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Twenty years of investigation with the case of prosopagnosia PS to understand human face identity recognition. Part I: function

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Abstract

Following traumatic brain injury in adulthood, Pierrette Sapey (PS) became suddenly unable to recognize the identity of people from their faces. Thanks to her remarkable recovery of general brain function, liveliness, and willingness to be tested, PS's case of prosopagnosia has been extensively studied for more than 20 years. This investigation includes hundreds of hours of behavioral data collection that provide information about the nature of human face identity recognition (FIR). Here a theory-driven extensive review of behavioral and eye movement recording studies performed with PS is presented (part I). The specificity of PS's recognition disorder to the category of faces, i.e., with preserved visual object (identity) recognition, is emphasized, arguing that isolating this impairment is necessary to define prosopagnosia, offering a unique window to understand the nature of human FIR. Studies performed with both unfamiliar and experimentally or naturally familiar faces show that PS, while being able to perceive both detailed diagnostic facial parts and a coarse global facial shape, can no longer build a relatively fine-grained holistic visual representation of a face, preventing its efficient individuation. Her mandatory part-by-part analytic behavior during FIR causes increased difficulties at extracting diagnostic cues from the crowded eye region of the face, but also from relative distances between facial parts and from 3D shape more than from surface cues. PS's impairment is interpreted here for the first time in terms of defective (access to) cortical memories of faces following brain damage, causing her impaired holistic perception of face individuality. Implications for revising standard neurofunctional models of human face recognition and evaluation of this function in neurotypical individuals are derived.

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I. Introduction

On August 14 1992, two weeks before her 42nd birthday, Pierrette Sapey¹ 's head was violently hit by (the mirror of) a London bus on Tower Bridge, leaving her with a life-threatening closed head injury. Despite the severity of the injury and the extensive brain damage (**Figure 1**), following a long recovery and neuropsychological rehabilitation, she was left with remarkably preserved sensory, motor and cognitive functions. However, she forever lost her ability to recognize people's identity by their faces.

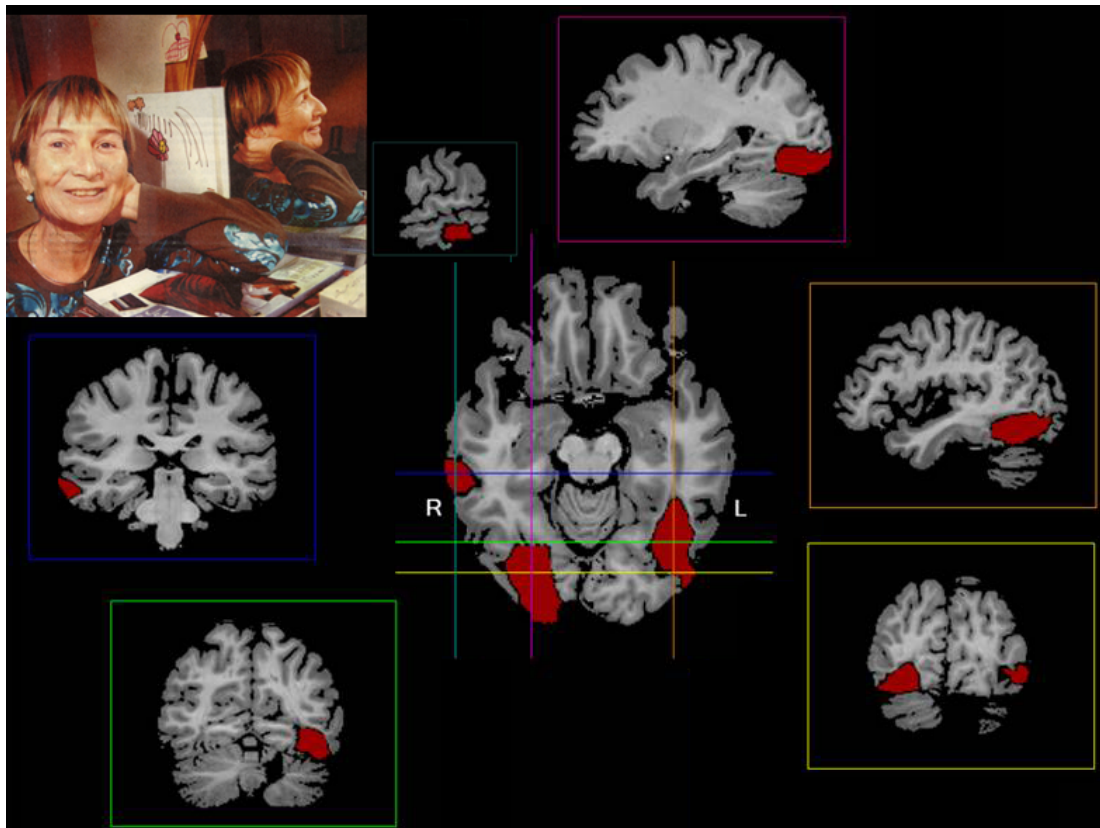


Figure 1. **A.** *Pierrette Sapey, known as the prosopagnosic patient PS in the scientific literature, here photographed at home around 2005.* **B.** *As illustrated in this figure (from Sorger et al., 2007), PS underwent severe brain damage mainly in the right inferior occipital gyrus and the left middle fusiform gyrus, as well as in the left cerebellum (bottom panels). A small third cortical lesion, in the right hemisphere (close to the “R” label in the central figure) is present in the lateral section of the middle temporal gyrus.*

Her neuropsychological case, as the patient PS, was described briefly by the late Eugene “James” Mayer as an attempt to help her improving her ability to recognize the children in the kindergarten where she was working (Mayer et al., 1999). Through James Mayer, I met PS in

¹ This is the real name of the patient, which is indicated here with her formal consent.

January 2000 seven-and-a half years after her accident, to systematically investigate her face identity recognition impairment. As early as the first meeting, she struck me as being potentially extremely informative to clarify the specific nature of human face recognition. Indeed, while her face identity recognition deficit was massive, her visual recognition abilities, including reading and topographical orientation, appeared to be intact, or at least remarkably well preserved: she came to this testing session by herself, taking the bus from her home in a village a few kilometers away, and then from the bus stop in town walking her way to the neuropsychological unit of the hospital. When we asked her to perform a few computer tasks, she sat immediately in front of the computer screen, could identify and use the keyboard keys as well as read written instructions without any difficulty. PS appeared lively and intelligent, understanding instructions to perform visual recognition tasks straight away. She also claimed that despite her inability to recognize people's identity by their faces, she had no difficulties at all at recognizing any other object forms, including animals, fruits or vegetables in real life, as corroborated by her family and friends.

The selective inability to recognize the identity of faces following brain damage, unaccountable by low-level sensory defects or general intelligence problems, was defined by the German neurologist Joachim Bodamer (1947) as *prosopagnosia* (from the Greek 'prosopon', *face*, and 'a-gnosia', *without knowledge*), literally '*the lack of knowledge from the face*'. Back in 2000, when I met PS for the first time, *prosopagnosia* was still considered to be an extremely rare neurological condition. Nowadays, this term is rather routinely used to refer to a *symptom*, i.e., an individual's subjective complaint or below normal range performance at a behavioral face identity recognition test, with or even without neurological history. That is, while *prosopagnosia* implies a face identity recognition deficit, the scientific community now seems to have accepted the converse, i.e., that virtually any face identity recognition impairment – objectively or sometimes even only subjectively defined – should be called '*prosopagnosia*'. As a result, the term '*prosopagnosia*' has now entered the layman's lexicon: it was even used in the 2015 James Bond movie *Spectre*², and people who are not very good at face identity recognition without any neurological history sometimes spontaneously define themselves as having *prosopagnosia* (i.e., "*developmental prosopagnosia*" or "*congenital prosopagnosia*"; McConachie, 1976; for recent

² In the movie *Spectre* (2015), Bond is tortured using a head clamp fused with a robotic drill. Bond's nemesis says he is directing his drill to the fusiform gyrus to erase Bond's memory of faces by making him *prosopagnosic*. However, the drill aims below the mastoid under and behind the ear instead of just in front of 007's ear (Cusimano, 2015). Moreover, it targets the left hemisphere, which plays a secondary role in face identity recognition compared to the right hemisphere (see Rossion, submitted; PS review part II).

reviews see Bate & Tree, 2017; Avidan & Behrmann, 2021). Thus, the condition has become largely unspecific, with numerous so-called ‘cases of prosopagnosia’ studied in the scientific community, and even reports of cases of “prosopagnosia” following COVID-19 (Kieseler & Duchaine, 2021) (see Barton et al., 2021 for a recent review on broadly defined cases of prosopagnosia; see Rossion, 2018a for critical discussion of this symptom-based definition of prosopagnosia, an issue which will also be addressed at the end of the present review).



