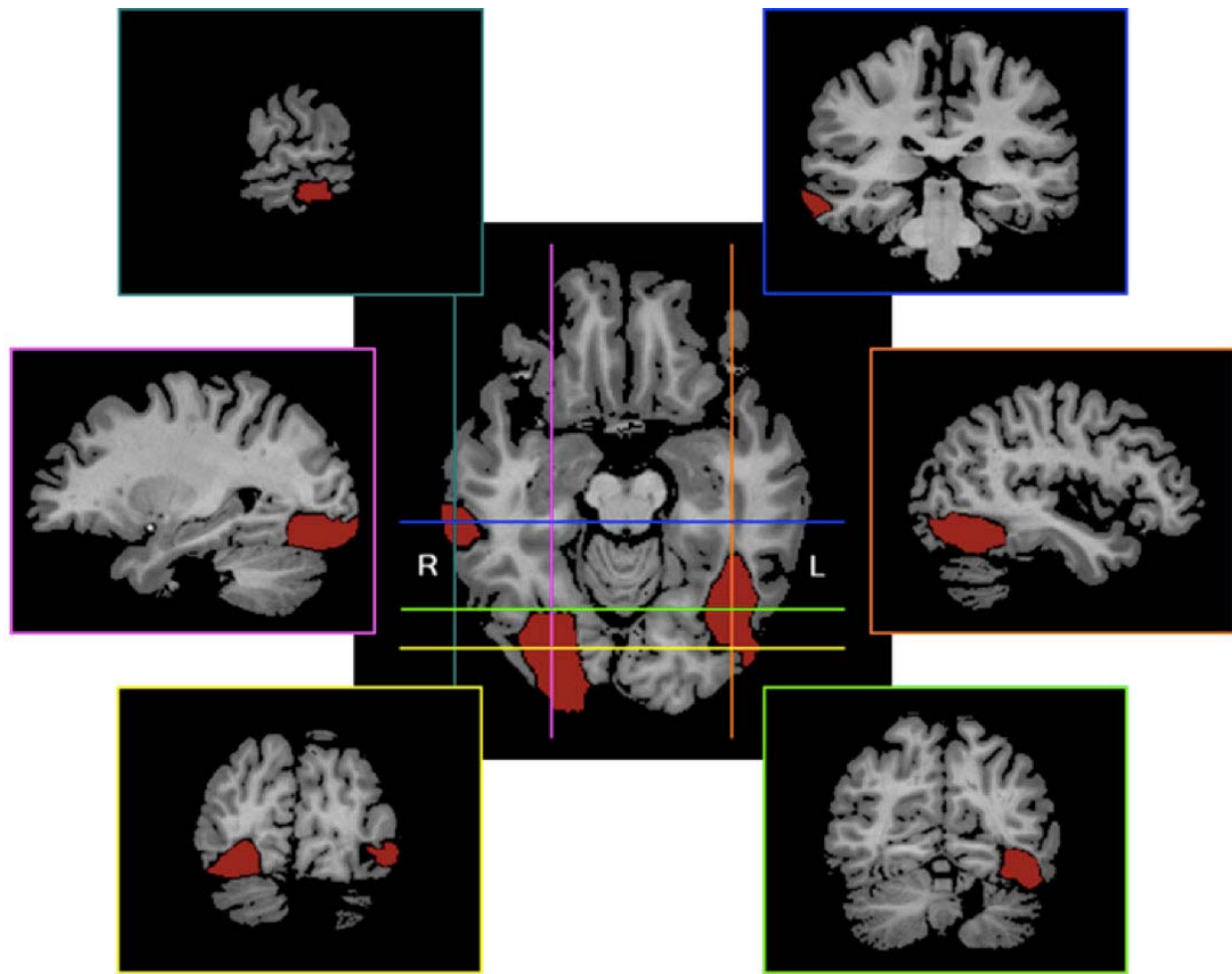
Figure 11. A detailed view of the brain damage of the patient PS, described in section 2 (adapted with permission from 86). Her lesions concern the lateral part of the right inferior occipital cortex, the left middle fusiform gyrus, a small lesion in the right middle temporal cortex and damage to the cerebellum. It is remarkable that despite extensive brain damage, this is a patient who shows severe prosopagnosia with preserved object recognition.

the occipital pole to the temporal pole, with a clear right hemispheric dominance (Figures 10, 13, see e.g., 62, 106).

Despite some regions being more critical than others, for instance the lateral part of the ventral occipital cortex of the right hemisphere, it is virtually impossible to identify a single cortical region that is damaged in all or most cases of prosopagnosia. Such a variable pattern of brain damage suggests that face perception depends on a wide network of regions, with many areas and their connections being essential components of the normal face perception system (85, 135).

However, it is particularly interesting that different patterns of brain damage have not been clearly associated with different functional impairments. For instance, it has been argued that perceptual contribution to prosopagnosia is greater when the lesions concern the posterior rather than the anterior sections of the ventral temporal cortex (62, 106). Yet, even a patient like LR, whose lesion concerns essentially the right anterior temporal lobe, presents with a prosopagnosia that qualitatively resembles cases of prosopagnosia with more posterior lesions, such as PS and GG (section 4, 92). While such observations may seem puzzling, they may in fact be quite informative, suggesting that the function of the face perception system should be understood as a whole rather than attempting to dissect it into components that may not have a meaningful function when considered in isolation. Unfortunately, the functional neuroimaging enterprise in this field of research, that we will overview next, has so far taken little notice of these clinical observations.

6. NEUROIMAGING STUDIES OF FACE PERCEPTION IN THE HEALTHY BRAIN

In this section, I will try to summarize the contributions of the functional neuroimaging studies of face perception carried out in the normal brain, in particular the identification of several small areas in the visual ventral
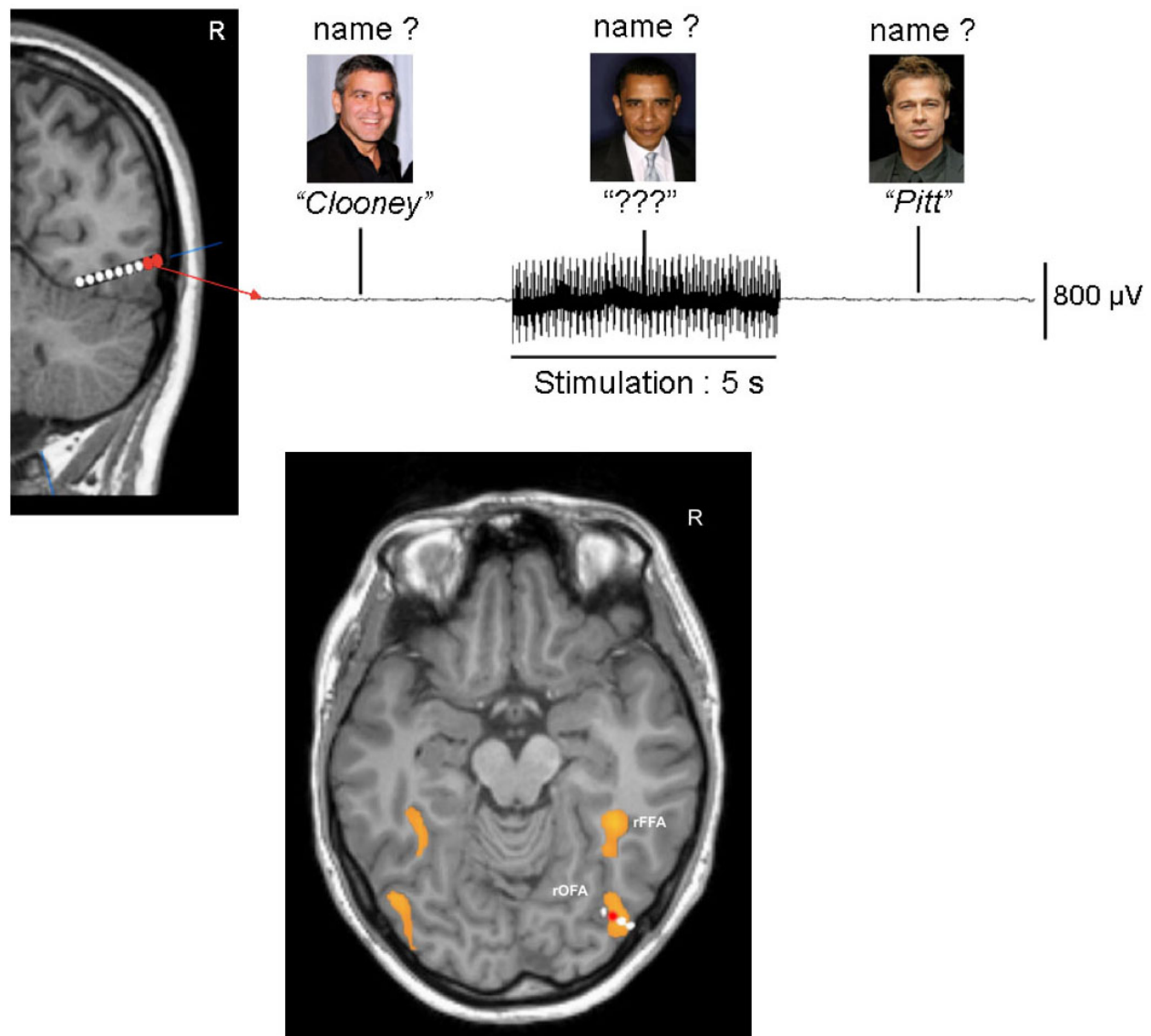
Figure 12. A case of prosopagnosia following focal cortical electrical stimulation (adapted with permission from 134). This epileptic patient – who had normal face recognition as assessed by neuropsychological tests - was electrically stimulated in the right inferior occipital cortex, a region where face-selective responses were observed both in fMRI ("occipital face area", see section 4) and ERPs (N170, 318, 323 for review). During electrical stimulation of this region only, and only for faces, the patient failed to recognize famous faces that she was able to recognize without stimulation. Videos are available at *http://face-categorization-lab.webnode.com/products/patient-kv-famous-face-recognition-pictures-/*

stream that respond preferentially to faces, to which I will refer extensively when discussing the functional neuroimaging studies of brain-damaged cases of prosopagnosia in the last section of this paper. I will first start by providing a little bit of context from the studies of face perception in the nonhuman primate brain and intracerebral electrophysiological recordings in the human brain.

6.1. The context

The second (historically) source of information regarding the neural basis of face perception comes from the study of single neurons responding selectively to faces in the monkey infero-temporal cortex (IT, 136). Ten years after this first report, single cell studies performed during the 80's reported large proportions of face-selective neurons in the monkey IT (e.g., 137-141; for more recent studies see e.g., 19, 142, 143; and the historical and comprehensive review of Weiner and Grill-Spector (144)). Specifically, face-selective neurons were found in concentrations of 10%-20% in many cytoarchitectonically defined areas of the upper and lower banks of the superior temporal sulcus, in the monkey infero-temporal cortex (141, 144).
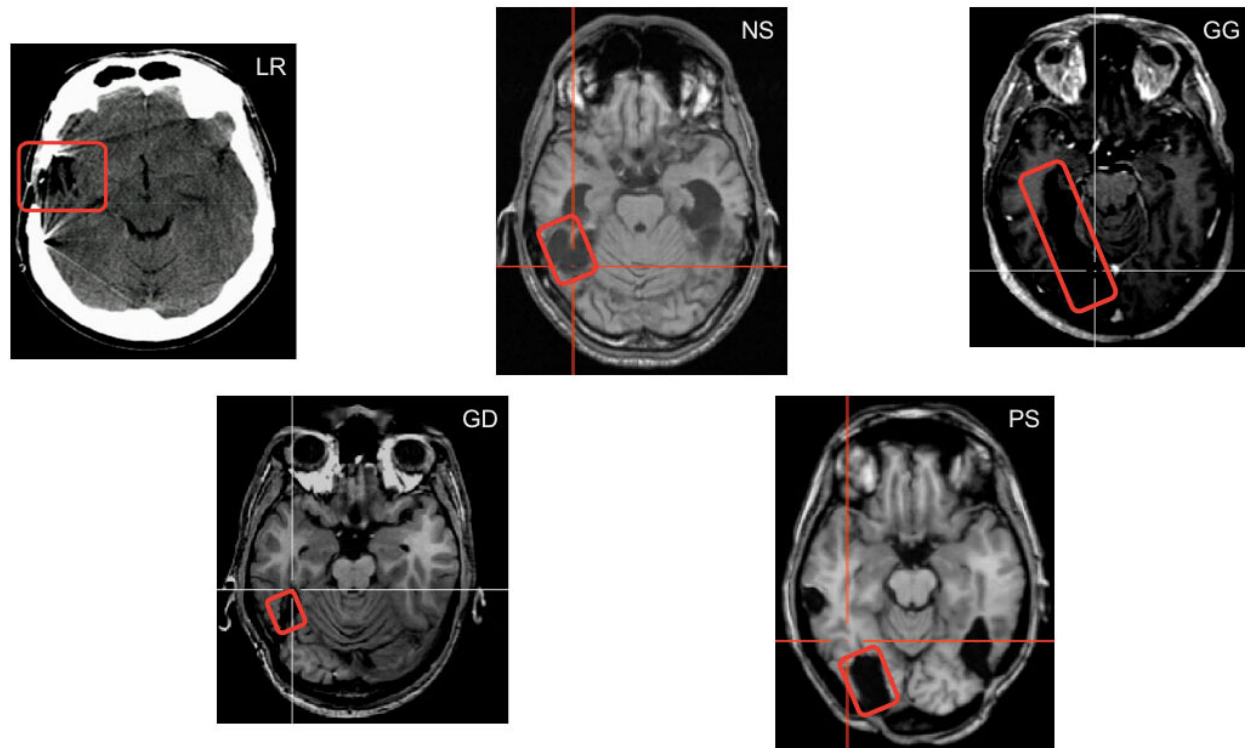
Figure 13. Example of the variability of brain damage leading to prosopagnosia in five cases with the main, or only, lesion highlighted (in the right hemisphere). PS (trauma with multiple hemorrhages), GG (stroke) and LR (trauma) present with pure prosopagnosia and have been reported in several papers. NS has bilateral damage following trauma, and has a general form of visual agnosia, with impairment at both face and object recognition (73). GD presented with a prosopagnosia and metamorphopsia following a small metastasis in the right middle fusiform gyrus (337).

In the human brain, the wide distribution of face perception in the human ventral occipito-temporal cortex suggested by the study of prosopagnosia received further support by the observation of largely distributed face-selective responses over the ventral occipitotemporal cortex as recorded with subdural grids of electrodes ("Electrocorticography", ECOG, 145), or depth electrodes (Stereotactic electroencephalography, "SEEG", 146), implanted in epileptic patients (Figure 14; for more recent ECOG studies, see 147 for ECOG and 134, 148 for SEEG). These studies also suggested that populations of neurons responding selectively to faces were clustered in the ventral-occipito-temporal cortex rather than being intermingled with columns responding to all object categories (149; Figure 14).

6.2. The early neuroimaging studies: a large set of areas

The first neuroimaging studies of face perception in the healthy brain were performed by means of positron emission tomography (PET; 1, 150, 151; see also 152 for an early study that used faces to dissociate the ventral and dorsal visual processing streams). These studies used perceptuo-cognitive tasks derived from a classical functional decomposition of face processing stages (153). They reported a right hemispheric dominance for face compared to object perception, in particular at the level of the midfusiform gyrus. They also reported more anterior activations in response to familiar (famous) than unfamiliar faces, specifically in the right parahippocampal gyrus (Brodmann area 36) and the anterior region of the temporal lobe, including the temporal pole (1). In their conclusions, the authors of these studies interpreted their findings in the context of prosopagnosia (1). In particular, they emphasized the large size of the set of areas involved specifically, or preferentially, for face stimuli, stating, for example: "A first conclusion concerns the large cortical volume activated during the processing of faces … Even if all the involved areas are not specific to face processing, the activated regions extend from the occipital to the temporal poles, and engage the ventro-medial parts of the brain … This extensive neuronal network underlying the processing of faces may appear disproportionate … and it may be suggested that this large cerebral space inherent in the processing of faces … is necessary for face identification to be achieved with such efficiency and apparent automaticity" (1; text in bold by the author of the present paper).

The early fMRI studies of face perception also reported widely distributed responses to faces as compared to control stimuli (scrambled faces) in the midfusiform and inferior temporal gyri, middle occipital gyri, and
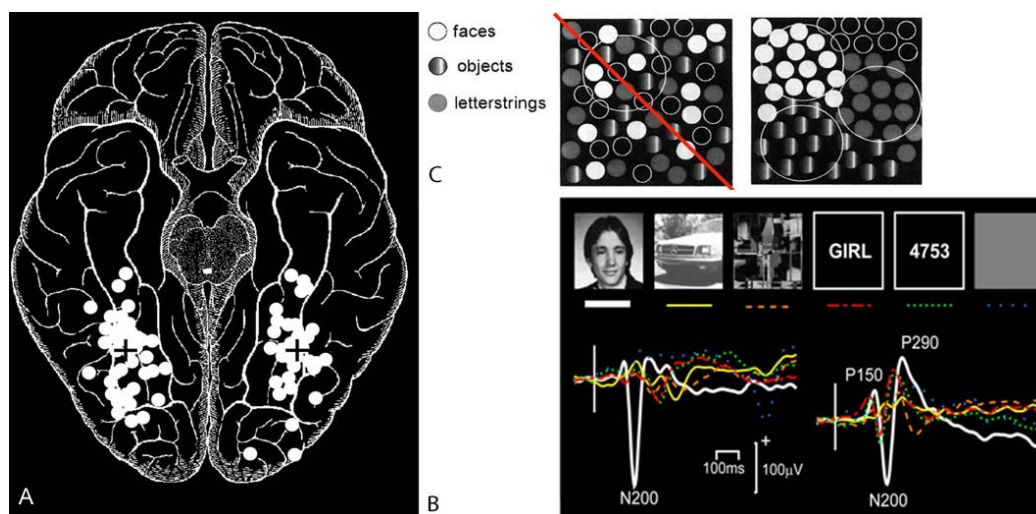
Figure 14. Figure adapted with permission from Allison *et al.* (149), showing the sites where face-selective responses (N200, in B) were observed in 99 patients implanted with grids of subdural electrodes on the ventral occipito-temporal cortex. The first reports of such electrical brain responses were made by Allison *et al.* (145) and by Halgren *et al.* (146), the latter study using depth electrodes and reporting face-selective responses (P180) in the fusiform gyrus (see also 134). C. Because the N200s were elicited exclusively for faces on electrodes that had a 2.2mm diameter, Allison and colleagues (149) suggested that cortical columns of neurons coding selectively for faces were probably clustered in the ventral-occipito-temporal cortex rather than being intermingled with columns responding to all object categories.

superior temporal or lateral occipital sulci (154, 155). Thus, the identification of a large set of brain areas involved in face perception in early neuroimaging studies fully agreed with the neural basis of prosopagnosia described above, and human electrophysiological studies.

6.3. The functional localizer approach and the FFA
 The fMRI study of Kanwisher *et al.* (156) modified this perspective in two ways. First, this study introduced the functional localizer approach in fMRI, in which one or several functional run(s) comparing the presentation of faces to control stimuli (usually pictures of objects) are presented to participants performing the same task on the two kinds of stimuli. An area responding significantly more to faces than objects in an individual brain is usually defined as being "face-selective", in analogy with the face-selective cells identified in the monkey IT[8]. This functional region of interest (ROI) can then be used in subsequent fMRI experiments to test more specific hypotheses about how faces are represented. Currently, this approach is widely used in neuroimaging studies of face perception. The second contribution of that study was to limit the conclusion to a *single* functional area across individuals, namely to the area showing the strongest face-selective response. This area, labeled the "fusiform face area" ("FFA", Kanwisher *et al.*, 1997; Figure 15; see also 157), is of a few mm³ in size, and can be localized in the right middle fusiform gyrus of individual brains. This FFA, also more rarely referred to as *FG* (for fusiform gyrus, 158), *MFG* ("Middle Fusiform Gyrus", 88) *MidFus* area or *FFA1/FFA2* (159, 160) has probably become the most well known functional area in the whole community of fMRI researchers.

The FFA has been the topic of specific reviews (161), specific methodological contributions regarding the functional localizer approach (162), and intense scientific debates (163, 164). The main debate about this area concerns its domain-specificity. Indeed, even though its preferential response to faces is undisputed, the FFA responds more weakly to object categories, and shows differences in activation between these categories (e.g., 165, 166). FFA activation increases for nonface objects of visual expertise, such as car pictures or bird pictures in car or bird experts, respectively (167, 168). These results have been taken as evidence against the domain-specificity of the FFA: the area would carry out certain perceptual processes that are important for faces but which could be potentially applied to other nonface object stimuli following expertise training, even in adulthood. However, in adults, several studies have failed to report such changes of FFA activation to nonface visual objects of expertise (e.g., 167-170).

A major problem of this debate is that it focuses almost exclusively on the FFA, as if results obtained at the level of this area could be taken as evidence for or against the domain-specificity not only of this area, but of the function in general. This limitation also applies to a number of studies that have attempted to understand the neuro-functional basis of face perception by focusing only on the FFA. This is problematic because even if the FFA is certainly a key component of the face perception brain network, there is no evidence that this area is more important for this function than other brain areas responding preferentially for faces, which will be described next.
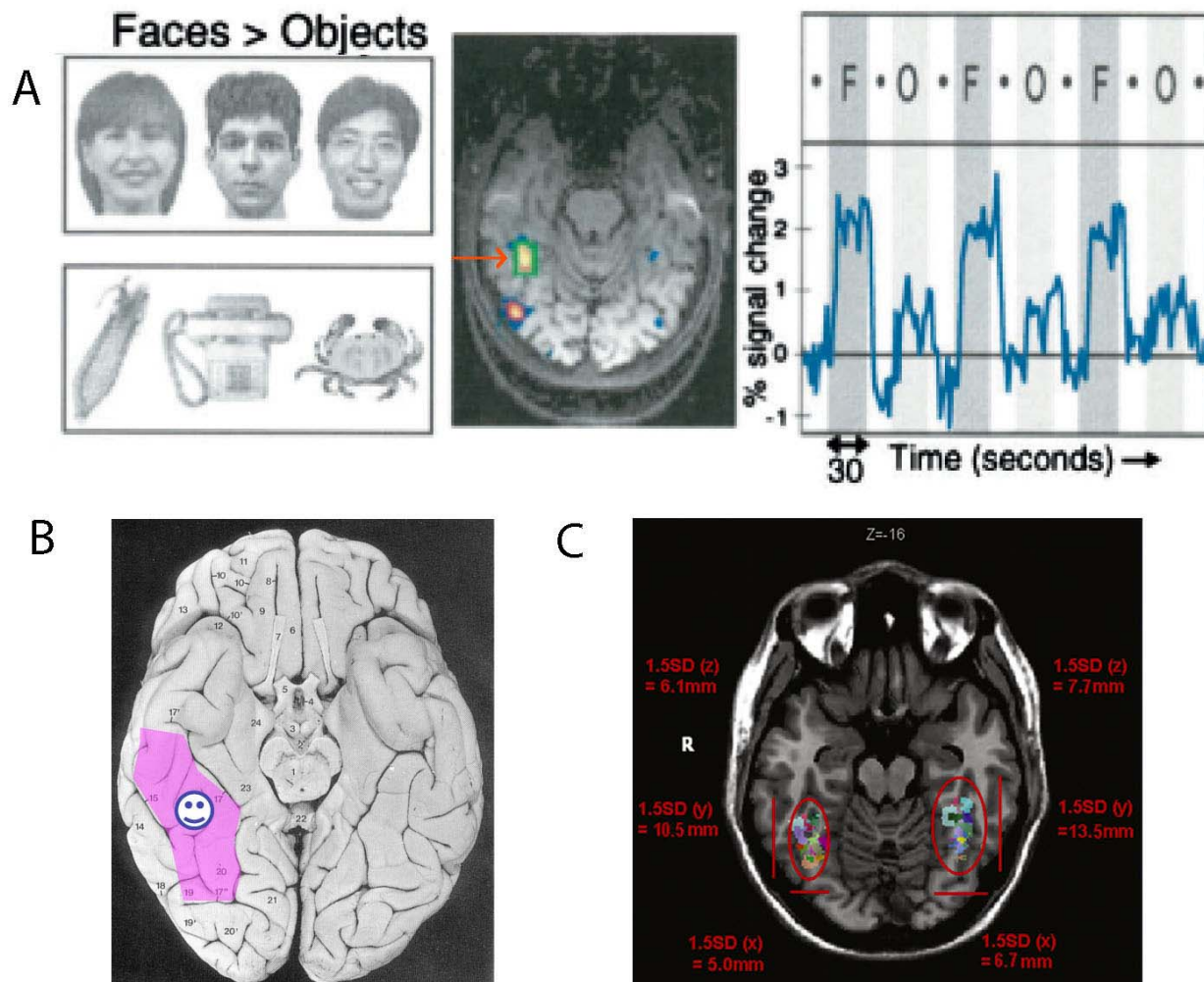
Figure 15. The right "fusiform face area", defined by Kanwisher *et al.* (156, adapted with permission) as a small cluster of contiguous voxels in the middle fusiform gyrus responding much more to faces than objects in fMRI. A. Figure adapted from the original study of Kanwisher *et al.* (156) showing the stimuli used, the region activated in a representative individual brain (right FFA indicated by the red arrow) and the magnetic signal change in this region. B. Schematic representation of the average location of the FFA on the ventral surface of the occipito-temporal cortex (fusiform gyrus in Magenta). C. Variability in localization of the individual FFAs of 36 participants (FFA defined by subtracting the response to nonface objects and phase-scrambled stimuli. Adapted with permission from (176).

6.4. The return of the network
6.4.1. A set of face-selective visual areas

In reality, despite the emphasis on the FFA in this field, the comparison of faces versus other object categories in fMRI leads to at least three bilateral spots of activation, or three face-selective areas, in both group and individual analyses. Besides the FFA, localized in the middle fusiform gyrus, there is a posterior face-selective response in the lateral part of the inferior occipital cortex (IOG or "occipital face area", OFA; 167), and an area in the posterior part of the superior temporal sulcus (pSTS; 171) (Figure 16a). Hence, as pointed out early on, the FFA needs *"a little help from its friends"* to perform its job in face perception (172). According to the model of Haxby and colleagues (173) (see also 174, 175), these three areas form the 'core' system for face perception, providing inputs to an extended system, i.e. to temporal and prefrontal regions involved in emotional and semantic processing associated with person recognition (Figure 16b). Importantly, these three areas, which are bilateral but present a strong right hemispheric dominance on average (176), are defined functionally (faces *vs.* object categories; or *vs.* scrambled faces, preserving all low-level visual features of face stimuli): they are located outside of the retinotopic visual cortex and their borders are not defined anatomically (177; although see 160). They also present a large inter-individual variability in terms of location, spatial extent, and hemispheric dominance (176: Figure 15c).

6.4.2. Extending the core set of areas
6.4.2.1. The right temporal pole, precuneus and prefrontal cortex

Beyond the three functional areas mentioned above, face-selective responses in fMRI have also been
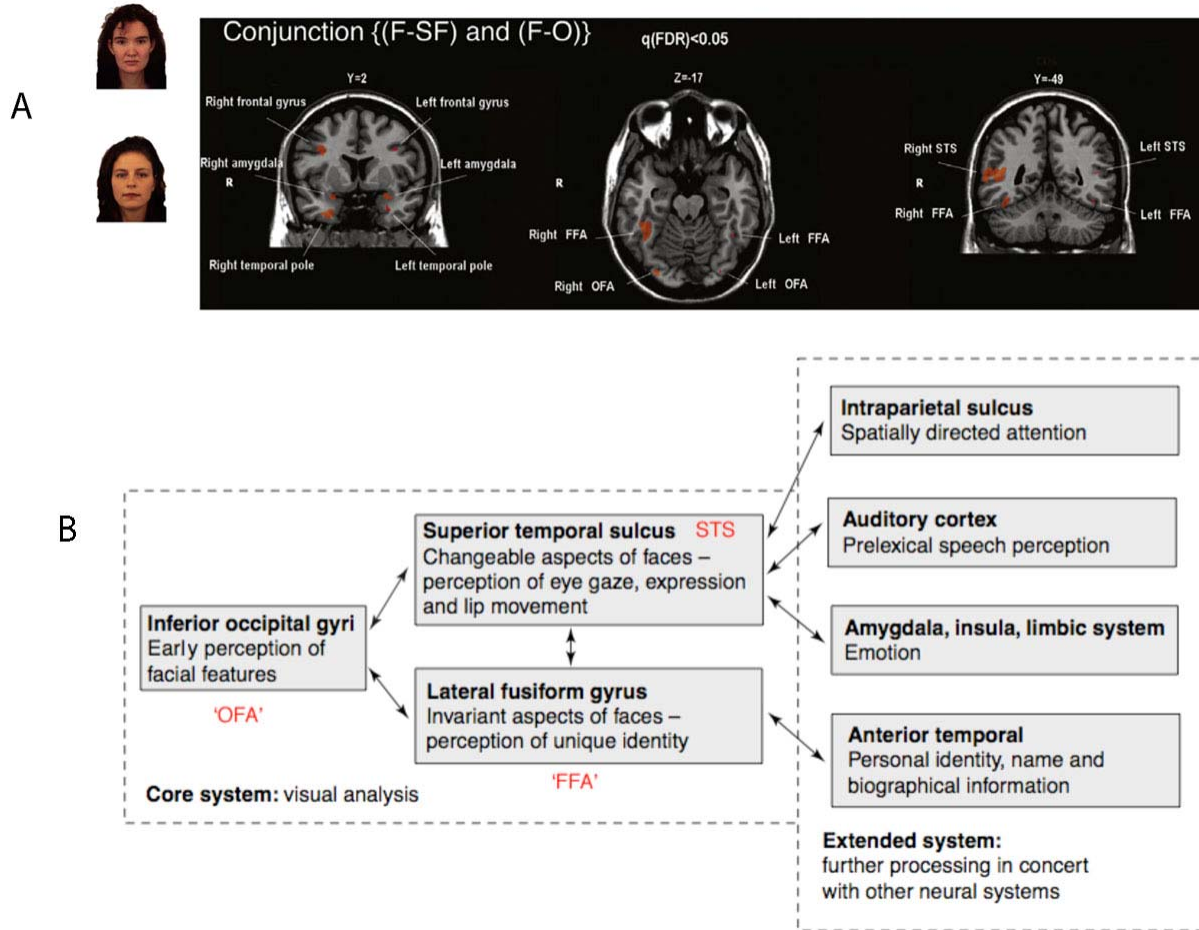
Figure 16. A. Whole-brain (group) analysis of a large number of subjects (N=36) presented with faces, scrambled faces and objects (cars) (adapted with permission from 176). Even though the group analysis only reveals the overlapping face-selective clusters in (normalized) individual brains, many face-selective-clusters are recorded throughout the brain (here FFA, OFA, pSTS, amygdala, temporal pole, prefrontal cortex, all with a right hemispheric dominance). B. Haxby *et al.* (173)'s neuro-functional model of face processing, postulating a hierarchy of face-selective areas with a core system of three areas (FFA, OFA, STS) being involved in deriving a face percept (Adapted with permission from from 173).

reported in the temporal pole, or the anterior section of the infero-temporal cortex (AiT), again with a robust right hemisphere advantage (176, 178). Either this region is not covered in conventional fMRI studies of face perception, or the signal in this area suffers from magnetic susceptibility artefacts, preventing the disclosure of face-related activations. It is a region whose role in face recognition is well known from lesion studies (section 5) and studies of patients with the right variant of fronto-temporal dementia (179). This region has also been reported in PET studies of face perception (1). Other face-selective clusters have been reported in several studies in the precuneus and prefrontal cortex, again with a right hemispheric dominance (176).