Figure 2. *PS has been tested at home or at her workplace (the kindergarten, in the top left) for her face identity recognition impairment but has also traveled around the world to be tested. She is pictured here in the kindergarten where she worked all of her career, on a bridge in the city of Bruges in Belgium (2006) and in Belgium, The Netherlands and the UK with various researchers involved in studying her behavioral and neural responses to face stimuli.*

Since impairment in face identity recognition can be due to many causal factors, this broad, symptom-based, definition of prosopagnosia has caused more confusion than clarity in our understanding of the nature of the condition and, most importantly, of face identity recognition (Rossion, 2018a). In spite of this confusion, classical cases of prosopagnosia such as PS, i.e., an adult person without neurological history who suddenly loses FIR ability following brain damage, with preserved general visual, memory and intellect function, as well as visual object recognition, remain extremely rare. As I will try to illustrate in the present review, and in line with the topic

of the present special issue, even in the age of big data – or perhaps *especially* in the age of big data (Medina & Fischer-Baum, 2017) - such single cases can be extremely important to understand how the human brain recognizes individuals by their face, an astonishing ability which is fundamental for social life, especially in the human species. Of course, when I first met PS, I could not anticipate that the research on this patient would be carried out so intensely and regularly for the next 20 years, and is still ongoing these days, with that many people getting involved in this research. PS has now been tested for hundreds, if not thousands, of hours, mainly in my laboratory, but also in other research centers all around the world. She has been tested in numerous behavioral experiments mainly with computers, recording her motor responses to various tasks, but also her eye movements and electro/magneto-encephalographic signals. PS has also been tested with functional magnetic resonance imaging (fMRI) for more than a hundred hours in total, in various neuroimaging centers around the world (**Figure 2**).

PS's case has been described extensively in scientific publications spanning from 2003 to 2022, i.e., in 34 papers with experimental data in total (to my knowledge) (**Table 1**).

1. **Rossion, B. et al. (2003). *Brain*, 126, 2381-2395.**
2. **Caldara, R. et al. (2005). *Journal of Cognitive Neuroscience*, 17, 1652-1666.**
3. **Schiltz, C. et al. (2006). *Cerebral Cortex*, 16, 574-86.**
4. **Sorger, B. et al. (2007). *NeuroImage*, 35, 836-852.**
5. **Orban de Xivry, J.-J. et al. (2008). *Journal of Neuropsychology*, 2, 245-268.**
6. Dricot, L. et al. (2008). *NeuroImage*, 40, 318-332.
7. Dricot, L. et al. (2008). *Behavioral Neurology*, 19, 75-79.
8. Rossion, B. (2008). *NeuroImage*, 40, 423-426.
9. Steeves, J. et al. (2009). *Neuropsychologia*, 47, 2584-2592.
10. **Rossion, B. et al. (2009). *Journal of Neuropsychology*, 3, 69-78.**
11. Peelen et al. (2009). *Soc Cogn Affect Neurosci.*, 4, 268, 277.
12. Farivar et al. (2009). *Journal of Neuroscience*, 29, 5336-5342.
13. Righart et al., (2010). *Cerebral Cortex*, 20, 1878-1890.
14. **Ramon, M., & Rossion, B. (2010). *Cortex*, 46, 374-389.**
15. **Ramon, M. et al. (2010). *Neuropsychologia*. 48, 933-944.**
16. **Busigny, T. & Rossion, B. (2010). *Cortex*, 46, 965-981.**
17. **Busigny, T. et al. (2010). *Neuropsychologia*, 48, 2051-2067.**
18. **Busigny, T. & Rossion, B. (2010). *Behav Neurol.*, 23, 229-231.**
19. **Van Belle, G. et al. (2010a). *Neuropsychologia*, 48, 2609-2620.**
20. **Van Belle et al. (2010b). *Behav Neurol*. 23, 255-7**
21. **Busigny, T., Rossion, B. (2011). *Journal of Neuropsychology*, 5, 1-14.**
22. **Jiang, F. et al. (2011). *Visual Cognition*, 20, 865-882.**
23. **Rossion, B. et al. (2011). *Frontiers in Human Neuroscience*, 4:225.**
24. Prieto, E.A. et al. (2011). *Front Hum Neurosci*. 2011;5:138.
25. Simon et al. (2011). *Cortex*, 47, 825-838
26. **Quadflieg, S. et al. (2012). *Visual Cognition*, 20, 865-882.**
27. **Van Belle, G. et al. (2015). *Cognition*, 136, 403-408.**
28. **Richoz, A-R. et al. (2015). *Cortex*, 65, 50-64.**
29. **Liu-Shuang, J. et al. (2016). *Neuropsychologia*, 83, 100-113.**
30. Fiset, D. et al. (2017). *Soc Cogn Affect Neurosci*. 12, 1334-1341.
31. **Ramon, M. et al. (2017). *Visual Cognition*, 24, 321-355.**
32. **Ramon et al. (2018). *Cognitive Neuropsychology*, 35, 304-313.**
33. Gao, X. et al. (2019). *Cortex*, 119, 528-542.

34. Fysch, M.C, & Ramon, M. (2022). *Neuropsychologia*, in press.

Table 1. List of publications with data on the prosopagnosic patient PS to date (2022), including 31 full papers and three short reports (see bibliography for full references). In bold, papers containing relevant behavioral data as summarized and discussed in the present review (part I).

This makes PS, to my knowledge, by far the most documented case of prosopagnosia in the scientific literature and arguably one of the most studied neuropsychological case ever. In addition, her case study has formed the basis of several theoretical reviews on prosopagnosia and human face recognition (Rossion, 2008; Rossion, 2014; Rossion, 2018a), has led to the development of many experiments applied to other single case studies of prosopagnosia (patient GG: Busigny et al., 2010a; Van Belle et al., 2011; patient LR: Busigny et al., 2014; also patient KV as the first case of transient prosopagnosia due to intracranial stimulation: Jonas et al., 2012) and, as summarized in the second part of this review on PS, inspired entire lines of research on the neural basis of human face recognition with fMRI but also transcranial magnetic stimulation (TMS).

Although PS's case of prosopagnosia has been described in numerous publications, there is no integrated review of studies performed with her published to date. The present contribution aims at filling this gap, providing a structured review of about 20 years of intense research carried out with PS. Most importantly, the goal of the present review is to show how the systematic and detailed study of PS has inspired and constrained theoretical views about how the typical adult human brain recognizes the identity of people by their faces, as well as contributed to substantial improvement of methodological paradigms to measure face identity recognition in the neurotypical population. This theory-driven review is divided in two parts. In part I, the present text, behavioral, eye movement and some EEG studies on PS (compared to neurotypical control participants) are reviewed, with the goal of describing the understanding of the *functional nature* of PS's face identity recognition impairment, i.e., how specific is her recognition deficit to the category of faces?, is it perceptual or memory-based?, what kind of facial cues are difficult to recognize for her and why?, etc. The main body of the review is organized in separate sections that follow the progress made in understanding the nature of PS's impairment, and the implications for studies on prosopagnosia and face identity recognition in neurotypical individuals. Part II of the review of PS's case (Rossion, submitted) is devoted to a review of the neural basis of human face recognition from studies of PS's prosopagnosia, i.e., how her case study directly and indirectly inspired and constrained neurofunctional models of human face recognition.

II. Face identity recognition (FIR)

The present theoretical review focuses on *face identity recognition* (FIR), which is the primary impaired function for PS. In psychology, the term “recognition” is often used to refer to the judgment of previous occurrence (specifically “*the ability to identify information as having been encountered before*”, APA Dictionary of Psychology; see also Mandler, 1980). In psychological research on human faces, the term ‘face recognition’ is even often restricted to the judgment of a previous occurrence of specific *identities* of faces, therefore of *familiar* (or familiarized) faces only. As we shall see later, this restrictive definition causes considerable conceptual confusion, for instance implying that all forms of recognition are necessary due to experience, creating an insurmountable barrier between unfamiliar and familiar faces or between ‘perception’ and ‘memory/recognition’, and is therefore not adopted here. Instead, FIR is defined here more generally as *the production of a unique response to a given face according to its individually distinctive characteristics*. FIR so defined involves visual *discrimination* (from many other signals, i.e., individual faces) and *generalization* (of the same individual face across substantial changes of appearance) and applies to both familiar and unfamiliar faces. It is the most precise form of recognition, involving and requiring unique (combinations of) cues.

In humans, the face is the visible body part which carries the richest, i.e., most diverse across individuals, signals for identity, at a genetic and morphological level (Sheehan & Nachman, 2014). In our species at least, FIR is a key brain function, which requires many processes, including the extraction and combination of low-level visual cues; the discrimination of an individual’s face as a unique visual pattern, concerning its shape, texture and color, from competitive similar patterns (i.e., faces of other individuals); the generalization of this face across substantial changes of appearance; the memory encoding, updating and implicit/explicit recollection of this face identity; and its association with specific semantic, lexical (i.e., names) and emotional information that cannot be extracted directly from the visual stimulus.