6.4.2.2. The many regions of the fusiform, STS and inferior occipital cortex

Recent fMRI studies have reported a second face-selective cluster located in between the FFA and the OFA,

in the posterior fusiform sulcus (159, 176, 180, 181). This cluster has been labeled as *FFA-1* (181), *pFus* (144, 159, 160) (Figure 17), to distinguish it from the more anterior cluster (labeled "FFA-2", "midFus" or "*aFFA*" in 180). Yet another face-selective cluster has been identified, in between the FFA and the temporal pole, in the anterior fusiform gyrus (*antFus*, 176; Figure 17). Two or even three different face-selective clusters have also been identified in the STS (176, 181), as well as two distinct face-selective clusters in the inferior occipital cortex ("OFA1", "OFA2", e.g., 176, 182). Hence, considering the whole ventral occipito-temporal cortex, from the inferior occipital gyrus to the temporal pole, at least six face-selective clusters, in addition to face-selective responses in the STS, can potentially be identified in an individual human brain. Interestingly, even if the monkey's face recognition system is certainly not as sophisticated as in humans, recent fMRI studies have also identified up to six face-selective clusters
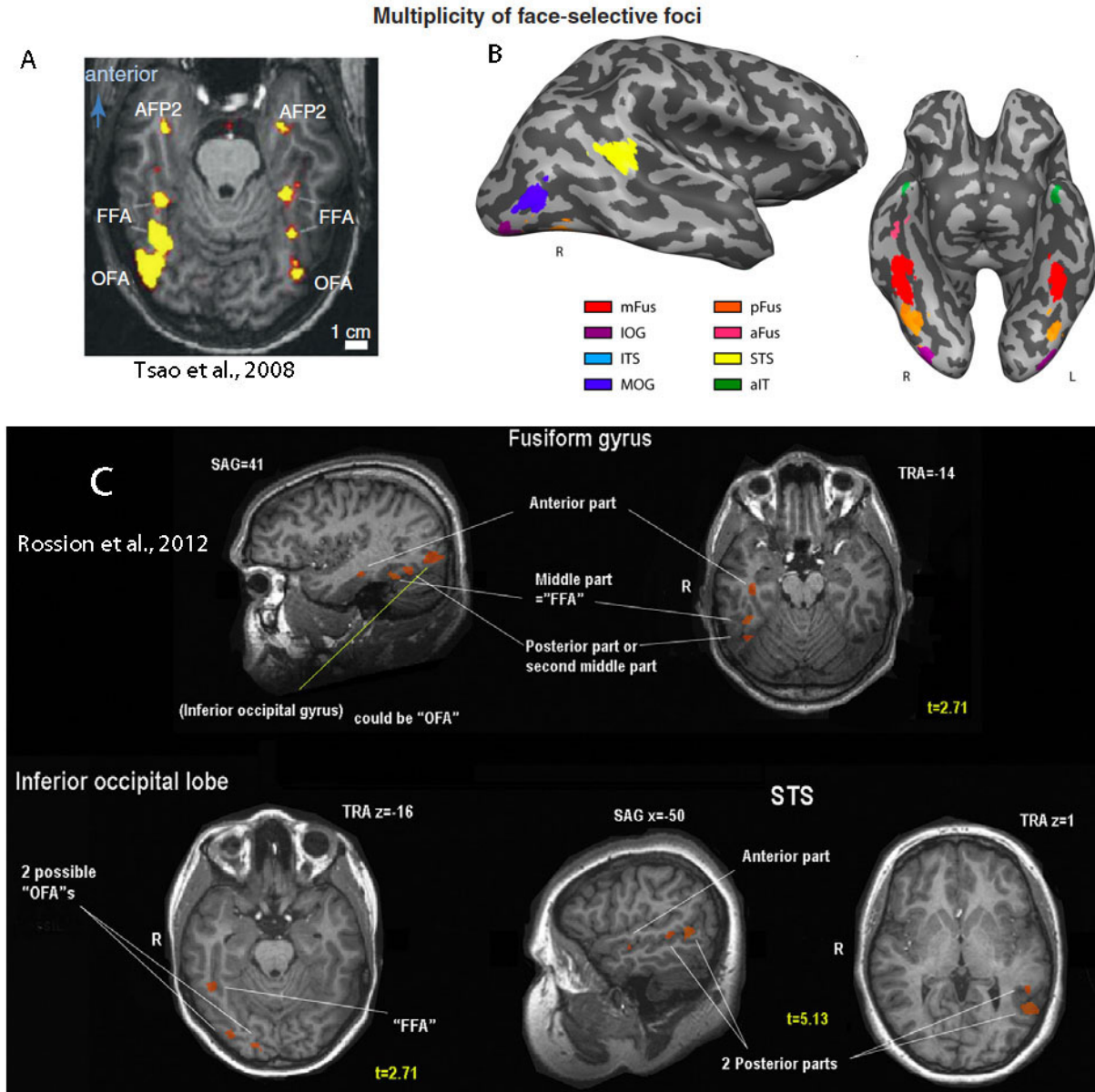
Figure 17. Figures extracted from Tsao *et al.* (183, with permission; A), Pyles *et al.* (182, with permission; B) and Rossion *et al.* (176, with permission; C) showing the multiple face-selective clusters that can be observed in individual human brains, from the inferior occipital gyrus to the tip of the temporal lobe, and also along the STS. Note that when multiple clusters are found in the occipital cortex or fusiform gyrus (A, right hemisphere), researchers are faced with the difficulty of choosing between separating or grouping these clusters (see 160, 176). Clusters that are in fact different may be both labeled "FFA" or "OFA" in different individual brains, making questionable the use of such labels (160, 176).

in the STS of the monkey brain (181, 183), and additional clusters may also be present in the monkey ventral occipito-temporal cortex (184).

6.4.2.3. How should the cortical face network be defined?

Admittedly, a majority of the recent studies that reported numerous face-selective clusters both in humans and monkeys do not use well-controlled stimuli when contrasting faces to nonface objects, so that the size and number of face-selective clusters may be exaggerated. Nevertheless, there seems to be converging evidence from several independent research groups for a large number of face-selective clusters in the human ventral temporal cortex. One may thus wonder why these numerous face-selective areas in the human brain were not identified in fMRI in the first place, and why few fMRI studies of face perception report and investigate all of these face-selective responses. There are various methodological, practical, or conceptual reasons for that. First, contrary to the initial

PET studies, some fMRI studies such as the study of Kanwisher *et al.* (156) scan only a limited portion of the brain. Second, whole brain (group) analyses identify only the face-selective clusters for which there is sufficient overlap across normalized individual brains. Whether or not spatial smoothing is used, closely located clusters are merged so that such group analyses typically report a single cluster in the middle fusiform gyrus (FFA), one in the lateral part of the inferior occipital cortex (OFA), and one in the posterior part of the STS (176). Third, individual brain analyses with conventional 1.5T or 3T scanners usually do not have the power to disclose all of the face-selective clusters at a significant level in every individual brain. This is especially the case because only one or two runs are usually used in a functional localizer to disclose these areas, the response properties of which are tested in subsequent experiments. Fourth, there seems to be a common belief in the neuroimaging community that the face-selective cluster that is activated the most is the most important for the function. For instance, at a given statistical threshold in a functional face localizer, the FFA is disclosed more consistently than other face-selective clusters, suggesting that this area is more important than other face-selective areas (156, 183). However, this could be due to many reasons that have nothing to do with the importance of this area for face perception: a larger overlap in localization across individual brains in a group analysis, larger blood vessels in the vicinity of this area, or less magnetic susceptibility artefacts in this area of the middle fusiform gyrus than in other areas. For such reasons, using the same statistical threshold to define all of the face-selective areas may not be adequate (176). More generally, functional neuroimaging cannot provide information about the respective importance of FFA compared to other face-selective areas. While some studies have reported that the FFA is the most face-selective area of the whole set (159, 183), an analysis of the response of these areas to both objects and phase-scrambled faces suggests that part of the FFA selectivity is accounted for by low-level visual cues (color and spatial frequency, 176, 185, 186) and this may not be true for other areas(176).

Another reason why most face perception fMRI studies focus on one or two cluster only is that there is a belief that each functional cluster is a brain area that has a definite function, or computational role, in a vast network of face-selective areas. According to this view, focusing on a single face-selective cluster should allow one to define its function (i.e., how it "codes" faces). At the end, one would just have to connect the nodes, or "modules" of the network, to understand the neural basis of the whole function (i.e., face perception). However, there are at least two limitations of this localizationist approach. First, given that up to six or more face-selective clusters can sometimes be identified in the ventral occipito-temporal cortex in individual brains, labeling each of these clusters is highly subjective. For instance, the region labeled "FFA" in different brains may in fact be different regions, and the "OFA" is often confused between face-selective clusters in the middle and posterior fusiform gyrus (e.g., 187, 188; fig 2; 182; see (160) for a discussion of this issue). Anatomical constraints and spatial relationships to other category-

selective responses (e.g., body parts) will have to be used increasingly to help defining regions such as the FFA across individual brains more objectively (160). Yet, it is unknown whether every face-selective cluster in the ventral occipito-temporal cortex has a specific anatomical signature (i.e., cytoarchitectony). Rather, a face-selective cluster may concern a *subset* of an anatomical area, and there is no reason to expect that all individual human brains, who can vary substantially in their expertise in face recognition (189), have the same amount of well-identified face-selective clusters in the ventral occipito-temporal cortex. Thus, although analyses performed at the individual brain level and the use of anatomical and functional constraints (e.g., selective responses to other visual categories such as body parts, 160) can help define functional face-selective clusters, it may prove difficult or impossible to objectively match all the different face-selective clusters across different individual brains. The second limitation of this approach is that a given cluster or area may not compute anything and have an intelligible function: it may simply represent faces (i.e., have a specific relation to a class of inputs of the visual world) and the process emerges from the dynamic reentrant combination of multiple representations across visual areas.

6.4.3. Neurofunctional decomposition, MVPA, adaptation and face individualization

At present, the function(s) of each of the face-selective clusters of the human brain remain(s) largely unknown, even when considering only the most consistently activated clusters, the "FFA", "OFA" and pSTS. According to Haxby *et al.* (173)'s neuro-functional model, the OFA is the first face-selective relay of information, being associated with the "*early perception of facial features*" (Figure 16). This area would feed information forward to the FFA and the pSTS for higher level processes. While the FFA would be associated with the invariant aspects of faces, in particular the perception of face identity, the pSTS would be involved in decoding changeable aspects of faces such as the perception of eye gaze and expression (Figure 16).

Overall, the role of the STS in changeable aspects of faces has been well supported, with studies showing its activation to changes of facial expressions and eye gaze direction (190-193) or to eye and mouth movements (171). Yet, the area showing sensitivity to changes of facial expression and gaze may be located more anteriorly in the STS, rather than in the face-selective pSTS area (190, 193). Other studies have also shown that the response in the pSTS, in particular, is larger to dynamic sequences of faces than static faces (194, 195).

According to Haxby *et al.* 's model (173), the OFA could be conceptualized as a sort of *face detection stage*. That is, an early area merely distinguishing faces from other object categories and sending information to higher-order areas involved in the decoding of facial identity. This face detection stage would be essentially based on the perception of the facial features/parts, such as
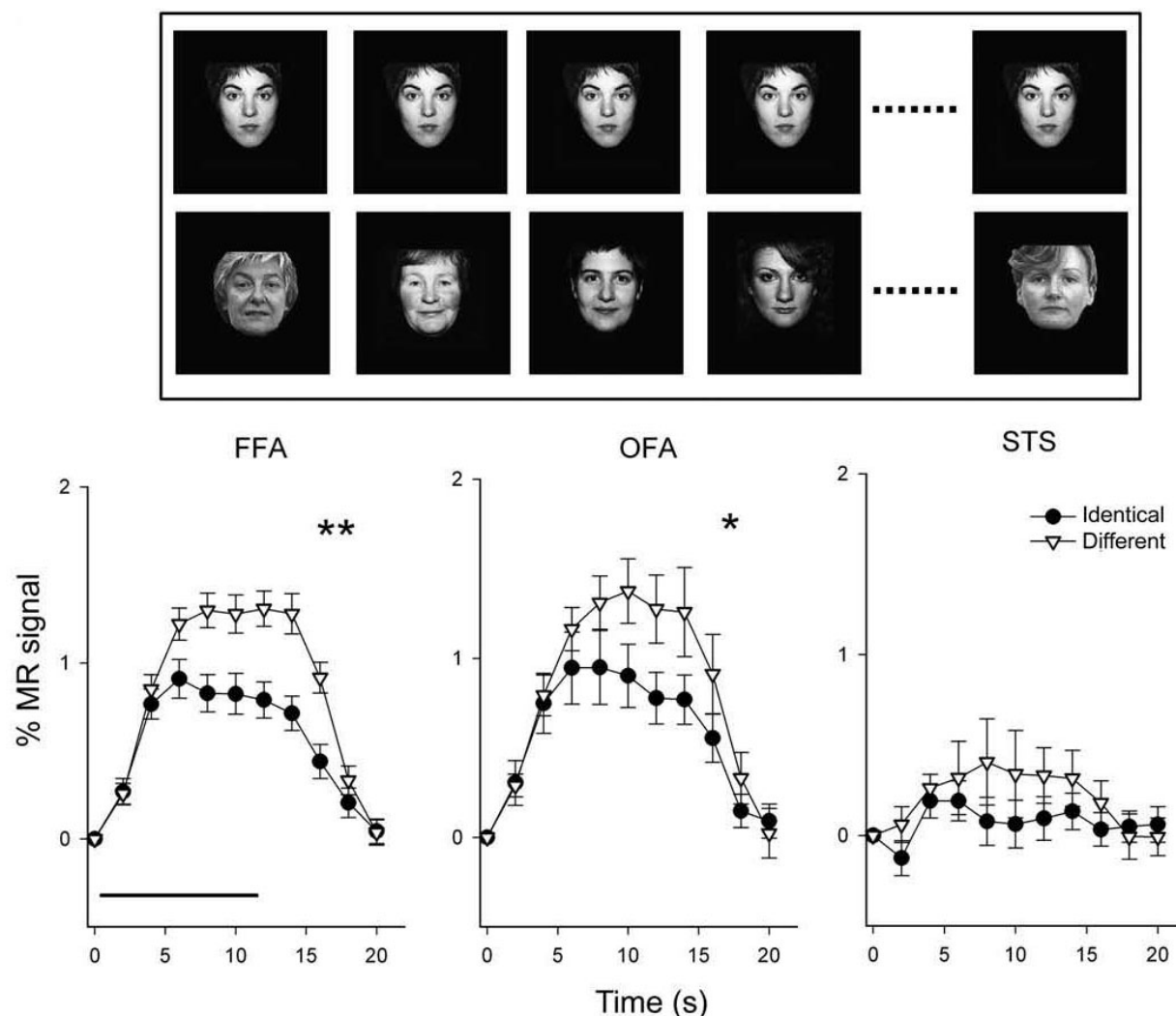
Figure 18. FMRI (BOLD) response in three major face-selective areas when presenting always the same face in a block as compared to the presentation of different faces. The response is significantly larger when different faces are presented (208). Here the exact same image is presented in the "Identical" condition, so that repetition suppression could be due to the repetition of low-level visual cues. However, at least in high-level visual areas, this repetition suppression effect is generalizable across substantial changes of size and position in high-level face-selective areas (e.g., 205, 238) and is abolished or reduced by inversion (161, 236), pointing to high-level visual processes.

the eyes, nose, or mouth. Currently, the view that the OFA is the first relay of information in a hierarchical network of face-selective areas, and that it codes faces in a part-based fashion, is quite dominant (e.g., 196-199; for a review, see 200). However, this view is not based on solid evidence, and poses a problem in accounting for functional aspects of face perception. Irrespective of this issue, there is evidence that the OFA is not only sensitive to faces as a category ('face detection'), but also contributes to discrimination among individual faces.

6.4.3.1. FMRI-adaptation

Evidence for this individual face coding comes essentially from the phenomenon of fMRI-adaptation, or repetition suppression, in which the neural response to a given stimulus is reduced when that stimulus is repeated

(201, 202). If this adaptation is released when two (or more) different stimuli are presented as compared to the repetition of the same stimulus, then one can assume that the area can tell apart the two kinds of stimuli. Such release from adaptation to face identity (i.e., face A preceded by face B *vs.* face A preceded by face A) has been found in many studies both in the FFA and OFA (e.g., 88, 203-207; Figure 18), but not, or only weakly, in the pSTS (e.g 161, 203, 208; although see 193, 209). This evidence that populations of neurons in the face-selective occipito-temporal cortex code for both the global 'face' category ('it's a face') and the fine characteristics of the individual face stimuli ('it's face X, not face Y') in healthy adults is in accordance with information analysis of single-cell populations in the monkey brain, which have shown that the very same neuronal population can subtend both functions (210), perhaps at different time-scales (211, 212)

**6.4.3.2. MVPA and the "decoding" of individual faces**

Over recent years, there has been a growing interest in the neuroimaging community for multivariate pattern analysis (MVPA). MVPA considers the pattern of variability across voxels within a given area (or a large cortical volume, or even the whole brain, e.g., 213), rather than merely the global response of the area (see 214 for a clear introduction to the approach; see also 215, 216). Although the implementation of the approach is variable (217), it is essentially a correlative approach by which a pattern of activation across voxels obtained in response to stimulus X is correlated with the voxel pattern obtained for other presentations of stimulus X *vs.* the pattern obtained for a stimulus Y. If there is a consistent pattern of activity across voxels for a given stimulus X, the correlation will be high between two presentations of the same stimulus X, and the correlation will be weak for the pattern associated with X and the pattern associated with Y. If this is the case, one can use the pattern to "predict" which stimulus is being presented on other (subsequent) trials. Although this approach can be valuable, its power is usually exaggerated, MVPA being described as a way to "predict", "identify" or "decode" neural representations, as opposed to a standard neuroimaging approach based on the measure of the averaged signal over regions of interest [9].

One of the main goals of researchers in this field is to "decode" face identity from a MVPA analysis of the FFA, OFA or all face-selective areas considered together. To be specific, the goal is to identify consistent patterns of activation for different faces in these areas (i.e., voxel patterns more correlated for the same identity presented several times than for different face identities). These attempts have not been very successful. For instance, Kriegeskorte and colleagues (218) failed to find such an effect in the FFA, concluding that this area is not involved in face identity but merely detects faces. However, this study reported such a replicable pattern difference between two very different pictures of a male and a female face in a non-face-selective area of the right temporal pole, suggesting that face identity is coded in that anterior region. More recent studies have apparently been more successful in "decoding" face identity information in posterior visual regions. One study showed that 4 faces were associated with systematic (i.e. reproducible) distributed patterns of activation in four very small clusters (middle and posterior fusiform gyrus, and bilateral temporal pole, 219). However, as in the study of Kriegeskorte and colleagues (218) most of these regions did not show face-selective responses (only two regions overlapped slightly with the bilateral FFAs). Moreover, the discriminative power of this limited set of faces was very low (just above chance), and every face was associated with a specific response key in the experiment, so that the weak decoding might have been increased by - or due to - this specific face-key mapping behavior. More recently, another study showed that 9 artificial faces could be discriminated just above chance level by using information from large face-selective clusters around the OFA, FFA and the anterior infero-temporal region (220). Again, the sensitivity was extremely low, indicating that one would not be able to determine which of 9 faces is

presented based on the pattern of activation, but would just be able to make a guess with a slightly better score than 1 out of 9.

What is surprising is not the lack of substantive findings of MVPA with respect to face identity decoding, but the energy that is put by researchers into this enterprise. In reality, these studies do not inform about how faces are individualized, but simply identify some clusters of voxels somewhere in the system that do not react the same way to different pictures of faces. This is not informative at all. We already know from lesion studies and fMR-adaptation in humans that some regions, in particular the face-selective areas but also other areas such as the ventral LOC (166), *are* involved in discriminating individual faces. More fundamentally, the level of organization at which face identity is coded is not the level of the voxel, or even the cortical column, so that an approach such as MVPA is inadequate for understanding the coding of face identity in the brain. Monkey physiology studies have shown for a long time that even in posterior areas of the STS, face-selective cells carry information about face identity: the magnitude of the response of one cell usually differs in response to different faces, suggesting that identity could be coded within a sparse populations of face-selective neurons (141, 221, 222; see also 223). Presumably, in the human brain, neighboring face-selective neurons also respond very differently to different faces. Given that in a single voxel there are millions of neurons, there is no reason to expect that a given voxel will respond more to face *A* than face *B,* and the next voxel more to B than A, etc. To put it differently, the difficulty of decoding face identity in face-selective areas by MVPA does not have anything to do with face identity not being coded in areas such as the FFA (218, 224): it results from an intrinsic limitation of the method. It is a matter of spatial resolution, or of level of organization that is relevant for face identity. Unfortunately for MVPA, this level of organization is not that of a cube of several mm^3. In fact, this level of organization is not even at the level of the cortical column, which could possibly be decoded in some low-level regions using MVPA (225; but see 226), but it is well below that of the voxel.

Despite this fundamental problem, there is a tendency when using this approach – at least in the field of face perception - to overinterpret null effects, and emphasize very weak sensitivity measures that will not be useful when looking for finer-grained discrimination and generalization across multiple views of the same identity. Rather than attempting to dismiss fMR-adaptation as a relevant tool to measure sensitivity to face identity and emphasize the importance of MVPA (227) it seems that more effort should be devoted to improve the former approach, making it even more sensitive, tightly controlled and understandable in terms of neural mechanisms. So far, fMR-adaptation has been much more successful than MVPA in providing information about the sensitivity to individual faces in face-selective areas, these findings being generally in agreement with the effects of brain damage [10].
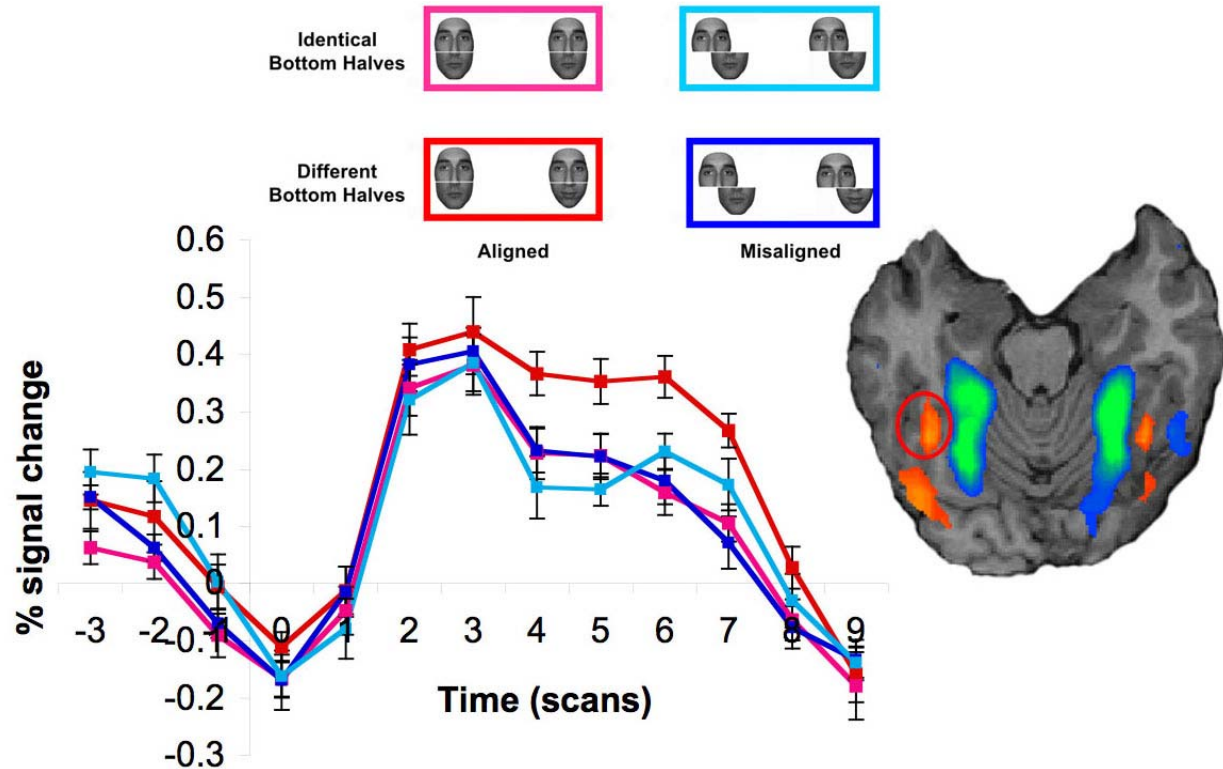
Figure 19. BOLD response in the right FFA to the presentation of composite faces. The exact same top half is repeated in all conditions, and attended. When the top halves are aligned with different bottom halves, they are perceived as different, leading to a release from adaptation. This effect is not found for misaligned faces, or when aligned faces are presented upside-down (88). Similar but weaker effects are observed in the other face-selective areas (see also 239).

6.4.3.3. How is face identity coded?

Many fMRI studies performed in the normal brain have attempted to clarify the *nature* of the individual face representations in the FFA, and also in the OFA, usually by means of fMRI-adaptation paradigms. Here, in keeping with the goal of the review, I will concentrate on the coding of face identity. Both the FFA and OFA are sensitive to changes of a subset of the facial parts when they are inserted in whole faces (44, 228-231). Some of these studies have also reported sensitivity to the *relative distances* between these parts in whole faces, either in both areas (230) or primarily in the FFA or fusiform gyrus (44, 231). Both the FFA and OFA also appear to be more sensitive to shape-based than surface-based information (i.e., texture and color, 232). However, repetition of the same unfamiliar face in a different viewpoint leads to a release from adaptation in both areas (168, 208, 233; see also 234), indicating that the individual face representations are largely viewpoint-dependent [11].

In line with the well-known difficulty at recognizing faces upside-down (e.g., 33, 235 for review), there is a higher response for different than identical faces for upright but not for inverted faces in both the FFA and OFA (161, 236; see also 237). A neural composite face effect is also observed in both regions, which show a larger response to the illusion of change of identity on the top halves of faces when these top halves

are aligned with different bottom halves, and only for upright faces (238; Figure 19). However, this effect is larger in the (right) FFA than in the OFA, and is found only in the right FFA in an event-related paradigm (239). These observations have been taken as evidence for holistic/configural representation of individual faces in the FFA in particular, a proposal supported by subsequent observations using fMRI adaptation (228, 240). Importantly, such observations do not mean in any way that the FFA is not sensitive to differences between facial parts, a common misunderstanding both in the neuroimaging and behavioral literature (34). They also go beyond the mere claim that "the FFA is sensitive to the presentation of the whole face", because they show that facial parts are *not* represented *independently* of each other (i.e., of the whole face) in these areas, and in the FFA more so than the OFA.

In summary, fMR-adaptation studies have generally found that the FFA is more sensitive than the OFA to various face cues or processes. The FFA represents individual faces more holistically than the OFA, and is more sensitive to relative distances between face parts. The only notable exception is a study that reported a higher sensitivity to subtle changes of facial identity in the OFA rather than the FFA (241), but two subsequent studies have shown the opposite result (207, 242). Contrary to the OFA, the FFA also generalizes across spatial scales to individualize faces (204[12]). However, for unfamiliar faces

at least, both areas do not generalize identity information across changes of viewpoint. With respect to the nature of the representation, it has also been suggested that the FFA codes individual faces relative to a norm in a face space (243), but this hypothesis was not tested in other face-selective areas, and the findings of this study are highly controversial (244, 245).

6.4.4. Are there truly part-based face-specific representations?

According to a popular view in visual and computational neuroscience, a complex visual stimulus such a face is first decomposed in parts that then combined to form larger parts and eventually a whole face (246-248). This is the analytical view described in section 1 of this paper. At first glance, this view makes sense because neurophysiological recordings in the monkey brain have shown that neurons in visual areas such as the primary visual cortex (V1) and early extrastriate areas (V2, V3, V4, MT) have small receptive fields and are sensitive to simple features such as contrast, orientation of line segments, spatial frequency, color or motion (249, 250). By contrast, higher-order areas of the inferior temporal cortex (IT) contain neurons with much larger receptive fields and strong selectivity for moderately complex stimuli (e.g., 139, 251, 252) or whole complex shapes, in particular faces (136, 140, 143; see 144 for a review and historical perspective).

In general, the neuroimaging community has transposed this hierarchical part-to-whole view to the neural representation of faces. In Haxby *et al.* (173)'s model, for instance, the OFA is described as representing "facial features", while higher areas such as the FFA and pSTS are thought to represent whole faces. This view has been explicitly formulated in a review of the OFA, a region described as the first face-selective relay in the human brain, representing faces by their independent parts (a nose, a mouth, an eye, etc.) (200; see also 19, 197, 199).

Is there evidence for such part-based, face-selective representations, in particular at the level of the most posterior face-selective area, the OFA? Studies that have attempted to answer this question fall into two categories.

On the one hand, some studies have shown that face-selective areas, the OFA in particular, respond to *changes* of single parts inserted in whole faces (228, 229, 253, 254; see also 255). However, since a given part cannot be perceived independently of the whole face (32, 40), it is incorrect to define these responses as being "part-based", or providing evidence for "part-based representations" (34). The exact same reasoning applies to the study of Pitcher *et al.* (132), in which transcranial magnetic stimulation (TMS) applied to the right OFA disrupted the matching of faces differing by local parts. Given that whole faces were presented in that TMS study, this finding cannot be interpreted in terms of evidence for part-based representations in the OFA (33, 34).

Other studies have directly compared the neural response to parts and whole faces, attempting to understand the nature of the representation in these areas. For instance, one study used restricted (aperture) viewing driven by the subjects of their experiments, and reported that the FFA responds even to small parts of a face (256; see also 197). Another study reported that the OFA responds more to a single part than to combinations of parts (i.e., the whole being less than the sum of the parts), while the FFA responded equally strongly to parts and whole faces (196). Using MVPA to decode neural representation of whole faces and parts, another study claimed that the OFA represents faces essentially by means of parts (199).

However, these studies are also inconclusive regarding the presence of representations of independent parts in the OFA (or other face-selective areas). Basically, what these studies show is that some parts, when presented in isolation, can activate the OFA or FFA consistently, often to a level that is at least as large as that of the whole face. While this is an interesting observation, it does not provide any evidence for part-based representations. The problem is that unlike objects that can be formed of simple meaningless elements (e.g., a triangle formed of 3 connected lines), a facial part such as an eye is meaningful in itself and is usually sufficient to activate other parts or an entire representation by completion. This is particularly true in the context of an experiment in which only, or mainly, faces are presented. Thus, none of these studies can exclude that a single part activates the whole face representation. This criticism also applies to monkey physiology studies arguing for part-based representation at an initial stage of processing (19, 223), but is even more valid for fMRI technique that measures brain activity over several seconds.

To illustrate this problem, let's imagine that one presents the left half of a face while recording fMRI. This presentation will activate the FFA and OFA, probably as much as to the presentation of the whole face. Does it mean that there is a representation of the left half of the face in these regions? This problem is exemplified in the study of Arcurio *et al.* (196) in which the OFA shows maximal activation with a single part. If anything, rather than summing up, activity in this area appears to decrease when adding face parts, making it very difficult to conceive that there is a representation of the facial parts in independent populations of neurons in this area.

In summary, the FFA and the OFA both responds preferentially to faces and show sensitivity to individual faces, with the effects being generally more robust in the FFA. The FFA represents individual faces more holistically than the OFA, and is more sensitive to relative distances between face parts. This could be because the OFA is positioned closer to the occipital pole than the FFA and shares many characteristics of retinotopic cortex, including increased position sensitivity and foveal-peripheral eccentricity maps (257-259). Hence, it makes sense that the OFA has smaller receptive fields, and shows less invariance to spatial position than the FFA. Other than that, there is little evidence to suggest that the two areas have

clearly different functional roles, and would compute independent face processing operations.

6.4.5. Connectivity and functional dynamics

Are the face-selective areas connected at the anatomical and functional levels, and if so, how? This question has been difficult to address, at least in the human brain (for evidence of functional connectivity between face patches in the monkey brain, see 260). At the anatomical level, diffusion tensor imaging (DTI) has been used to make inferences about the white matter tracts joining the different face-selective areas. These studies have suggested strong white-matter connections between the occipital face area (OFA) and fusiform face area (FFA) (182, 261), the latter study also reporting connectivity up to a face-selective cluster in the right temporal pole and between the FFA and several clusters in the lateral occipital cortex. No connectivity was disclosed between STS and FFA, or between STS and the other face-selective regions. A study conducted on subjects with a life-long impairment in face recognition has also found a massive reduction of white matter tracts in the ventral occipito-temporal cortex, suggesting that these connections are important for functionality (262).