Although many animal species have a face – a body part that developed originally for food prehension and sensory interactions with the physical world (McNeill, 2000) - and live in social groups, very few animal species may rely on face signals to recognize the identity of conspecifics (Sheehan & Tibbetts, 2011). Even nonhuman primates such as macaque monkeys, widely considered in the neuroscientific community as the best available animal model of human brain function (Passingham, 2009) including visual object recognition (DiCarlo & Cox, 2007), appear seriously limited at FIR compared to humans (Parr et al., 2008; Rossion & Taubert, 2019; Rossion, in press). In fact, no other species appear to rely on the face as much as humans for identity recognition, with such a high level of accuracy, automaticity and speed. Indeed, neurotypical

human adults are able to recognize at least thousands of identities from their faces only (Jenkins et al., 2018), they can recognize a face identity at a glance and without explicit instruction to do so (i.e., automatically) across a wide variety of viewing conditions (e.g., Visconti di Oleggio Castello & Gobbini, 2015; Zimmermann et al., 2019). In humans, FIR plays a key role in social interactions, and it has even been suggested that the face, in particular, has evolved throughout human evolution in part to maximize facial identity signals (i.e., maximize diversity even among genetically homogenous populations; see Sheehan & Nachman, 2014).

Despite an enormous amount of experimental research on human FIR since the 1960s' (Ellis, 1975 for an early review; more recently: Calder et al., 2011), the scientific community still has little understanding and agreement about the nature and neural basis of this function (Young, 2021). Nowadays, besides a substantial amount of research on artificial FIR systems mainly for security and control (Christakis et al., 2021) human FIR is studied in typical human observers in hundreds of laboratories across the world, both with behavioral and neural measures. The current trend in the scientific community is to collect large data samples and use sophisticated psychophysical, neural and computational techniques of recording and analysis, for instance to characterize interindividual variability in FIR and its neural basis in the typical population (e.g., Zhen et al., 2015; Rostami et al., 2017; Wilmer, 2017; McGugin et al., 2018; Parker et al., 2022), or “decode” face identity signals at various scales and levels of brain organization (e.g., Nestor et al., 2011; Dobs et al., 2019). This type of research is not only performed in humans, but also in other animal species, especially macaque monkeys (e.g., Chan & Tsao, 2017).

However, here, along the lines of detailed case studies in neuropsychology that have provided a wealth of information about the mechanisms of learning and memory in the medial temporal lobe (the patient HM; Scoville & Milner, 1957; Corkin, 2013), visual object recognition (HJA; Humphreys & Riddoch, 1987), or the dissociation between vision for object recognition and for action (DF; Goodale & Milner, 2004) for instance (see Code et al., 1996), I will try to show that systematic observations and data collected in a *single human neuropsychological patient*, are uniquely valuable, and perhaps even critical, in constraining and inspiring our understanding of human face (identity) recognition. Although careful observation, replication, intuition and interpretation are key to the success in this endeavor, thanks to the impressive technological progress made in cognitive neuroscience over the past two decades and the willingness of PS to participate in many experiments, this research also blends a traditional single-case approach in neuropsychology with sophisticated techniques of psychophysics and cognitive neuroscience.

In part I of this review, the case of PS will be used to inform a number of major issues about human FIR such as *whether faces are recognized by specific processes in the human brain*, if so, *what is the nature of these processes* and how can they be best understood. The review will also address the issue of whether there are fundamental differences in the recognition of familiar and unfamiliar faces, and what is the relationship between (visual) *perception* and *recognition* of faces. I will discuss the controversial issue of the definition and evaluation of prosopagnosia, and why I think that single case studies of this kind, despite the challenges that they constantly face, can be much more informative scientifically about the nature of FIR than group studies of brain-damaged patients or of individuals with neurodevelopmental deficits at FIR.

III. A massive impairment at face identity recognition

Structural scans of PS's brain carried out many years after her accident revealed extensive posterior brain damage due to severe hemorrhages: in the right inferior occipital gyrus, the left mid-ventral occipito-temporal cortex (i.e., midfusiform gyrus), together with the left posterior cerebellum and a smaller lesion to the right middle temporal gyrus (**Figure 1**; Rossion et al., 2003; see Sorger et al., 2007 for detailed neuroanatomical data; and part II of the review on PS). Despite the posterior damage, which includes part of the primary visual cortex in the right hemisphere and most likely white matter fibers from the inferior longitudinal fasciculus and optic radiations, the patient's low-level visual function is well preserved. Her visual acuity, contrast sensitivity and color vision as evaluated by classical measures are in the normal lower range (Rossion et al., 2003; Sorger et al., 2007). Notably, however, PS has a left paracentral scotoma of about 2° by 3° as defined by static and dynamic perimetry (**Figure 3**; see Sorger et al., 2007 for details). Such left superior visual field defects are typical of classical cases of prosopagnosia, and served in fact as the first clinical indicators for the right hemispheric dominance in human face (identity) recognition (Hécaen et al., 1957; Hécaen & Angelergues, 1962; see also Bouvier & Engel, 2006; Rossion & Lochy, 2022). PS's performance at standard clinical and neuropsychological tests of visual perception was initially reported in Table 1 of Rossion et al. (2003) and Sorger et al. (2007).

Even if the field of human face recognition is surprisingly short of information about the minimal low-level visual capacities that are necessary for FIR, it is safe to say that this function does not require a full visual field, high visual acuity as well as perfect contrast and color vision (e.g., Yan et al., 2021). Thus, in line with demonstrations of clear dissociations between (prosop)agnosia and low-level visual defects (de Haan et al., 1995), it is fair to say that PS's core FIR deficit, which is spectacular as we shall see shortly, is not due to these low-level visual difficulties: she can explore faces very well and describe their features (including eye color for

instance) as well as anybody. Regarding this issue, it must be noted that prosopagnosia is not, as often erroneously defined, a deficit of FIR *in the absence* of low-level visual defects. Instead, it is a deficit of FIR that *cannot be explained* by putative low-level visual defects. Yet, slight low-level visual defects can be present and potentially affect PS's performance at a specific task (i.e., a small stimulus presented briefly at fixation would be partially occluded by her scotoma as illustrated on **Figure 3**). Therefore, these defects must be carefully considered when designing experiments to directly contrast her visual recognition performance to typical individuals.

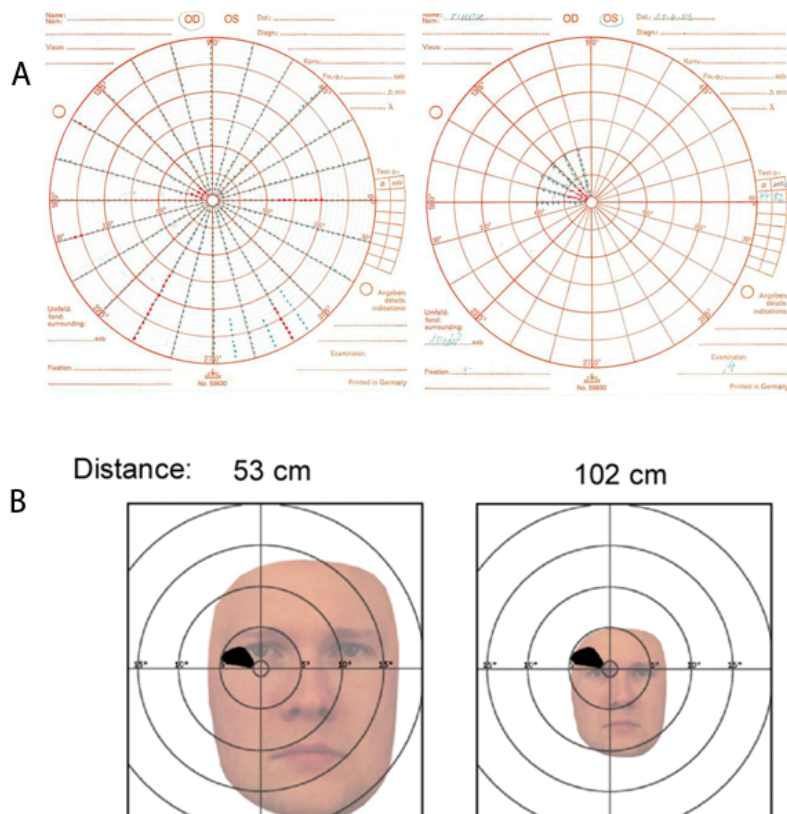


Figure 3. A. Due to brain damage, PS has a left paracentral scotoma, as defined with static and dynamic perimetry (Sorger et al., 2007 for details). A left upper visual field defect scotoma is relatively common in reported cases of prosopagnosia (Hécaen & Angelergues, 1962; Bouvier & Engel, 2006), this observation forming the basis of our knowledge regarding the right hemispheric dominance of human face recognition (Hécaen & Angelergues, 1962; see Rossion & Lochy, in press). In B, the effect of the scotoma is schematized here for a fixation point on the picture of a face in a typical experiment presented at two different distances ($15^\circ \times 10^\circ$ of visual angle on the left; from Van Belle et al., 2010).

Despite the extent of brain damage, since her accident and to this date, PS's only continuing complaint concerns her impairment at recognizing people's identity by their face, including those of family members, as well as her own. To determine a person's identity, she usually relies on contextual information, her excellent general semantic and episodic memory, and non-facial cues such as the person's voice, posture, gait, etc. Providing that there is no context

given, i.e., that she does not expect to be shown pictures of specific people she knows, and that the stimuli do not have obvious singular cues for identity, her ability to tell whether a face is familiar or not is close to zero (Rossion et al., 2003; Simon et al., 2011; Busigny et al., 2014a). Importantly, she does not suffer from a naming impairment or a lack of knowledge of famous people: she watches TV almost every day, surfs on the internet, read magazines, and can recognize celebrities from their name without difficulty (Busigny et al., 2014). To illustrate, she was tested relatively recently (late 2017) at a task requiring finding the famous written person's name among three options: she was flawless (100%) at this task. In contrast, when the names were replaced by natural, clearly visible images of the faces, she scored at chance level (33%) (**Figure 4**).

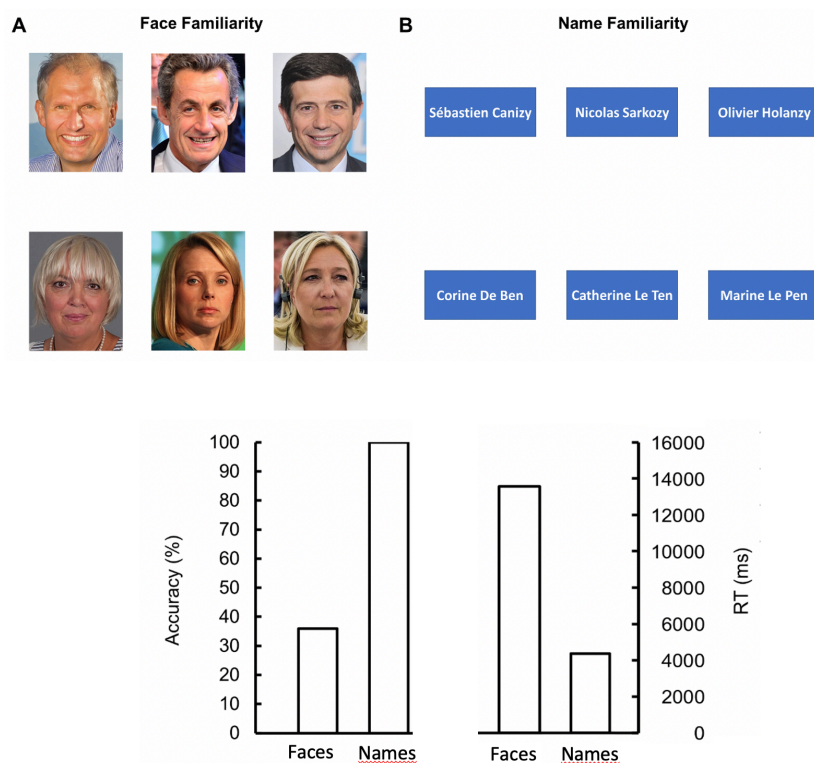


Figure 4. An illustration of PS's face identity recognition inability (Volfart, Michel & Rossion, in preparation). Despite watching TV or surfing on the internet almost every day and being exposed to a wide range of famous faces in Switzerland and France in particular, PS (tested here in December 2017) scored at chance level when she had to choose a famous face identity among three options. In contrast, she was flawless at finding the correct famous written name among three options (with two plausible distractor names transformed from the celebrity's name).

When PS is shown a limited set of pictures of faces of familiar people, and if she knows in advance some or all of the identities that should be included in the set, she is able to recognize a fair number of these identities from their face. For instance, she was presented with face pictures of 27 children one-by-one, knowing that every face is of a highly familiar child to her and belongs

to the group of kindergarten children where she works. In these conditions, PS was able to recognize about 60% of the children from their faces only, an impressive performance for her that is nevertheless much lower than her kindergarten colleagues' performance (Orban de Xivry et al., 2008; Ramon et al., 2017). Moreover, in these conditions, she takes an extremely long time relative to her colleagues to scrutinize each face and make guesses about the identity of each child. Interestingly, if pictures of the same familiar (children) faces are suddenly mixed up with a set of unfamiliar (children) faces, her performance at a familiarity decision task becomes close to chance level (Busigny & Rossion, 2010; Ramon et al., 2017).

This latter comparison shows that human FIR is not just about processing or 'decoding' information from the stimulus, and reflects the nature of the greatest challenge of FIR, in prosopagnosia or for typical observers: to be able to correctly recognize a (new view of a) familiar face identity among unfamiliar faces *rapidly* and *automatically*, especially when this familiar face is not expected, appears under unknown viewing conditions and in an undetermined context. Hence, it is fair to say that the context plays an important role in FIR (since early development, see Sugden & Moulson, 2019). For instance, PS will be able to recognize her husband, daughter or son from their face in her house, where she expects to meet them and cannot really confuse them. However, she has failed to recognize the same family members on several occasions where she did not expect to meet them (in town, at a theatre intermission, on the beach after they had moved to a new place, ...), especially when they were mixed up with unfamiliar people (Mayer et al., 1999).

Importantly, when PS is asked to recognize pictures of *unfamiliar faces*, she also has major difficulties. For instance, she was impaired at the widely used Cambridge Face Memory Test (CFMT, Duchaine & Nakayama, 2006), which requires explicit encoding and recognition of individual faces among distractors (Ramon et al., 2016; but see Fysh & Ramon, 2022). Even when there is no explicit encoding procedure and requirement to hold an individual face in memory in the absence of the stimulus, PS is impaired at individuating faces, for instance at the Benton Face Recognition Test (BFRT, Benton & van Allen, 1968), requiring matching pictures of unfamiliar faces across head rotation and lighting direction changes. However, she performs well above chance level at these tests, and her deficit appears only clearly when considering her extremely prolonged response times (RTs), for instance at the electronic version of the BFRT (BFRT-c; Rossion & Michel, 2018; see also Busigny & Rossion, 2010; and Fysh & Ramon, 2022 for a recent discussion of this issue). Relative to typical participants, PS's impairment in accuracy rates and RTs at matching/discriminating pictures of unfamiliar faces for their identity has been documented in tens of experiments, as shown for example in section 4 below.

In summary, while, for obvious reasons, her FIR impairment is expressed only to familiar faces in real life, it can be evidenced for pictures of both familiar and unfamiliar faces, and across a wide variety of tasks, with or without delay between pictures to recognize. While, on this evidence, PS could be defined as a case of *apperceptive* (rather than associative) prosopagnosia according to standard neuropsychological models of human face recognition (Bruce & Young, 1986; see Davies-Thompson et al., 2014), this distinction does not rest on solid evidence (Davidoff & Landis, 1990; Farah, 1990), and is considered as being problematic rather than useful here. Therefore, it will not be adopted in the present review to define PS's case, as discussed and justified more extensively below (section X).