The face-selective areas appear to be highly correlated with one another, especially within the same hemisphere (263, 264). The strength of the correlation at rest between the OFA and FFA is also related to face but not object perception tasks (265). Studies using dynamic causal modeling (DCM; 266) have attempted to estimate the direction of this correlation or the effective connectivity (or functional coupling) between occipitotemporal regions. Some studies have reported evidence in favor of a simple feedforward relationship between face-selective regions of occipitotemporal cortex (i.e., input entering OFA and then modulating FFA) (267-269). However, these studies assumed that driving input enters OFA only and did not test alternative models in which input enters other visual regions. Contrary to these studies, another study using DCM without any constraints on the model areported intrinsic bilateral connections between the right inferior occipital gyrus and middle fusiform gyrus during face perception (231). A limitation of these studies, however, is that the regions tested were not limited to face-selective responses. In particular, Fairhall and Ishai (268) defined the "OFA" as a large area responding more to faces than scrambled faces, i.e., including the entire lateral occipital cortex, without isolating face-selective responses. Most recently, there have been reports of both OFA-to-FFA and FFA-to-OFA interactions in DCM studies, these interactions being weighted differently according to the kind of repetition suppression effects observed (across changes of face size or not, (205)). Overall, there seems to be a lot of discrepancy between these studies, which reach ambiguous conclusions about the direction of face-selective processing. A fundamental problem remains the low temporal resolution of fMRI. It is very likely that dynamic reentrant anatomico-funcitonal connections exist between these areas and may be weighted differentially depending on the kind of task performed. However, when the stimulus is presented abruptly, the process of individual face perception, and even face recognition, takes place essentially within the first 200 ms (205, 270, 271). Thus, during transient stimulation, a dynamic model of face perception cannot rest on evidence based on the normal brain, where information can flow almost freely in multiple directions of a network during several seconds after the presentation of the stimulus.

6.4.6. Summary-conclusion

In summary, even without relying on high-resolution fMRI, functional neuroimaging studies have refined the human neuroanatomical map of face perception to a level that is well beyond the spatial resolution offered by lesion studies of patients with prosopagnosia. These studies have shown that there are multiple clusters, or areas, in the STS and in the ventral occipito-temporal cortex, that respond more, or almost exclusively, to faces than other visual objects. However, the neuroimaging community in this field has not made an enormous amount of progress beyond that, and has often neglected knowledge coming from other approaches that would inform about, and would constrain, the interpretation of neuroimaging findings of face perception. There are also a number of issues on which there has been little progress, and there are some points for future direction that I would like to address.

First, the neuroimaging community in this field still focuses too much on a single area of this set, namely the FFA. This is unfortunate because it is very unlikely that important issues such as the domain-specificity of faces, or the nature of perceptual face representations, will be answered at the level of a single area. Moreover, the FFA is not even necessarily the most face-selective area, and does not appear to be more critical for face recognition than other face-selective areas. In particular, there is now converging evidence that the lateral part of the right inferior occipital cortex is a necessary component of the intact face perception system, perhaps the most critical of all (118, 134).

A second issue is that there is not enough emphasis on the dominance of the right hemisphere for face perception in the neuroimaging community. For instance, Haxby *et al* (173)'s influential neurofunctional model of face perception, which is largely inspired by neuroimaging, treats the two hemispheres indifferently (see also 158, 159, 175). Yet, studies of prosopagnosia clearly show the dominance of the right hemisphere in this function. This discrepancy suggests that the left hemisphere may contribute to face perception but that it is not *necessary* for this function. However, many neuroimaging studies, including both PET and fMRI, have also reported a right hemispheric dominance in face perception. This right lateralization is an important factor to consider because the processes localized in the right hemisphere are probably those that make faces special compared to other object categories (98, 101, 272-275). In this respect, the apparent absence of right hemispheric dominance in the monkey brain in fMRI studies (181, 183, 276; but see 277) is quite puzzling[13]. Indeed, the view that right hemispheric dominance in humans is related to language lateralization

(128, 129) can only be partly true: with the exception of the FFA, this right hemispheric dominance is identified even in all left-handed brains tested (130).

A third issue concerns the identification of the face-selective regions of interest in different studies. It is clear that there is an enormous amount of interindividual difference in the localization of these areas. Given that up to six or more face-selective clusters can be identified in the ventral occipito-temporal cortex in some individual brains, the labeling of each of these clusters becomes very subjective and is open to interpretation. For instance, the regions labeled "FFA" in different brains may in fact be different regions, and the "OFA" may be confused between face-selective clusters in the middle and posterior fusiform gyrus (188, 278; fig 2; 160, 182 for a discussion of this issue). Anatomical constraints and spatial relationships to other functional areas will have to be used increasingly to help defining regions such as the FFA across individual brains more objectively (161) However, it is not entirely clear why every single human brain should have the same amount of well identified face-selective clusters in the same way as a primary visual cortex can be identified in every single brain. Rather, it is likely that different individuals have different amounts of face-selective clusters, of different sizes, which reflect their visual experience with faces and other visual entities. This points to analyses performed at the single subject level, and perhaps avoiding forcing some correspondence between labeled clusters across different individual brains, until or unless we have well-established anatomico-functional criteria to do so.

A fourth issue is that there seems to be too much focus on "cracking" the code of a given area, in the sense of understanding what specific computations it performs. MVPA has been touted as a powerful, new and exciting tool in this endeavor, and combined with increases in MR field and spatial resolution, it seems to have convinced the community that this is the adequate way to understand how the system works. As indicated above, I am highly skeptical about that. It does not seem to me that we have learned much about the nature of face representation from MVPA studies of face perception. This is partly because these studies neglect other sources of knowledge and tend to overinterpret null results. It is also because face identity is not coded at the level of resolution of the voxel. And it may also be because the representation of an individual face is not a fixed "code" or a fixed "pattern" of activation in a given population of neurons. Indeed, the representation of an individual face changes all the time, depending on our exposure to that that face but also to other faces which other faces ("face adaptation or aftereffect"; 279, 280). Thus, *the direction of the change of activation* rather than the "pattern" itself may be more important in "decoding face identity". If the representation of a face is not static but relative and dynamic, this is another reason in favor of an approach such as fMR-adaptation compared to MVPA. In addition, the "code" or the functional role of an area may be entirely dependent on other areas, and make sense only when considering the synchronous activity of other reentrant areas. In this perspective, an individual holistic face representation would only emerge from a network of reentrant integration between populations of neurons distributed in various areas. Therefore, one would need to consider the whole network to understand the function.

In the last section, I will discuss how combining neuroimaging studies with investigations of brain-damaged cases of prosopagnosia could help to clarify these issues. Hopefully, this approach will challenge the view that we need to treat these areas as components ("modules") that compute independently and feed the outcome of these computations into each other in a hierarchical manner. Rather, I will argue that understanding face perception cannot be achieved by considering face-selective areas in isolation, and that they are as interdependent on each other as the parts of a face.

7. UNDERSTANDING HOW THE HUMAN BRAIN PERCEIVES FACES BY COMBINING LESION STUDIES AND FUNCTIONAL NEUROIMAGING: THE CASE FOR A NON-HIERARCHICAL VIEW OF FACE PERCEPTION

7.1. Necessity and connectivity

By itself, functional neuroimaging of the healthy brain is unable to indicate whether the areas activated during the presentation of face stimuli are *necessary* for their successful perception. Hence, in principle, the precise identification of the lesions causing prosopagnosia remains important to understand the neural basis of face perception. However, as indicated above, relying on the lesion method (i.e., correlating neuroanatomical data and clinical symptoms) as a means to establish the neuroanatomical basis of prosopagnosia is associated with a number of weaknesses, most notably a lack of precision due to the extent and variability of functional and anatomical impairments of the patients (1).

Another difficulty is that brain regions that may appear structurally intact, and, thus, not considered to be critically associated with the impaired function(s) in a prosopagnosic patient, may in fact be functionally depressed because they do not receive normal inputs from lesioned regions ('diaschisis', 281). An illustration of this phenomenon was provided early on by Sergent and Signoret (62), who reported a case of prosopagnosia with no structural damage to the right parahippocampal gyrus. Yet, a PET measurement of the patient's brain indicated a functional depression of this region, presumably because this area was deprived of normal inputs from other lesioned parts of the cortex. Thus, any attempt at correlating behavioral deficits of the patient due to the hypofunction of the parahippocampal gyrus with visible structural damage would have been flawed.

However, this observation highlights the interest of studying cases of prosopagnosia, or brain-damaged patients in general, with functional neuroimaging: such studies may not only improve the accuracy of associations between function and brain localizations, but they may also offer a powerful tool to investigate the relationship(s) between brain areas identified in the normal brain, and test hypotheses regarding their functional relationships (281,
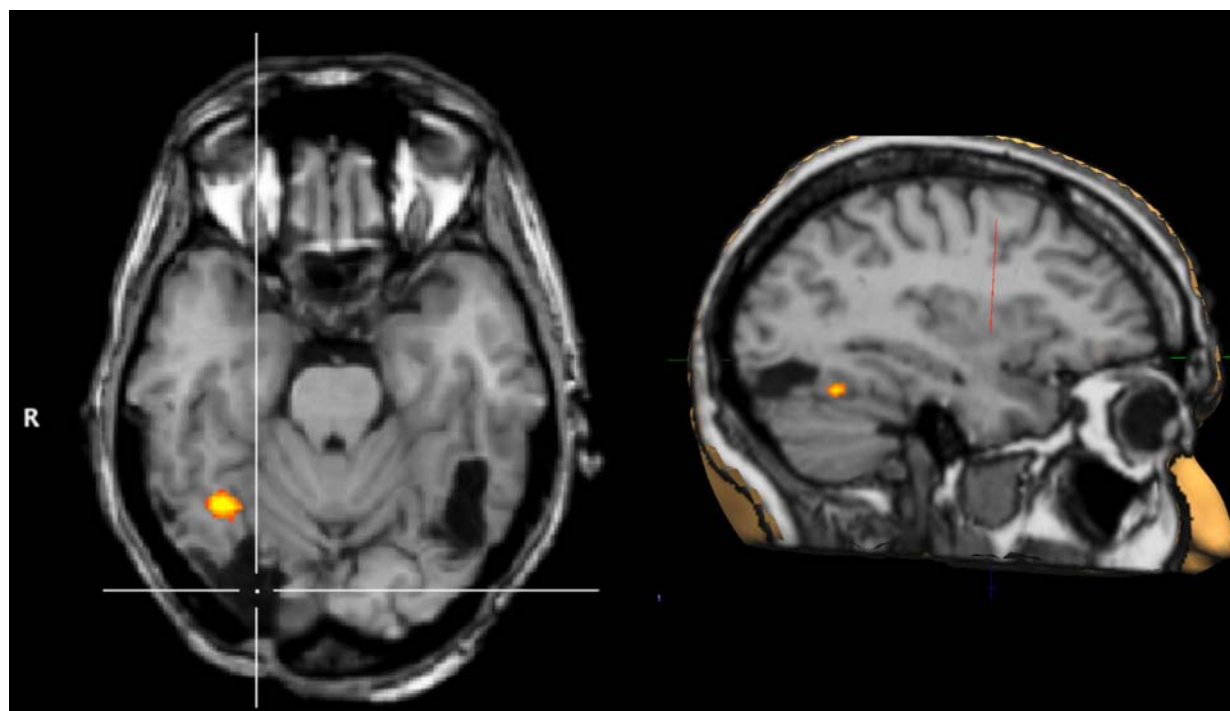
Figure 20. Face-selective response in the right middle fusiform gyrus of the prosopagnosic patient PS, despite brain damage to the ipsilateral inferior cortex and no evidence of posterior face-selective clusters.

282). For instance, if the OFA is truly the front-end of the core face perception system, as proposed by Haxby and colleagues (173; Figure 16), then a lesion to this area should prevent the flow of information to higher visual areas such as the FFA and the pSTS. The opportunity to test this hypothesis was offered to us when we encountered the prosopagnosic patient PS described in section 2.

7.2. Preserved face-selectivity in the right middle fusiform gyrus (FFA) despite ipsilateral OFA lesion
Where are PS' brain lesions located relative to the functional areas that are described in Figures 16 and 17, and that are thought to be particularly important to perceive faces? Her largest lesion is located in the right hemisphere and concerns a substantial part of the lateral inferior occipital cortex (Figures 10 & 11; 86). This localization corresponds to the site of maximal overlap of lesion localization in several cases of prosopagnosia (118; Figure 10), suggesting that this right inferior occipital lesion is instrumental in causing PS' face perception impairment.

Most interestingly, PS' right posterior lesion entirely spares the middle and anterior sections of the fusiform gyrus, exactly where the right FFA is usually disclosed in normal participants when comparing the response to faces and objects in an fMRI localizer (Figure 15). This pattern of damaged and spared brain tissue in a case of prosopagnosia offered us a unique opportunity to test one of the key features of the hierarchical neuro-functional model of face perception: the hypothesis that the OFA is the front end of the system, providing the early inputs to higher visual areas such as the FFA and pSTS

(Figure 16, section 6). If the hierarchical model was correct, damage to the right OFA should have prevented face preferential activation in higher visual areas of the middle fusiform gyrus ("FFA") and the pSTS.

In contrast to this model, our very first fMRI investigation of the patient PS, using a simple functional localizer, showed a preferential activation for faces in the middle fusiform gyrus (i.e., right FFA) in the absence of any face preferential activation around the lesioned area of the right inferior occipital cortex (i.e., no right OFA) (85; Figure 20). Hence, we found that the right middle fusiform gyrus (FFA) may show a larger response for faces than objects, without possibly getting any inputs from the ipsilateral inferior occipital cortex. This observation suggests that in the normal brain, the FFA may show face-selectivity independently from face-selective activation observed in the posteriorly located area in the inferior occipital cortex, the OFA (85). This proposal has been reinforced by several observations:

- The activation of the right FFA for the patient PS is a robust effect that has been replicated many times, in different laboratories, with 4 different scanners (1.5T and 3T) and different acquisition parameters (block design or event-related paradigms) (85, 86, 88, 101, 166).

- Compared to control participants in our experiments, the right FFA of the patient PS is in the normal range in terms of size and localization (85, 86, 101).
- The response amplitude difference between faces and objects is overall in the normal range for PS'

FFA (85), even though it can be in the lower range in some experiments, perhaps because of an absence of release from identity adaptation in her FFA (see section 5.4 below).

- The FFA activation in the patient PS' brain is observed whether the patient is impaired at performing the task (e.g., one back face matching task) or is able to perform the task normally (e.g., color detection task, see 85, 88, 101, 166).

- FFA activation with no evidence of OFA activation has been replicated in a case of visual agnosia due to *bilateral* damage to the inferior occipital cortex, the patient DF (112). Remarkably, the damaged area that is common for both PS and DF is the right OFA (283).

- Besides right FFA activation, the right pSTS of the patient PS also shows preferential activation for faces in the absence of OFA inputs (86).

Overall, the observation of right FFA activation in a patient with ipsilateral OFA damage suggests that, in the normal brain, the FFA may potentially be activated preferentially for faces *independently* of inputs coming from the posteriorly located face-selective OFA. That is, both the OFA and FFA might be activated in parallel in the normal brain, independently from each other, such that a lesion to one of the areas does not prevent face-preferential activation in the other area. Or, more intriguingly, the FFA could be activated *before* any putative contribution from the OFA. That is, the onset of face-selectivity in the normal brain may appear first in the middle fusiform gyrus (FFA), and then in the lateral occipital cortex (OFA). This reverse hierarchy would be in complete contrast to the proposal of a hierarchical feedforward model of face perception (173, 200).

Even though this latter hypothesis requires further support, there is additional evidence in its favor. First, the right FFA activation is unlikely to originate from face preferential inputs coming from the OFA of the left hemisphere (e.g. through transcallosal connections), because left OFA activation was rarely found in PS' data and because her right FFA activation is larger and peaks earlier for contralateral than ipsilateral face stimulation (see Figure 6 in 46). Second, another brain-damaged (prosop)agnosic patient (NS; 73) has a lesion in the bilateral parahippocampal gyri and the right fusiform gyrus, with largely preserved brain tissue in the lateral inferior occipital cortex. Despite an excellent signal-to-noise ratio, there was no evidence whatsoever of face-preferential activation in the bilateral ventral stream, neither around the lesion in the fusiform gyrus (FFA), nor in the inferior occipital gyrus (OFA). In fact, there was only a hint of face preferential activation for faces in the pSTS of the patient (see Figure 7 in 46). Hence, in the absence of the right fusiform gyrus, there was no evidence for right OFA activation.

In summary, neuroimaging investigations carried out on PS and also other brain-damaged cases of prosopagnosia suggest that in the normal brain: (1) *the*

posteriorly located right OFA is a necessary component of the face perception system; and (2) *rather than being an early component, its preferential activation for face stimuli may in fact follow, and be dependent on, inputs originating from the higher-level ipsilateral FFA.* Admittedly, one cannot exclude that these observations made on single cases of brain-damaged prosopagnosic patients may reflect some kind of peculiar reorganization of neural function, and we must remain cautious in deriving general conclusions about normal brain functioning from these observations alone. Nevertheless, these observations have enough merit to challenge the conventional hierarchical view of face perception, and have inspired subsequent neuroimaging studies of the healthy brain that reinforce this view and will be described next.