IV. A category-specific face recognition impairment: prosopagnosia

Since its first written report in a scientific journal (Quaglino & Borelli, 1867) and for almost a century, a sudden impairment at FIR following brain damage, for instance a stroke, was considered only as an element, or a *symptom*, of a more general impairment at visual object recognition, i.e., *visual object agnosia* (e.g., Charcot, 1883; Wilbrand, 1887), even when the FIR impairment was emphasized (e.g., Millian, 1932; Donini, 1939). However, Bodamer (1947) defined *prosopagnosia* as “*The selective disturbance in grasping physionomies, both of one's own face as well as of those of others, which are seen, but not as the physiomy of a particular individual*”, claiming next that “*It appears in varying strengths and together with the various forms of agnosia, but can be separated from these from the outset*” (Bodamer, 1947, p.10, text underlined here; see Ellis & Florence, 1990 for partial translation of the original paper)³. Hence, technically, questioning whether prosopagnosia is truly a deficit of visual recognition limited to faces, sparing object recognition, is questioning whether prosopagnosia exists or not (Rossion, 2018a). While Bodamer (1947) was unable to provide any convincing evidence in support of his

³ In fact, the very existence not only of prosopagnosia, but of visual agnosia in general remained heavily contested for decades after this definition. Eberhard Bay (1950; 1953) in particular, but also others (Critchley, 1964; Bender & Feldman, 1972), argued strongly against a defect of recognition that could be specific to a given sensory modality (i.e., vision) and yet not accounted for by a deficiency of the sensory organs themselves or of the pathways conveying sensory information to the brain, which was considered to be the seat of amodal higher cognitive functions. This issue was progressively resolved only in the second half of the 20th century by showing that low-level visual impairments alone could not account for object recognition deficits in visual agnosia (Ettlinger, 1956; de Haan et al., 1995).

audacious proposal, the FIR disorder appeared as the primary complaint and symptom in other cases reported in subsequent years after his contribution (see the early review of Hécaen & Angelergues, 1962). Thus, despite continuous skepticism, not only about the existence of prosopagnosia but also visual agnosia², the term prosopagnosia remained used after Bodamer (1947) to define brain-damaged patients with a FIR impairment in the context of visual agnosia, or to refer to the symptom itself (e.g., “*the patient X has visual agnosia and prosopagnosia*”, see e.g., the review of Farah, 1990).

Before meeting PS, I was skeptical about the existence of prosopagnosia, or “pure prosopagnosia” (an expression generally used, including by myself in the past, but technically incorrect, as explained above), i.e., a deficit in FIR with preserved object recognition. Part of this skepticism was based on a number of reports on the patient LH defined by many authors as a case of prosopagnosia (e.g., Etcoff, 1991; Farah et al., 1995a; 1995b; Barton, 2008), but whose ability to recognize real objects and pictures had been largely overestimated (e.g., Farah et al., 1995a). In reality, if LH was able to recognize the majority of pictures of common objects presented to him through vision only, he required several seconds to recognize each object, and he was largely impaired at recognizing living things, animals in particular (Levine & Calvanio, 1989; Farah et al., 1991) (see Rossion, 2018a for a recent criticism of this case).

In contrast, PS never complained nor presented any difficulty at recognizing nonface objects in real life and, throughout all these years, I never saw her hesitating or mistaking a non-face visual object for another one in real life circumstances, whether she had to recognize living or nonliving things. When questioned about it, her family and colleagues never reported her misidentifying or asking the identity of an object from vision, even though they were all well too aware of, and witnessed many times PS’s struggle at FIR in real life circumstances. In fact, PS is surprised that we tested her so much at recognizing nonface visual object stimuli over several years.

Formally, PS was tested without time constraints in various object recognition tasks and performed extremely well (Rossion et al., 2003). For instance, we asked her to name out loud, as accurately and rapidly as possible, the full set of the 260 colored drawings of Snodgrass and Vanderwart (Rossion & Pourtois, 2004) presented one by one. Although some of these objects are not easy to recognize from the (old) drawings and it is a difficult task for which she cannot correct herself, PS named each object in turn without hesitation. She made only a few mistakes or failures to recognize, i.e., on 8 stimuli out of 260, with no systematic difficulties: she did not recognize a poor drawing of a pepper (which she named correctly and rapidly on another drawing), a lobster drawn from the top, an ant, a cloud (poorly drawn); a bee was named as a fly with

hesitation, but there also the poor drawing and ambiguous color make it understandable. A violin was too rapidly named a guitar. She also could not recognize the raccoon and black-footed ferret, animals that she simply did not know about and never encountered before in her environment. Excluding these last two, her score on rapid naming of animal pictures was of 49/52, and her score was of 23/24 for naming fruits and vegetables⁴. While recognition of fruits and vegetables pictures is often impaired in other reported cases of prosopagnosia (e.g., 9 out of 10 patients reported in Barton, 2008), PS was able to name another set of such stimuli without any mistakes and quickly⁵.

On this basis, it must be clear that PS does not suffer from basic-level visual object recognition impairment. Most recently, we completed this investigation with a test of her ability to recognize a large set of pictures of objects presented under canonical or noncanonical views (Ghose & Liu, 2013): her recognition of these objects was almost flawless (114/120), with no difference whatsoever of accuracy and speed between canonical (56/60, mean RT 1877ms) and noncanonical (58/60, mean RT 1863ms) views of the same objects (Rossion & Desruet, unpublished data). Hence, PS truly appears to be a classic case of prosopagnosia (i.e., according to the definition of Bodamer, 1947): an impairment of visual recognition restricted to the category of faces.

V. Damasio's error

Of course, there is an important potential confound to consider when comparing PS's failures and successes at face and object recognition respectively: she is impaired at *individual level* face recognition (e.g., John's face) but has no difficulties at generic or *basic level* object recognition (e.g., a table, a tomato, etc.). Hence, her deficit may not be at recognizing faces *per se* but at recognizing *individual exemplars* of visual categories in general. Since most objects in the visual environment do not have to be recognized at the level of specific exemplars, her recognition deficit may superficially appear as being specific to faces.

In apparent support of this view, PS has no difficulties at *generic face recognition*: she readily recognizes visual stimuli as faces, and is in fact very good at that (Rossion et al., 2011; Liu-Shuang et al., 2016). While I will elaborate on her ability to perform generic face recognition

⁴ See here <https://face-categorization-lab.webnode.com/products/ps-object-naming/> for a full video of PS naming the objects one by one (in French). The video was filmed a few years after the original report of PS's performance at naming the Snodgrass and Vanderwart stimuli (Rossion et al., 2003).

⁵ See here <https://face-categorization-lab.webnode.com/products/propopagnosic-vegetable-identification-control-/> for a full video of PS naming the fruits and vegetables one by one (in French).

in later sections of this review, how about the recognition of individual exemplars of nonface object categories? In real life at least, PS does not seem to have any difficulty at recognizing individual exemplars of nonface categories: she could recognize Dr. Mayer's tie for instance, and once even remarked that her neighbor had a new dog (this neighbor then complained that PS could recognize dogs' identities but not her).

This view of prosopagnosia as reflecting an impaired *process* (i.e., the recognition of individual exemplars of a visual category) rather than a specific type of signal (i.e., faces) was initially proposed by Faust (1947; 1955), a contemporary of Bodamer. This view emerged from, and appeared supported by, the observation of brain damaged patients who were impaired at FIR together with difficulties recognizing various types of chairs (Faust, 1947; 1955), food items and animals (Pallis, 1955), different car brands (Macrae & Trolle, 1956), different fruits (De Renzi et al., 1968), horses (Newcombe, 1979), similar birds (Bornstein, 1963), individual cows (Bornstein et al., 1969) or plants and mountain peaks (Clarke et al., 1997) (see Barton & Corrow, 2016).

Damasio and colleagues (1982) championed this view, arguing that reported cases of prosopagnosia often emphasize the recognition impairment for faces because 1) faces are highly similar to each other, i.e., they form a visually homogenous category and 2) in the human species at least, it is often mandatory to recognize them at the individual level, for social reasons. In contrast, objects may be usefully recognized following a coarser level of analysis ('generic', or 'basic-level' recognition/categorization; Rosch et al., 1976). Therefore, according to Damasio and colleagues (1982; 1986), "prosopagnosic" patients would have no difficulty at basic level object recognition, or even at identity recognition of visual stimuli belonging to groups in which different members have a different visual structure. However, they would have difficulties recognizing all visual stimuli, not just faces, belonging to classes in which numerous members are physically similar and yet individually different (Damasio et al., 1982; 1986).

While these authors never provided any data to support their view, Gauthier et al. (1999) provided apparent empirical support for this *within-category/visual similarity recognition* account of prosopagnosia with two brain-damaged patients (SM & CR) tested with matching tasks in which the similarity of a distractor to the target item was manipulated (e.g., a duck to discriminate either from a chair, a pelican or, most importantly, another individual duck). Although the authors concluded that the two patients showed disproportionate decreases of performance relative to controls, as manifested in particular by abnormally increased response times (RTs) with increasing levels of visual similarity between the target and the distractor, their data was not convincing at all (see the criticisms in Busigny et al., 2010a; Rossion, 2018a).

In particular, as argued in these latter papers, this visual similarity/within-category account of prosopagnosia is not well supported because the patients who complain and show increased difficulties with similarly looking objects, such as the two patients tested by Gauthier et al. (1999), already have clear difficulties at basic-level object recognition to start with. That is, they are clear cases of visual object agnosia (Behrmann & Williams, 2007). While such patients do not readily recognize objects, they are more likely to make visual underspecification errors, in particular for living things, which have much more similar shapes than manmade objects (e.g., the visual agnosic patient LH, see Levine & Calvanio, 1989). Importantly, this does not mean that their impairment concerns a putative generic individual recognition process in the visual modality. Indeed, testing this hypothesis, i.e., testing the *within-category/visual similarity account* of prosopagnosia, requires first identifying a clear case of prosopagnosia, i.e., a patient without basic-level object recognition difficulties to *then* evaluate his/her identity recognition of nonface objects (Rossion, 2018a). The patient PS, who has no difficulty recognizing fruits and vegetables presented altogether, and can spontaneously match similar visual shapes in video memory games⁶, offered us this unique opportunity.

To do that, we first used a delayed 2-alternative forced-choice (2AFC), which showed that PS was able to discriminate among individual exemplars of several nonvisual categories (pictures of cars, birds, boats, houses) as accurately and rapidly as age-matched controls (Schiltz et al., 2006; **Figure 5**) (see also Farivar et al., 2009 for PS's learning of a homogenous set of pictures of chairs). In contrast, her performance at the same task for faces, which were not the most difficult items for normal controls, was significantly impaired (**Figure 5**). These results contrast with those of the reported prosopagnosic patient LH mentioned above, who was impaired both for FIR and object identity recognition (OIR) at these tasks (see Rossion et al., 2018a).

⁶ See here for a full video of PS matching similar shapes in the “memory” game: <https://face-categorization-lab.webnode.com/products/ps-memory/>. Filmed in one branch of the popular Dutch bookstore chain Selexyz, inside of a 13th century Dominican church in Maastricht, Holland.

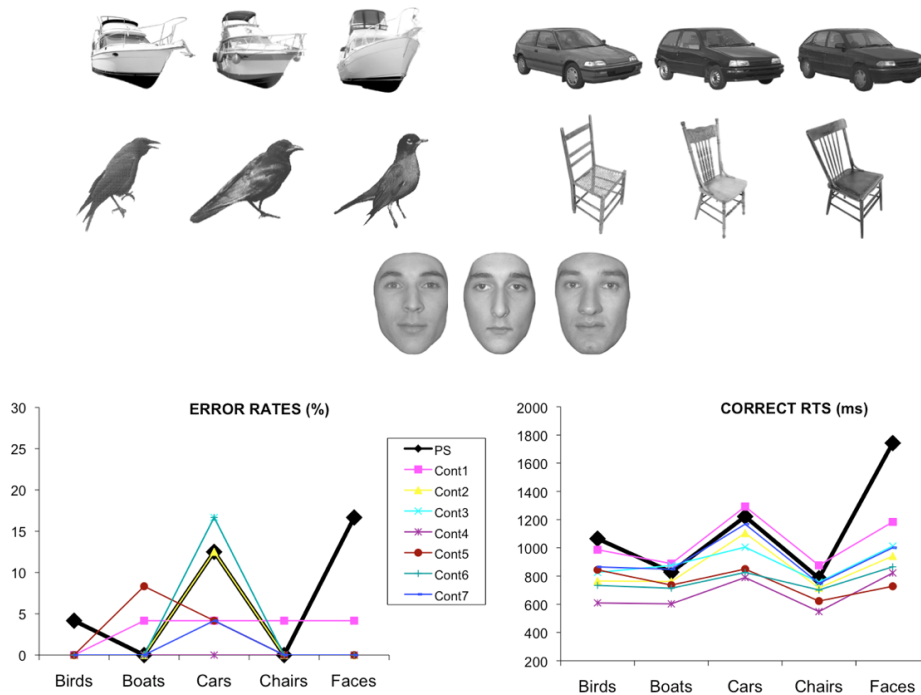


Figure 5. Within-category delayed discrimination task as reported in Schiltz et al. (2006) for testing the patient PS. **A.** Exemplars of the five categories of stimuli used, in which a target is shown first, followed by the same target and a distractor. **B.** PS made more mistakes than controls only with faces. **C.** Relative to normal controls, PS was slowed down only for faces. The visual agnostic patient LH tested at the same task made more mistakes than controls not only for faces, but also for nonface object categories, being significantly slowed down for all categories (see Rossion, 2018a).

To evaluate more systematically the *within-category/visual similarity account* of prosopagnosia, PS was then tested with specific delayed forced-choice matching tasks with exemplars of the same category in which the similarity of the distractor to a target was systematically (i.e., parametrically) manipulated (**Figure 6**; Busigny et al., 2010a).

In three separate behavioral experiments, we tested single shapes (“geons”, Biederman, 1987), nonface artificial objects from both living or nonliving categories, and photographs of a well-known category (cars). In these tasks, PS was shown with a single stimulus for 500 ms (geon shapes, objects) or 2000 ms (cars), which was replaced after a brief blank screen by the same object appearing next to a distractor, until the response was made. The most important thing was to assess whether any slight decrement of performance at baseline level for PS would increase *disproportionally* with increasing visual similarity between a target and its distractors, as postulated by the visual similarity account of prosopagnosia (Faust, 1955; Damasio et al., 1982; Gauthier et al., 1999).

In all of these experiments, PS did not show increasingly lower accuracy or higher (correct) RTs with increasing levels of visual similarity relative to controls. In fact, her

performance was undistinguishable from typical observers', at *all* levels of physical similarity between the target and its distractors (Busigny et al., 2010a; **Figure 6**). These observations were made despite the tasks being quite difficult for typical observers, as judged by their error rates and RTs, with some of the discriminations truly requiring fine-grained analysis of the stimuli (**Figure 6**). Hence, they directly contradict the view that PS's prosopagnosia is due to a general difficulty at recognizing shapes belonging to a visually homogenous category.

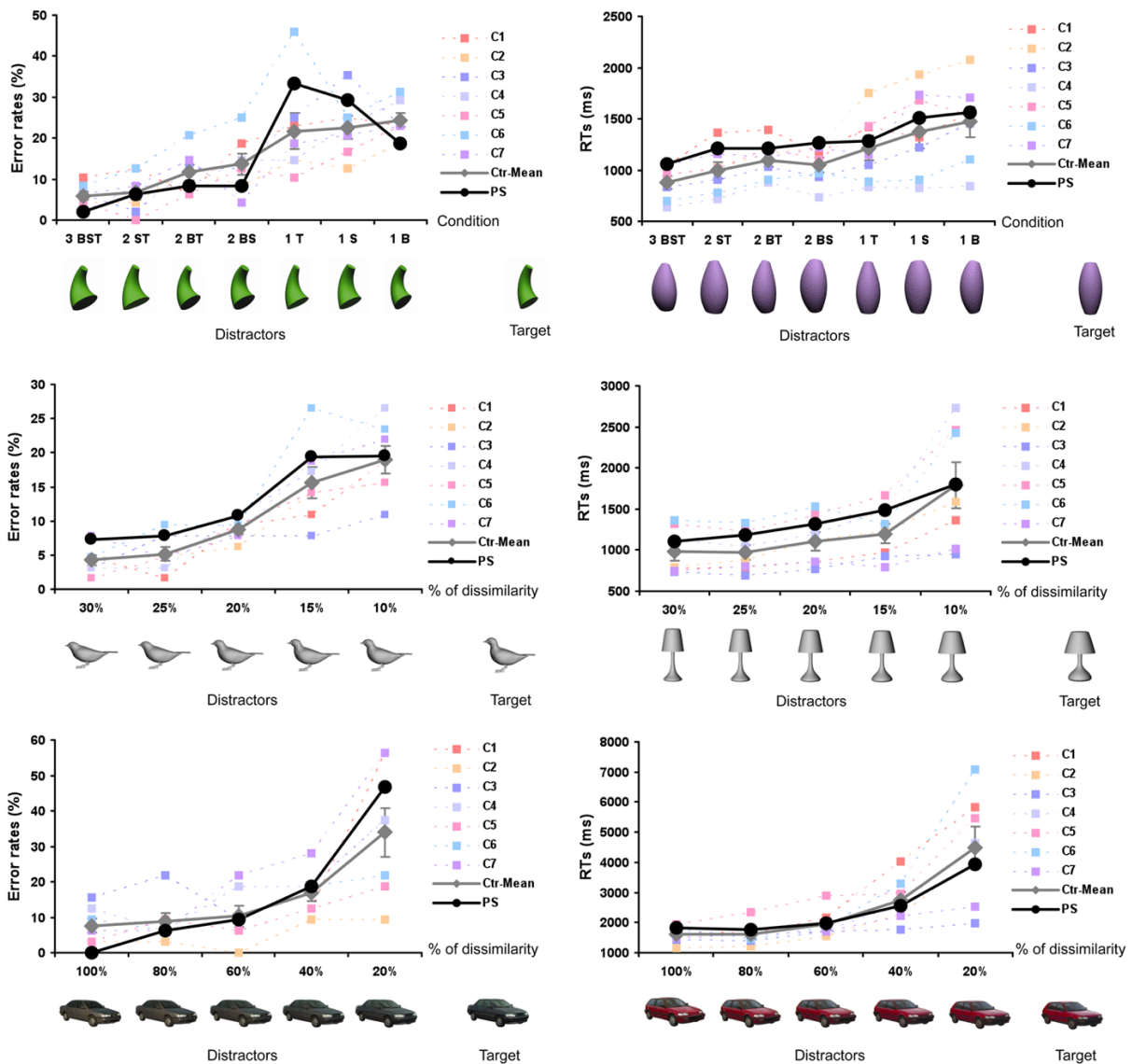


Figure 6. PS's performance compared to normal controls at three separate experiments testing the matching of single shapes (top row; 12 shapes in total in the experiment), morphed living and non-living objects (8 by category), and morphed photographs of cars (20). Parametric increases in visual similarity between the target and a distractor leads to increases in error rates and RTs, with no difference in slope between PS and age- and gender-matched typical controls (from Busigny et al., 2010a).