7.3. From brain-damaged patients to the dynamics of perception in the healthy brain and back

Why would face-selectivity arise initially in a higher-order area of the middle fusiform gyrus rather than in a lower-level area of the inferior occipital cortex? While it is difficult to understand in the context of a hierarchical feedforward model, it makes much more sense in a coarse-to-fine model of face perception, as introduced in section 2. According to this view, the initial face-selective representation is not that of isolated parts, but it is the *whole face*, at a coarse level. While populations of neurons in higher-order areas such as the middle fusiform gyrus probably have receptive fields that are large enough to generate such a global representation, this might be impossible for populations of neurons located in lower-order visual areas of the inferior occipital cortex. As mentioned earlier, the OFA is positioned closer to the occipital pole than the FFA and shares many characteristics of retinotopic cortex, including increased position sensitivity and foveal-peripheral eccentricity maps (257-259). In other words, while populations of neurons in the middle fusiform gyrus might be able to "see" a whole face at once, this may require the time-consuming combination of activation of many subpopulations of neurons in the inferior occipital cortex.

7.3.1. Mooney and Arcimboldo face perception emerges in the right FFA

To test the hypothesis that initial face-selective representation is that of the whole face in higher-order areas such as the FFA, we turned to a visual stimulus that can be readily categorized as a face even if it does not contain clear elementary facial parts, its faceness being defined solely or primarily by the global organization of its elements. A classical example is provided by the two-tone "Mooney" images of faces depicted in Figure 3. In a Mooney image, the local parts are too ambiguous to be recognized as face-like individually. Rather, these local parts must be disambiguated based on their context within a global configuration. Moreover, since two-tone images of novel objects do not lend themselves to volumetric interpretations, the correct perception of a Mooney stimulus appears to depend on previously stored representations in memory, or a top-down application of a 2D global face template (30, 284, 285). Indeed, when a Mooney picture is presented upside-down, the face is usually not perceived,
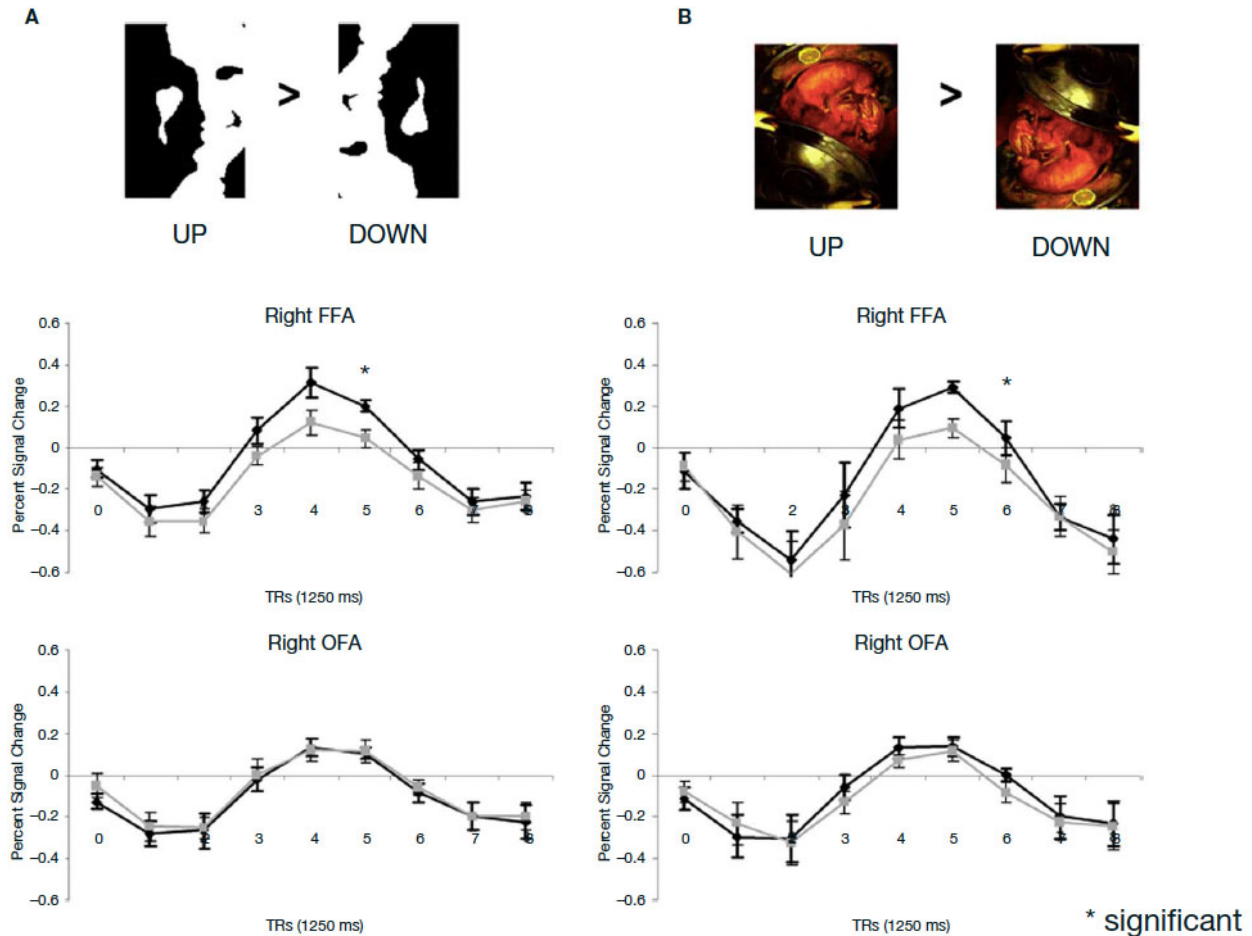
Figure 21. When visual stimuli cannot be categorized as face-like based on their parts, but only on the basis of their global configuration (A, Mooney faces; B; Arcimboldo paintings), face perception activates the right FFA without activating the right OFA (adapted with permission from 101). This observation indicates that even in the normal brain face-selectivity can emerge in a higher-order area without face-selective inputs from a posterior area. These observations contradict a hierarchical neuro-functional model of face perception.

presumably because the visual input cannot be disambiguated without the help of internal 2D global representations (i.e., top-down processes) which favor upright orientation. Consequently, contrary to face photographs, Mooney faces *require* an appreciation of global configuration (286-288): the stimulus needs to be processed as an integrated whole rather than as a collection of independent parts.

Given this, we reasoned that in the normal brain the response to Mooney stimuli should be much larger in the right FFA than the OFA, compared to the responses of these two areas to face photographs. This is exactly what is observed during a face/nonface categorization task in an event-related fMRI study: Mooney stimuli activate primarily the right FFA and pSTS, without face-selective responses in the OFA (101; Figure 21a). These observations indicate that categorization of a visual Mooney stimulus as a face is supported almost exclusively

by higher-order areas in the right hemisphere and does not rely on a lower-order visual area that is sensitive to segmented face photographs in a typical face localizer (OFA). Similar observations are made when using Arcimboldo stimuli, whose perception as faces also relies on a global configuration, not the individual parts (Figure 21b). Hence, in some way, these experiments reproduce the pattern observed with the patient PS: face-selectivity emerges in the middle fusiform gyrus (FFA) without concomitant face-selective responses in the inferior occipital cortex ("OFA"). Such observations are particularly difficult to reconcile with a hierarchical view of the neural perception of faces, a view that cannot explain how a Mooney face is seen as a face in the first place.

7.3.2. Coarse-to-fine face perception

The coarse-to-fine model of face perception has received further support by an event-related fMRI study (289). In this study, healthy participants were presented with face photographs that were flashed for various durations (75, 150 or 300 ms) and then masked. These
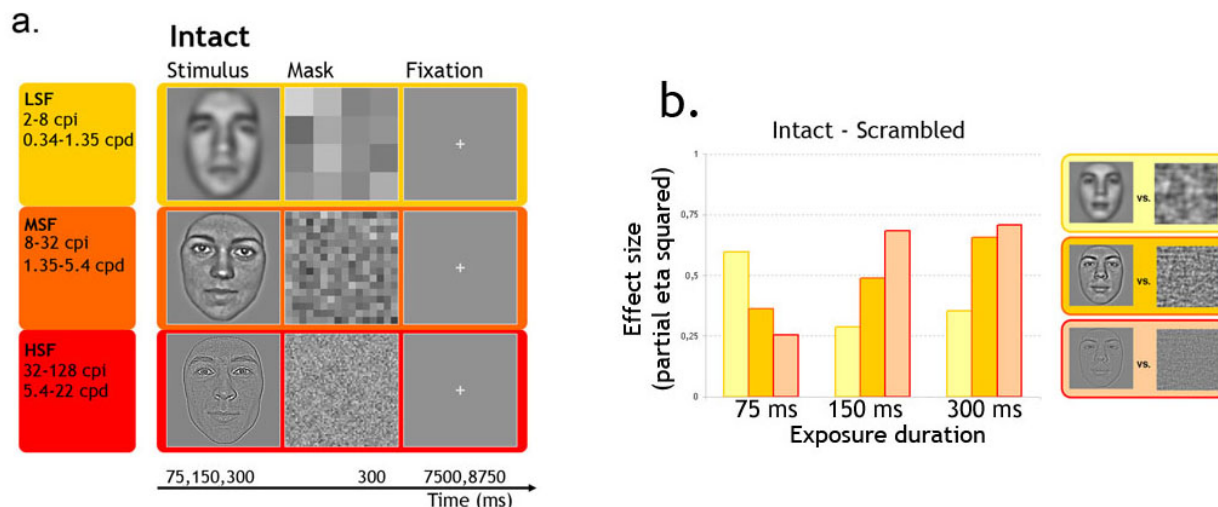
Figure 22. In the study of Goffaux *et al.* (289, figure adapted with permission), low-pass filtered (LSF, coarse scale information) faces presented briefly activate the FFA more than the same faces bandpass filtered (middle spatial frequencies, MSF) or with the low-spatial frequencies only (HSF). However, at longer presentation durations this pattern reverses, with LSF faces being associated with lower responses than MSF and HSF faces. These results support a coarse-to-fine processing of faces in the FFA.

photographs contained only coarse information (low spatial frequencies, LSF), or more details (middle and high spatial frequencies, MSF and HSF, respectively). At a very short duration of time (75 ms), LSF evoked larger responses in the rFFA than HSF and MSF faces; this pattern reversed for longer durations (Figure 22). These observations indicate that there is a temporal dynamic of processing in the FFA that may follow a coarse-to-fine scheme. Moreover, the rOFA did not show any face-selective response (faces *vs.* scrambled faces) to LSF faces at any exposure duration. This latter observation is in line with the findings described above, showing first that face-selectivity can emerge in the FFA without such effects in the OFA, and second that the OFA shows face-selectivity only when face-likeliness can be extracted from local information.

### 7.3.3. The spatio-temporal rise of face-selectivity

Testing directly the hypothesis that face-selectivity can emerge in the FFA before the OFA in the normal brain is challenging. Indeed, the low temporal resolution of fMRI (290) does not allow separation of the time of activation in two visual areas such as the FFA and OFA, separated by about 2 cm of cortex, and whose earliest face-related responses might be isolated by a few tens of milliseconds at most during face perception.

Despite this intrinsic limitation of the technique, we took advantage of a large number of participants (36) to perform a BOLD latency mapping (BLM) analysis to compare the time-course of activations across areas (176). For all face-selective areas, the onset time of the response to the first face in each block of faces (432 trials in total) was estimated using a piece-wise linear trapezoidal model for the response without forcing a return to baseline (291). Interestingly, the right FFA showed the earliest onset response, its mean onset time preceding that of the right OFA and emerges as early as the ventral posterior part of the lateral occipital (LO) complex, an area that does not

respond more to faces than other objects (Figure 23). Although this observation must be interpreted cautiously, it suggests that face-selectivity may emerge in the right FFA before the right OFA.

To further reveal differences in the onset time and duration of processes in visual areas with more power, we used the approach of slowing down visual stimulation in fMRI, which may reveal timing differences between visual areas (292-295).

Specifically, we used a paradigm of gradually revealing information in successive continuous steps, that is, a dynamic sequence (Figure 25; video at: *http://face-categorization-lab.webnode.com/products/face/*) (296). In this study, as in the previous studies, the meaningful picture was not present at the onset of stimulation and was instead gradually revealed throughout a long dynamic sequence (20 seconds). The low-level image properties, such as luminance and frequency spectra, were held constant by progressively de-noising only the phase spectrum of the visual stimulus (297). Strikingly, among the face-selective regions identified based on a standard localizer, the right FFA showed the earliest difference between the BOLD response for faces and cars. In particular, differential activation in the FFA was observed *before* differential activation in the more posteriorly located occipital face area (OFA) (Figure 24). A whole brain analysis confirmed these findings, with a face-sensitive cluster in the right fusiform gyrus being the only cluster showing face preference before successful behavioral detection (296). These findings support the view that following generic low-level visual analysis, a face stimulus presented in a gradually revealed visual scene is first detected in the right middle fusiform gyrus ("FFA"), only after which further processing spreads to other face-selective areas (including the OFA).
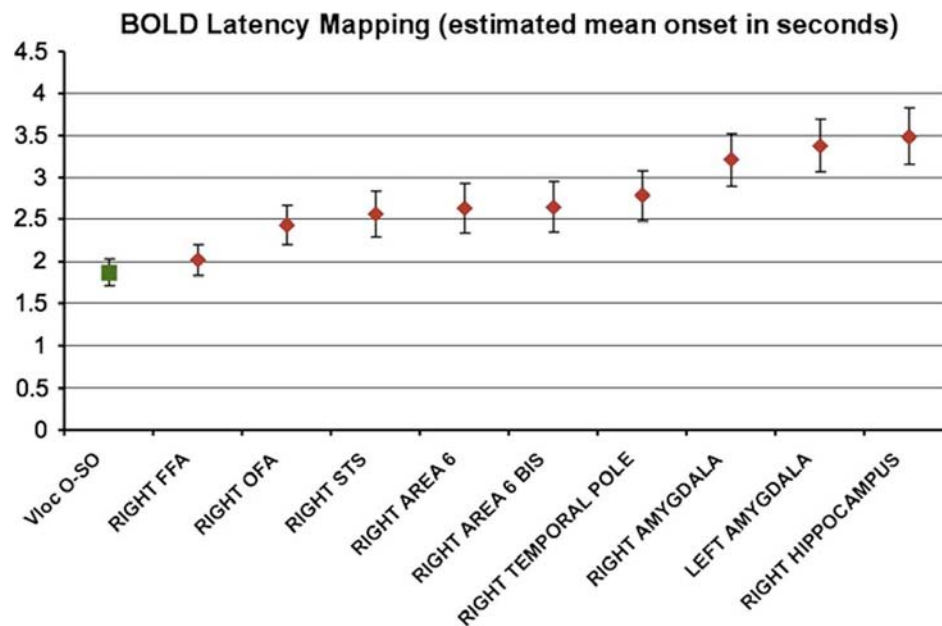
Figure 23. Results of a BOLD Latency Mapping (BLM) analysis (mean onset in seconds and 0.05% confidence interval) performed on 36 individual brains (adapted with permission from 176). Onset time of the response to first face in each block (432 trials in total) across all the face-selective areas and in the posterior ventral part of the lateral occipital complex (LOC), an area that does not respond more to faces than objects. Among all areas responding preferentially to faces, the right FFA shows the earliest onset response, significantly before the OFA. It is activated as early as the ventral part of the LO complex.
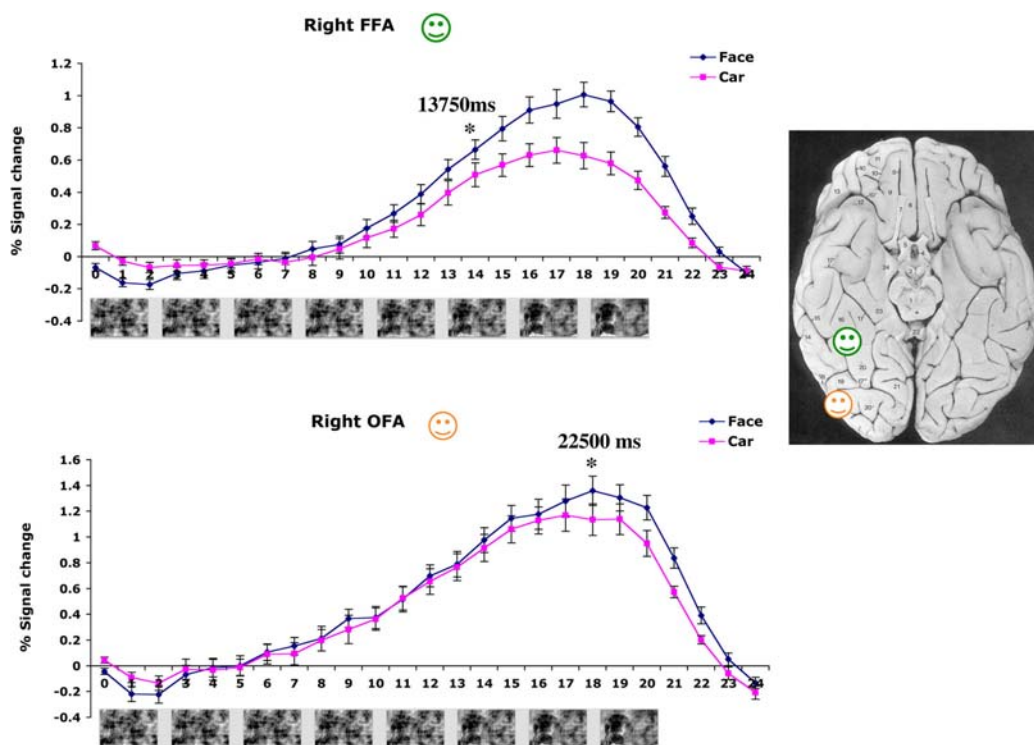
Figure 24. Slowing down the appearance of a face and keeping constant the low-level stimulation points to a temporal reverse hierarchy in the emergence of face-selectivity in the human brain (296). Note that the absolute activation starts in the OFA (volume 6, corresponding to 7500 ms for repetition times (TRs) of 1250 ms) ahead of the FFA (data point 9). However, strikingly, this initial activation does not differ between faces and cars. The onset of the difference between faces and cars emerges earlier in the FFA (significant at 1350 ms) than the OFA (significant at 22500 ms).
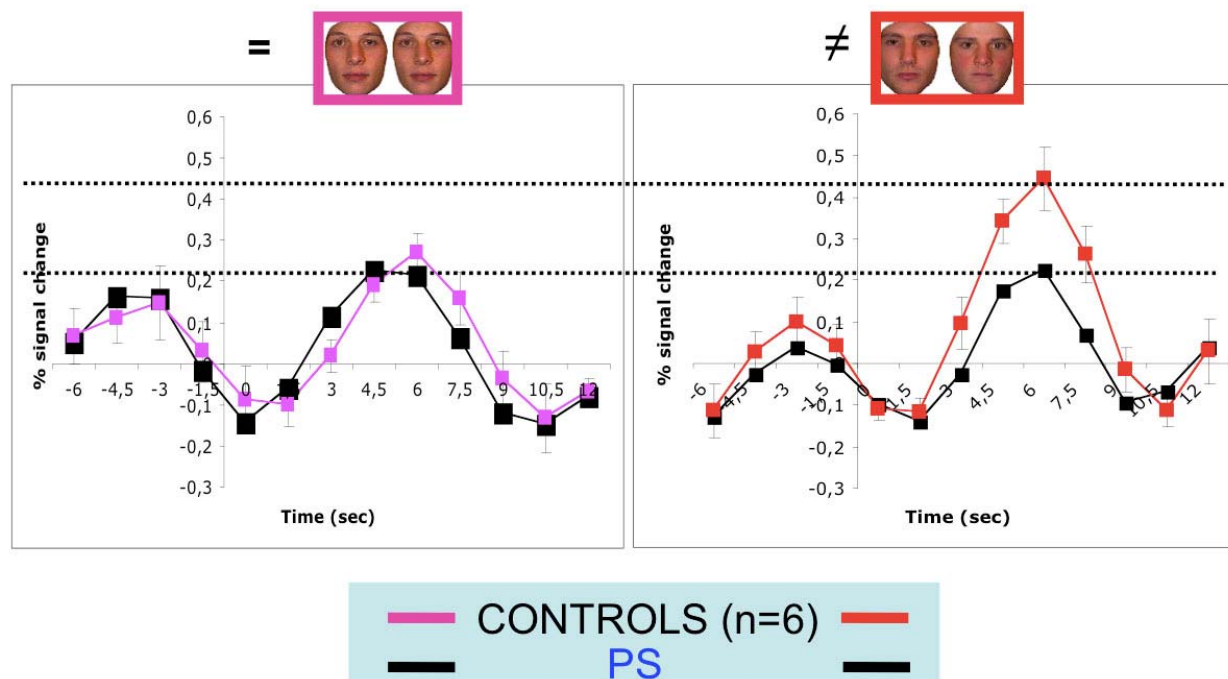
Figure 25. Lack of release from adaptation in an event-related fMRI paradigm in the patient PS' right FFA when different faces are presented in succession as compared to the presentation of the exact same face (88; see also 166). It is as if the faces were not discriminated by this face-selective area in the patient's brain (for individual data of the normal controls, see 88). In a replication of this study, the lack of release from adaptation was confirmed, even when using faces with external features (hair; 166). However, release from adaptation was found in the intact right ventral LOC, both for the patient and normal observers, suggesting that the patient's reduced ability to individualize faces is supported by general processes.

### 7.4. Holistic and fine-grained discrimination of individual faces: a role for an FFA-OFA reentrant loop?

If the FFA can be activated without a contribution of face-selective inputs from the OFA, then what is the contribution of an area such as the OFA? Why would the system need to have such a posterior face-selective cluster? To provide a tentative answer to this question, we should first ask how a patient like PS can be deeply prosopagnosic and yet show a preferential response for faces in the FFA (and in the pSTS) that looks perfectly normal in terms of localization, size and magnitude of the differential fMRI signal between faces and objects. To understand this apparent paradox, one should be reminded that FFA activation emerges by differentiating pictures of faces and nonface object categories ("a face localizer"). This is something that the patient PS is perfectly able to do behaviorally (e.g., 88), and which does not require the integrity of the OFA (see e.g. a recent TMS study, 133). Like other cases of prosopagnosia, her difficulties are apparent when she has to process *individual exemplars* of faces, either to discriminate different individual faces or to recognize an individual familiar face. Hence, populations of neurons in PS' FFA can carry out the categorization of a stimulus as a face, even when it is extremely simplified or degraded (101). However, unlike populations of neurons in the same area of the normal brain (section 6), they may be unable to code for individual faces.

7.4.1. A right FFA that does not discriminate individual faces

This intriguing hypothesis was tested with the patient PS using fMRI adaptation to facial identity. That is, PS and control participants were presented with blocks or pairs of identical face stimuli, as compared to the successive presentation of different face stimuli. Whereas neural activation was lower for repeated facial identities in the right FFA of normal participants, in line with many studies (section 6), there was no significant difference in the level of activation for the patient PS whether different or identical face identities were presented successively (88, 166; Figure 26). That is, despite showing a larger response to faces than objects in the normal range, PS' right FFA showed an absence of face identity adaptation effect. To be more accurate, the level of signal in PS' right FFA was as large as in normal participants when identical faces were presented repeatedly, but failed to show a release from adaptation when different faces were presented: her FFA appears to treat different face identities as being identical.

Hence, contrary to what our initial observations suggested, PS' right FFA does *not* work normally: while being involved in the categorization of the stimulus as a face (as opposed to other objects), the signal in this area does not carry sufficient coding information to discriminate individual faces. Originally, these observations were made during an orthogonal task that the patient was able to perform as well as control participants (color change
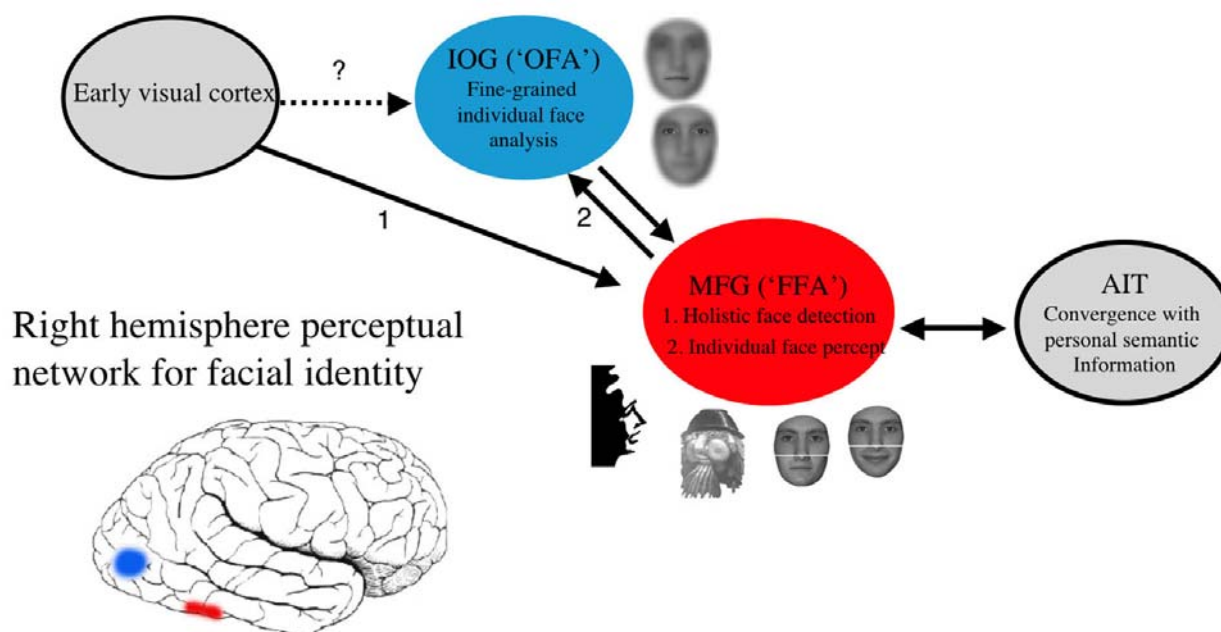
Figure 26. A reverse hierarchical neural model of individual face perception (adapted with permission from 33). Following early visual processes, input is sent to the middle fusiform gyrus, both through the inferior occipital gyrus and independently from it. If the input matches a face representation in this region, even coarsely (template-based matching), face-selectivity emerges ("FFA"; 1. Holistic face detection, illustrated by Mooney and Arcimboldo faces). The representation is then refined through reentrant interactions between this higher-order area and lower-level visual areas, where face-selectivity emerges later. Through this reentrant interaction, a full holistic representation of an individual face is built (2. Individual face percept, illustrated by composite faces). The whole process takes no more than 200 ms. Note that due to intra-area inhibitory processes, the IOG/OFA is not thought to represent faces as independent parts, but population of neurons in this area can emphasize finer-grained information at a local level. In this framework, independent part-based face-selective representations do not exist in the system. Note that this is only a schematic representation and that there are many more face-selective clusters along the ventral occipito-temporal cortex.

detection task) both in a block and an event-related (ER) paradigms (88). Interestingly, they stand out even during an ER individual face discrimination task in the scanner, for which the patient performs well below controls (lower accuracy, slower response time), but better than at chance (166). Again, these results have been recently replicated with the patient DF, also showing (bilateral) FFA activation without release to face identity adaptation (283).

The observation of a dissociation in the same brain area between intact face detection and defective individual face discrimination has several implications. First, one cannot merely consider the level of activation in response to face stimuli in this area in the normal brain to conclude that faces are treated normally: an apparent normal response to faces may in fact be associated with impaired fine-grained coding, as revealed by fMR-adaptation. Second, and more directly related to our findings, the anomalous activation to conditions with different faces in the FFA of the prosopagnosic patient PS, in line with her behavioral impairment, points towards a *critical* function of this region in individual face perception. This is additional information revealed from functional neuroimaging studies of brain-damaged patients

(281): the FFA is not simply involved in individual face perception, as indicated by fMRI studies on normal participants, but it appears to be *necessary* for this function. Finally, and most importantly, these observations suggest that successful individual face discrimination in the FFA may require the right OFA to be intact: without a contribution of the right OFA, which also shows face identity adaptation effects in the normal brain (section 6), the coding for facial identity is impaired.

To summarize, these studies have shown that the preferential activation for faces in the lateral part of the right middle fusiform gyrus (rFFA) can arise in the absence of face-preferential inputs coming from posterior areas, such as the right OFA. However, without any contribution from the right OFA, the activation level in the rFFA when different faces are presented drops down to the level of identical faces[14].

7.5. The neural microgenesis of face perception

Based on these observations, we suggested a reformulation of the neuro-functional organization of face perception in the human brain (298; Figure 26). Following early and crude visual analysis in striate and extrastriate

visual areas, face stimuli would be initially and directly categorized in high-level visual areas of the fusiform gyrus (and possibly pSTS), leading to the earliest face preferential response at a relatively anterior location in the ventral visual stream ("FFA"). Neurons in this non-retinotopic visual area presumably have a relatively large receptive field, as in the area TE of the monkey IT (between 30 and 50 degrees, 299, 300) allowing an initial representation of the whole face stimulus, even when it is perceived out of the foveal view (i.e. a face popping out in a visual scene). This initial representation would be rather coarse, sufficient for accurate detection and categorization of a stimulus, such as a face, but insufficient for the fine-grained analysis required to discriminate identity. This initial face categorization process is preserved for the patient PS, who shows normal behavioral and neural face categorization/detection function, even for degraded high-contrast stimuli such as Mooney faces (101).

However, in the normal brain, following this initial categorization process, a face representation would be progressively refined to allow the extraction of local features and their integration to form a full percept of an individual face supporting identification (a "structural encoding code", according to the terminology of Bruce and Young (153)'s functional model of face processing). This is where lower-visual areas such as the OFA may be called upon in order to play an important role during this microgenesis of face perception (48). That is, the higher order face-sensitive populations of neurons in the FFA may contribute through reentrant signaling to the emergence of functional face preferential responses in lower level visual areas, i.e. the OFA, where populations of neurons with smaller receptive fields would help to refine face representation. In other words, global and coarse information in higher visual areas would serve as a header to set up the processing of fine information related to facial identity in lower visual areas. Given their smaller receptive fields, neurons in the OFA may be fine-tuned to subserve such fine discrimination, which is critical in real-life situations (e.g., recognizing the same identity across age differences, changes in lighting, discriminating siblings or twins, etc.). Reentrant connectivity between these two areas would then support the full extraction of individual face representations (Figure 26).

If we consider the patients PS, the initial categorization of the stimulus as a face in the right FFA, which allows her to categorize faces *vs.* objects, to detect faces in visual scenes, or even to perceive a whole Mooney stimulus as a face, cannot be followed by an integration with lower visual areas in the right hemisphere to refine the initial face representation. Consequently, facial identity discrimination cannot be performed in the FFA of PS, and there is a decrease of the hemodynamic response in the absence of sustained reentrant interactions with the right OFA (Figure 25).

Generally speaking, this proposal of the neural microgenesis of face perception, starting with coarse categorization in high visual areas followed by refinement through reentrant interactions with lower visual areas is in agreement with the presence of massive cortical bi-directional connections (301) and the hypothesis of reentrant phasic signaling between areas of the visual cortex (302). Even though, to my knowledge, it has not been previously formulated for face perception and has certainly not been derived from brain-damaged patient studies, it is a proposal that is inspired from several sources. Starting with Mumford (303), a number of authors have indeed suggested that through feedback connections, higher-level perceptual computations and representations that involve high resolution details, fine geometry and spatial precision may involve lower visual areas (303-306). These proposals have perhaps been more extensively formulated in the reverse hierarchy theory (RHT) of visual perception proposed by Hochstein and Ahissar (307). According to RHT, explicit perception begins at high-level visual cortex, representing "the gist of the scene" or an object at the basic level. This is performed on the basis of a first order approximation of low-level inputs. The details are not represented at this stage, and the representation is then refined by recruiting lower visual areas with smaller receptive field neurons through feedback connections. RHT has been derived from perceptual learning experiments and has been proposed to account for many phenomena of vision and attention, such as the initial and fast perception of object categories (including face detection), feature search "pop out" effects, and whole superiority effects (307).