To complete this demonstration, we also tested PS in the exact same paradigm with pictures of *faces*, i.e., parametrically manipulating physical similarity of the individual face

distractors with image morphing. This time, PS clearly performed below age-matched controls, both in accuracy and RTs (**Figure 7**).

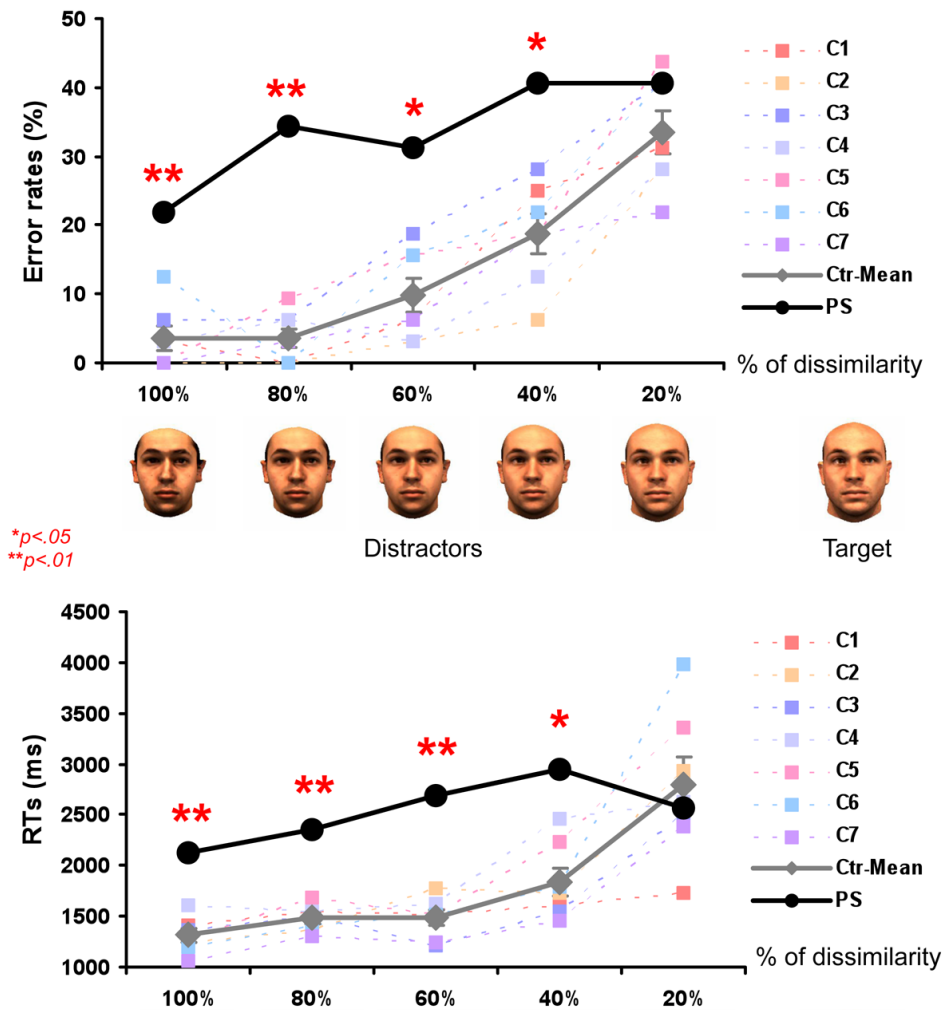


Figure 7. Performance of the prosopagnosic patient PS at the same delayed matching task as tested with nonface objects (Figure 6), here with morphed face stimuli. Despite the task being, if anything, relatively easier than with pictures of cars for normal controls, here PS showed clear difficulties, which were apparent even at the easiest individual face discrimination level (i.e., 100% difference on morph continua). Thirty-two individual faces were used in the experiment (see Busigny et al., 2010a for details about the stimuli and procedure).

Moreover, for typical observers, the task was even slightly easier than the exact same task performed with pictures of cars (compare **Figures 6 and 7**, see also Busigny et al., 2010a), leading to a double dissociation between PS's and the typical participants' performance. This experiment is also important because one could claim that PS's ability to recognize object shapes as illustrated on **Figure 6** is due to the use of identical images at encoding and recognition, therefore relying on simple image-based cues. If this were the case, the patient could have also used simple image-based cues to perform as well as controls with faces; yet she was unable to match their performance.

Strikingly, with faces, PS was impaired even at the *lowest* level of similarity between exemplars, i.e., when faces were the most different from each other. In fact, relative to normal controls, PS was impaired *the most* when the faces were clearly different (100%), and was not impaired when the faces were as similar as twins (20% morph difference); despite performance being above chance level both for her and in the normal population in this condition (**Figure 7**).

Taken together, these observations rule out an account of PS's prosopagnosia as a defect in recognizing individual exemplars of visually homogenous categories in general. Rather, they demonstrate that a visual recognition deficit suddenly occurring in a mature visual recognition system can truly be limited to the category of faces.

VI. Further remarks on face specificity and visual expertise

6.1. The meaning of a face-specific recognition impairment

Let me clarify a few issues at this stage. First, how could someone like PS, with such extensive brain damage (**Figure 1**) present with such a *specific* disorder of visual recognition, i.e., limited to the category of faces? To be clear, what is meant by “face-specific” is that FIR is impaired but visual object recognition is preserved, including OIR. Without drawing unwarranted conclusions at this stage (e.g., “this implies a face recognition “module” in the brain”, e.g., Kanwisher, 2000), a conservative interpretation of this pattern of observation on PS indicates that in the adult human brain there is a region, or a network of regions, which is/are necessary for FIR but not for visual OIR.

However, it is clear that PS has other deficits than her inability to recognize face identity. She has a cerebellum lesion, which has affected her motor balance early in her recovery and required physical therapy to improve her postural ability. Most importantly, her ventral occipito-temporal lesion (**Figure 1**) appears to encompass the typical region in the fusiform gyrus/occipito-temporal sulcus where the location of selective responses to prelexical or lexical combinations of visual letters are found in the normal brain (i.e., the so-called visual Word Form Area, vWFA, Petersen et al., 1989; Cohen et al., 2002). This region is thought to be critical for reading (Cohen et al., 2016) and in the initial neuropsychological examination of PS, less than three weeks after her accident, she is described as suffering from letter-by-letter alexia (without reported data; Mayer et al., 1999). However, PS reads correctly (as also shown by her correct identification of famous names; **Figure 3**) and although she may be slowed down in some tests, this effect is quite subtle and is not indicative of letter-by-letter reading. As tested recently (late 2021), she also impressively shows large and typical left lateralized selective electrophysiological responses to

visual words presented very briefly (100 ms, 10 Hz) among stimulation sequences of pseudoletters, nonwords or pseudowords (original experiment of Lochy et al., 2015; unpublished data of PS by Marchive, Lochy & Rossion). In fairness, the nature of any putative reading impairment of PS remains unclear due the presence of the left paracentral scotoma, which makes her sometimes miss the first letter of a word (or the first number of a written price) and can slow her down. Interestingly though, since her accident, she claims to have lost her ability to tell if a written word is spelled correctly or not, i.e., which could reflect an impairment at visual orthographic skills. For instance, she says that she cannot tell anymore if the word “carotte” in French (carrot) has two ‘rs’ or two ‘ts’) because, in her own words, she cannot “mentally visualize a word” anymore, something that she could apparently do very well before her accident. However, this deficit may be very subtle and/or very well compensated so that, unlike her clear and stable impairment at FIR, we have not been able to formally demonstrate it. Most importantly, given the quantitative and qualitative differences between PS’s FIR impairment and any subtle potential difficulty at visual word recognition, there is no reason to think that a commonly impaired functional process would be involved, as argued on the basis of studies in bilaterally lesioned patients with general visual object agnosia (Behrmann & Plaut, 2014; see Susilo et al., 2015)

The point that I want to make here is that “face-specificity”, i.e., prosopagnosia, does not mean that FIR must be the *only* brain function impaired. What it means is that *nonface visual object recognition*, including the recognition of the *identity* of nonface objects within a category, is preserved (Rossion, 2018a).