The revised cortical model of face perception proposed is in agreement with this RHT framework. In fact, faces are perhaps the best candidates for a "coarse-whole to fine-parts" scheme: faces are often detected very far away, out of foveal vision, without and before any detailed analysis and decomposition of their individual features (48, 308). In visual scenes, faces can be detected extremely rapidly (309), and they appear to pop out (310). More to the point, a whole face is perceived readily even when there are no facial features apparent, or when these features are not easily discernable, such as in a painting of Arcimboldo or in a two-tone Mooney face (Figure 3). Besides being compatible with multiple sources of evidence, initial, rapid, feedforward categorization of a stimulus as a face followed by reentrant interactions with lower visual areas is thus (eco)logically valid and highly plausible. This initial categorization and the reentrant interactions between high and low level visual processes would probably take place predominantly in the right hemisphere for faces, in line with evidence from early face categorization and individual discrimination effects, which are observed most significantly in this hemisphere (e.g., 311).

With respect to the RHT, the present proposal differs according to three points at least. First, it is not necessary for initial, feedforward processing of visual information to go through the hierarchy of visual areas, as proposed in the RHT framework, in order to obtain a first approximation of the face stimulus in high level visual areas. That is, direct connections between low-level visual areas, such as V1/extrastriate cortex, and high-level visual areas, such as the middle fusiform gyrus, could bypass the hierarchy of the visual pathway, e.g., excluding the lateral

inferior occipital cortex. Otherwise, there would not be any activation of the FFA in brain-damaged patients with posterior occipital lesions, such as PS and DF. Second, contrary to RHT, the feedforward initial processing of visual information does not lead to an implicit or unconscious representation only. For instance, the patient PS, who is presumably using only this initial feedforward initial processing of visual information, is fully aware that a face is present, and she can consciously define the stimulus as a face. Hence, reentrant interactions with lower visual areas are not necessary to elicit a conscious representation, although they are necessary to refine the percept. Third, it may be incorrect to refer to "feedback" from the FFA to the OFA, as we also initially proposed (85). Rather, in this framework, the initial *input* to the OFA would originate from the FFA. Consequently, rather than feedback between these areas as leading to a full individual face percept it is more correct to refer to phasic *reentrant* connections (302). Reentry is different than feedback in the sense that the relevant areas are not considered as performing independent computations that are sent back and forth between them. Rather, the areas would dynamically synchronize their activity in a functional loop, with functionality emerging from this dual, or multiple, inter-areal synchronization.

Importantly, the present scheme does not imply that, in the normal brain, the visual region of the OFA does not receive inputs from lower level visual areas. However, our hypothesis is that *face-selective* activation leading to OFA activation is driven by inputs from the FFA, rather than the reverse. Finally, rather than a two stage, serial model, this neuro-functional framework should be viewed as a continuous accumulation of evidence for visual categorization (312, 313) within a network of reentrant areas.

The view advocated here has received recent support from an fMRI study showing bidirectional functional connectivity between the OFA and FFA in the context of fMR-adaptation (205). Interestingly, in this study, for both familiar and unfamiliar faces, repetition of identical face images (same size) was associated with changes in "forward" connectivity between the occipital face area and the fusiform face area (i.e., OFA-to-FFA). In contrast, fMR-adaptation across image size was characterized by altered reversed connectivity (i.e., FFA-to-OFA). Although such observations must be considered very carefully given the low temporal resolution of fMRI, they are encouraging, especially since the changes of connectivity were related to individualization of faces. Moreover, the nonhierarchical neural model of the microgenesis of face perception is also compatible with neurophysiological evidence. For instance, single cell recordings in the monkey brain have shown that the representation of a face in IT, which emerges rapidly (70-130 ms, average latency of 100 ms in the monkey brain; 314), is that of a global face, because the stimulus cannot be decomposed into parts without altering the cell's response (139, 315). The very same neurons in these areas appear to carry out both coarse and fine-grained categorization of faces at different time-scales (100-150 ms, 139, 211, 212, 315).

Event-related potential (ERP) recordings on the human scalp as well as the latency of saccadic reaction times also indicate that objects and faces are detected in visual scenes well before a perceptual decision at 150 ms (309, 316, 317). EEG and magnetoencephalogram (MEG) studies indicate that segmented faces are reliably discriminated from other object categories at about 130 ms (onset of occipito-temporal N170 peak; 318-320 for review), and such early face-selective responses (N170/M170) can be observed on the scalp of the patient PS (321). In normal participants, individual representations of faces are discriminated slightly later, at about 160 ms, within the time window of the same component (311, 322, 323). Thus, overall, a reasonable amount of evidence supports the possibility of rapid, coarse categorization of the face stimulus in high level visual areas, such as the right fusiform gyrus (FFA), followed by refinement through reentrant interactions with lower visual areas, in particular the ipsilateral OFA.

8. SUMMARY, CONCLUSIONS AND FUTURE DIRECTIONS

In section 3 of this review, I summarized the two main views about how humans perceive faces: either analytically/part-by-part, or as an integrated whole (i.e., holistically/configurally). The analytical view is popular in psychophysics, computational science and neuroscience. Generally speaking, researchers that are outside of the field of face perception advocate this view. The holistic/configural view, which receives more support than the analytical view within the field of face perception, is based essentially on phenomenology (e.g., the observation of visual illusions such as the composite face illusion) and demonstrations of interactivity between the processing of different face parts in behavioral experiments.

In section 4, we saw that some patients with right posterior brain damage can be massively impaired at face recognition while their object recognition is preserved: *pure prosopagnosia*. Studying such patients offers a unique opportunity to understand the nature of the critical process that is missing in such patients, and consequently that is at the heart of our expertise in face perception. These studies suggest that face perception is qualitatively different than object perception because only face perception requires a holistic perception at a fine-grained level of resolution. Holistic perception at a coarse level of resolution, or local fine-grained perception, can be preserved in cases of pure cases of prosopagnosia, allowing these patients to recognize objects using either their global shape or detailed local parts. In contrast, the construction of holistic fine-grained representations is necessary for individualizing faces efficiently.

In section 5, we saw that such cases of pure prosopagnosia may have vastly different brain lesions, from the lateral occipital pole to the temporal pole of the right hemisphere. This observation suggests a wide distribution of function, which presumably had to develop this way in order to cope with the extreme difficulty of individual face recognition. An unfortunate consequence of this wide

distribution is that the system is particularly fragile: all of the components and their interactions are necessary to perform face recognition at a satisfactory level of performance. In this context, it is rather surprising that acquired prosopagnosia is very rare in the neurological population. However, I would like to argue that this apparent rarity is due to the criteria that are used to define acquired prosopagnosia in the scientific community. Usually, this label is given to patients who complain spontaneously only of face recognition impairments, and who are unable to recognize virtually *all* familiar faces when they are tested (such as the patient PS described extensively in this review). Such patients are indeed extremely rare. However, if one rather considers the kind of criteria that are sometimes used to define cases of congenital/developmental prosopagnosia (e.g. a score below 2 standard deviation of the normal population at face recognition tests), then there is a large proportion of patients with posterior brain damage, especially of the right hemisphere, who could be labeled as cases of prosopagnosia. For instance, Valentine and colleagues (324) tested 91 patients at least 6 months after brain injury and reported a large proportion of patients who were impaired across face learning/recognition tests (between 21% for the least sensitive test and 80%). A large proportion (50%) of patients also felt they would be unlikely, or definitely unable, to recognize people that they had met only a few times, prompting the authors of the study to conclude that it is very common for people with brain injury severe enough to necessitate admission to a rehabilitation unit to have some difficulty with face recognition. Substantial face recognition difficulties also result from right temporal lobe epilepsy (325), atypical development, fronto-temporal dementia, or Alzheimer's disease.

Section 6 summarized two decades of functional neuroimaging of individual face perception in which the focus has been, and still is, essentially on a single area of the middle fusiform gyrus (FFA) that lights up preferentially for faces over other object shapes. The field has only recently acknowledged the wide distribution of the face-selective areas and focus increasingly on anatomical and functional connectivity between these areas. Yet, the dominant view is still that these face-selective areas are organized in a strictly hierarchical feedforward manner, each area computing/representing one aspect of faces that is transmitted in turn to the next area of the hierarchy.

Section 7 challenged this view by showing that face-selectivity can emerge in an area that is located at a spatially advanced stage in the network, the middle fusiform gyrus ("FFA"), despite lesions to posterior face-selective areas (inferior occipital gyrus). These observations made primarily in the prosopagnosic patient PS have inspired functional neuroimaging studies of the healthy brain, showing that face-selectivity can emerge first from the activity of higher-order areas such as the right middle fusiform gyrus ("FFA"), and then in lower-order areas of the inferior occipital cortex ("OFA"). The role of a putative reentrant pathway in lower-level visual areas may be to fill in detailed information to the initially coarse

representation initiated in higher order cortex, the full individual face percept emerging from the coordinated reentrant interaction between these areas.

Obviously, this view remains highly speculative at this stage and the model proposed serves essentially as a road map for future research. It is becoming increasingly clear that there are many face-selective clusters all along the entire ventral occipito-temporal cortex, both in the gyri and sulci, and they are certainly not there just by chance but contribute to the whole function. This brings numerous questions about the functional neuro-anatomy of face perception in the normal brain. For instance, one may wonder why there are so many of these face-selective clusters given that face identity could be coded in sparse populations of neurons? And why some of these clusters show stronger face-selective responses than others? Why responses that are exclusive to faces seem to be found at the level of neurons, columns of neurons or even clusters of columns but not at the level of entire cortical areas? What is the role of the left hemisphere, in particular face-selective clusters in this hemisphere, in normal face perception? Answering these questions will be fundamental to establish the neural dynamics of face perception at the system level in the human brain. While there are certainly multiple methods of Cognitive Neuroscience that will contribute to reach this goal, I believe that a fruitful and inspiring approach in this field is the combination of in depth single-case behavioral and functional neuroimaging investigations of brain-damaged cases of prosopagnosia (see also e.g., 120, 326-328). This methodology is important not only to characterize the function(s) of brain areas and to clarify the necessity of certain areas for a given function, but also to understand the dynamics of the functional connectivity between brain areas. Using this approach for a number of years, my colleagues and I have derived here a number of predictions about the functional neuro-anatomy of face perception. Even if these predictions and the simple scheme proposed here are proved wrong by future investigations, the approach itself should not be abandoned, as it is undoubtedly a very rich source of inspiration for deriving hypotheses about how the human brain perceives faces.

9. ACKNOWLEDGMENTS

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Endnotes: [1] Metric distances between face parts are sometimes referred to as being the "configural" or "configurational" features, in contrast with "local" features such as the shape of the mouth or the color of the eye (e.g., 329). However, attributing this "configural" label exclusively to metric distances is confusing because it suggests that "configural processing" concerns the processing of these relative distances only. In reality, what is meant by "configural" or "configurational" processing in classical studies (e.g. 32, 38) is the processing of the face as an integrated unit (i.e., "holistic processing"). In this perspective, processing a local part inserted a whole face is also a form of "configural/holistic" processing. To avoid this confusion, I suggested in previous reviews to understand the term "configural" as referring to *process*, as a synonym of "holistic", rather than using it to refer to relative distances between face parts (see 33, 34, 46; see also 47). Holistic/Configural processing is the processing as an integrated unit of both the local parts a*nd* their relative distances, without giving a particular status to the latter cues.

[2] This review concerns only acquired prosopagnosia, or prosopagnosia that follows brain damage in adulthood, after the face processing system has reached maturity. For reviews on life-long impairments in face recognition ("congenital" or "developmental" prosopagnosia), see Behrmann and Avidan (64) as well as Duchaine and Nakayama (330).

[3] Note that some brain-damaged patients may be unable to recognize faces although their performance at face matching tasks is in the normal range. However, these patients generally present with multimodal recognition disorders, so that their impairment is not limited to faces or even to the visual modality (see 331, 332).

[4] It could be argued that a central mask does not force a nomal observer or the patient to use the whole face and that local information outside of fixation can be used instead (i.e. a peripheral window). However, if this is the case, then performance should be lower in this mask condition than in the central window condition (109). This is the case for PS, but not for normal observers. An independent gaze-contingency experiment with upright and inverted faces in normal observers also suppors the association with holistic/analytic perception, showing a significant reduction of the mask vs. window difference in performance when faces are presented upside-down (110).

[5] Acquired prosopagnosia is considered as being a rare disorder in neurology, but it is probably because of the criterion that is used to define a patient with prosopagnosia. If the patient has to complain spontaneously, and only, of face recognition problems, and if the patient has to be completely impaired at face recognition, then acquired prosopagnosia is indeed very rare. If one rather defines a case of acquired prosopagnosia as someone who has an abnormally low performance at face recognition, then "acquired prosopagnia" is very frequent in the neurological population (324; see discussion section).

[6] Regarding the only right-handed patient with a left unilateral lesion, functional damage might have been also present in the right hemisphere due to inter-hemispheric spreading of epileptic seizures (333).

[7] Following this study, a patient electrically stimulated in the posterior and middle fusiform face-selective regions reported a perceptual distorsion of the clinician's face (334; a phenomenon previously reported during intracerebral stimulation of face-selective response sin the prefrontal cortex (335). However, there was no effect of electrical stimulation on the recognition of face photographs for the patient of Parvizi *et al.* (334), and the distorsion was not specific to faces, the patient reporting subtle distorsions with objects (e.g. a balloon, a TV). As acknowledged by the authors, the distorsion for nonface objects may be due to spreading of currents to other areas. Indeed, contrary to the study of Jonas *et al.* (134), which was performed with depth electrodes, the electrical stimulation of Parvizi *et al.* (334) was applied using relatively large eletrodes positioned on a cortical surface grid, requiring higher intensity currents to elicit perceptual phenomena.

[8] In the jargon of researchers in this field, "face-selective" does not mean that the region responds only to faces. An area such as the FFA for instance, responds also to nonface objects, yet it is defined as face-selective. The correct term should be "face-preferential" but the term "face-selective" has been used widely and will refer here to a significanty larger response to faces than other visual categories.

[9] In reality, MVPA is not more predictive or able to decode representations than any other method. Researchers using this approach simply choose to look at the data from the perspective of the brain rather than the stimulus. This is not something that is tied to MVPA. If the FFA is activated above a certain level in a given experiment, one is able to "predict" or "decode" that the subject sees, or even imagine, a face rather than a nonface stimulus. MVPA allows one to potentially refine the discrimination of signals by looking at variabilities at a finer scale of brain organization. However, it is not fair to say that contrary to a standard neuroimaging approach, MVPA has access to the "content of the representation" (e.g., 214).

[10] Admittedly, the power of fMR-adaptation has also been sometimes exaggerated, with some authors claiming that the technique could reveal the fine structure of subpopulations of neurons in a given area. In fact, release from FMR-adaptation can only inform that the area is able to discriminate between the items tested.

[11] Some studies have found that a simultaneous change to two properties (e.g., face viewpoint and identity of unfamiliar faces) does not lead to a bigger release from adaptation than a change to either of the two properties (e.g., 168, 208). These findings do not indicate that the regions are insensitive to identity because they could be due to celing effects of the release from adaptation. More generally, these findings could be interpreted as reflecting the coding of identity in a completely viewpoint-dependent manner.

[12] However, the regions were not defined based on face-selectivity in that study, but by the comparison of activity in response to faces vs. scrambled faces.

[13] Evidence of right specialization of face perception in other species (e.g. sheep) is also mixed (336).

[14] This was also observed in the face localizer experiment, where different facial identities were presented: initially, neural activation to faces in the right FFA of PS is as large as or even larger than in the normal brain, but the BOLD response is not sustained and drops down below normal range (Figure 10 in 88). Hence, averaging over the entire time-window of activation for faces may mask any difference between PS' and normal participants' right FFA during a face localizer. However, a closer look at the time-course of activation, in particular when long stimulation blocks and recording epochs are used, reveals an abnormally functioning FFA in the patient's brain. We have speculated that this non-sustained response of the FFA to the lack of reentrant inputs from the OFA contributes to individualization of face representations in the normal brain (a so-called "dynamic diaschisis" effect, 282 see the discussion section in 88).

Send correspondence to: Bruno Rossion, Institute of Research in Psychology and Institute of Neuroscience, Universite Catholique de Louvain, 10, Place Cardinal Mercier, 1348 Louvain-la-Neuve, Belgium, Phone: 32-10-478788, Fax: 32-10-473774, E-mail: bruno.rossion@uclouvain.be