6.2. Low-level visual defects

In the original report of PS, she was tested with difficult same/different matching tasks with pictures of cars (different viewpoints) or novel 3D objects (Rossion et al., 2003, Table 3 in that study). Her performance was generally as good as normal controls tested in the same tasks, although she took significantly more time in some of these tasks (see also Busigny & Rossion 2010, experiment 4). This has sometimes been interpreted as a problem with nonface object shapes, prompting some authors to suggest that PS’s recognition deficit “is not restricted to faces” (e.g., Riddoch et al., 2008 in a study of a reported case of prosopagnosia where RT measures were not even considered). However, a slightly lower performance or increased RT at such tasks could merely reflect the fact that PS has lower visual acuity than normal controls and, again and most importantly, a ~2 by 3 degrees left paracentral scotoma masking the initial view of an image (**Figure 3**). Moreover, same/different tasks are susceptible to response biases, which may differ between a neurological patient and neurotypical individuals.

In this case, it is important to compare the patient's performance to normal controls across the face and nonface object category of interest. For instance, while controls' performance is roughly identical for faces and cars in such tasks, PS' performance drops by almost 30% for faces, and she is almost two times slower for matching faces than cars (Tables 2 and 3 in Rossion et al., 2003). Most importantly, across experiments, a change of view between the pictures to match (for novel objects or pictures of cars for instance) never led to a relatively disproportionate increase in mistakes or RTs for PS relative to controls (Rossion et al., 2003). In contrast, across all studies performed with the patient, her performance at matching pictures of unfamiliar faces for their identity systematically decreased significantly when a change of view was introduced between the target images (Rossion et al., 2003; Busigny & Rossion, 2010; Busigny et al., 2010a; Rossion & Michel, 2018). This indicates again that PS's deficit is not in visual recognition in general, but rather that a face-specific process is selectively affected in the patient.

In summary, establishing normal visual object recognition abilities in reported cases of prosopagnosia requires careful and repeated observations, with various stimuli and tasks (e.g., forced-choice matching tasks to avoid response biases, stimuli of various and large enough sizes, etc.), consideration of individual data of typical observers at these tasks beyond population average measures, parametric variations and testing for generalization of recognition across views, as well as a comparison of performance across tasks. In principle, if such controls were readily available, PS's performance should also be compared to non-prosopagnosic *brain damaged* patients who would have similar low-level visual defects as her (e.g., a left paracentral scotoma) (de Haan et al., 1995). In fact, it is remarkable that even when comparing her to neurotypical individuals matched in age and gender who do not have any low-level visual effects, PS nevertheless scores in the normal range at object (identity) recognition.

Although I was initially very skeptical about the specificity of PS's visual recognition disorder for faces – I had in fact written in my PhD dissertation shortly before first meeting PS that real cases of prosopagnosia probably did not exist – I had to realize that I was wrong and that there was no point in trying to force her to slightly fail at visual object recognition in artificially difficult stimulus conditions and tasks at all costs. Rather, it seemed more constructive to acknowledge the astonishing specificity of her identity recognition impairment for faces (which is found across the board and does not require a difficult task and stimulus conditions, e.g., **Figure 7**), and try to understand why, despite the extent of her brain damage, such an extreme category-specific recognition impairment can occur. This will be the topic of section VII, following a brief discussion of the contentious notion of visual expertise.

6.3. Visual expertise

A domain-specific visual expertise

Prosopagnosia has sometimes been defined in terms of a deficit of visual expertise rather than a domain-specific impairment (Gauthier et al., 1999; Barton et al., 2009; Bukach et al., 2012). What does this mean exactly? Beyond prosopagnosia, this notion of visual expertise, introduced in human face recognition research by Diamond and Carey (1986), has plagued the field for four decades, causing a great deal of confusion. This confusion is due to a few reasons.

First, the notion of visual expertise has been radically opposed to domain-specificity (e.g., Kanwisher, 2000; Tarr & Gauthier, 2000; McKone et al., 2007). However, it does not have to be the case: one can be (and is often) expert at recognizing a specific type of signal. Indeed, contrary to PS, neurotypical human adults can be said to be *experts* at FIR: they are able to recognize thousands of faces, rapidly and automatically. This is no longer the case for PS: due to extensive brain damage in critical brain regions of the ventral occipito-temporal cortex, she lost her *domain-specific expertise* at FIR, as shown by her major difficulties at behavioral tasks with both familiar and unfamiliar faces. Other animal species who do not have the adequate neural circuitry in the first place, macaque monkeys for instance, are not experts at FIR (Rossion, in press). Hence, they struggle with simple FIR tasks even after being exposed and trained with thousands of presentations of the same face pictures (Parr et al., 2008; Rossion & Taubert, 2019), and there is no evidence of prosopagnosia in this species when their cortical face network is (bilaterally) lesioned (Heywood & Cowey, 1992). Even human children of a few years of age are seriously limited in their FIR ability compared to adults (Carey, 1992; Mondloch et al., 2002; Hills & Lewis, 2018), with performance improving throughout development together with an increase in the cortical space devoted specifically to faces in the ventral occipito-temporal cortex (VOTC) (Golarai et al., 2017; Nordt et al., 2021).

Although both a formal and an operational definition of visual expertise at FIR are lacking, perhaps the second reason behind the confusion⁷, it can be reasonably argued that most neurotypical human adults do not reach such level of expertise for recognizing exemplars of

⁷ It has been proposed that expertise at FIR is characterized by an ability to recognize familiar faces at the level of their identity as rapidly as at a superordinate level (“human” or “face”) of recognition/categorization (Tanaka, 2001). However, this is only true in very specific tasks (e.g., when a label precedes the presentation of a visual stimulus, allowing the search to be constrained, and with a small set of repeated images). In reality, recognizing a face as a face (generic face recognition, GFR) is systematically faster than FIR (see Quek et al., 2021 for recent references and further evidence).

another visual category. Thus, there is no opposition between a visual expertise account and a domain-specific account of prosopagnosia: neurotypical adults reach a level of expertise at identity recognition of visual entities *only* for the category of faces⁸. Due to the formidable challenge of FIR, this expert recognition level is only required for faces, so that sudden brain damage at adulthood can sometimes cause a recognition impairment restricted to the category of faces. In other words, a visual expertise account of prosopagnosia is not an alternative to the domain-specificity account of prosopagnosia, but merely proposes *a reason* why a face-specific deficit can occur: because visual expertise is domain-specific, i.e., restricted to the category of faces in typical human adults.

A third reason for confusion is because *expertise* has been repeatedly confused with *experience*, while the two concepts are orthogonal in reality: a living organism could be defined as an expert at a given task due to completely genetically determined neural circuits. Contrariwise, a great deal of visual experience does not entail expertise – since her accident, PS has had a great deal of experience with faces, certainly attempting with greater effort than anybody to individuate faces in real life and experiments. Yet, she has not improved at all and is clearly no longer an expert at FIR. The level of expertise at FIR shared by neurotypical human adults is likely due to a mixture of factors. On the one hand, genetic factors such as those that make human newborns pay increased attention or show higher sensitivity to facelike patterns (e.g., Goren et al., 1976; Morton & Johnson, 1991; Turati et al., 2002; Buiatti et al., 2019), provide a disproportionately large cortical space in the VOTC for rich categorization of visual entities in hominoids and in the human species in particular (Bryant & Preuss, 2018), and generate a large amount of interindividual phenotypic variability in our species' faces (Sheehan & Nachman, 2014) certainly play a key role. On the other hand, the overwhelming experience with faces since early in life (Sugden et al., 2014; Sugden & Moulson, 2019) and during human development, as well as the social requirements to individuate numerous conspecifics in the human species, also play a key role.

Finally, and unfortunately, contrary to the view exposed above, the term “visual expertise” in human face recognition research is usually associated with a *generic* expertise account: the view that there would be a generic “expert” system in the brain, which could be recruited to individuate virtually any type of visual entity at an expert level (e.g., dogs in Diamond & Carey, 1986; cars and birds, Gauthier et al., 2000; or even chess panels in chess players, see Bilalic,

⁸ In fact, the highest level of expertise is reached only for human faces of an experienced morphology, the phenomenon known as the “other-race face effect” (Meissner & Brigham, 2001; Rossion & Michel, 2011).

2017). According to a particular version of this view, this expert system would even be so flexible that it could become involved *in adulthood* for nonface multidimensional object shapes after learning to individualize these shapes for only a few hours (e.g., “Greebles”, Gauthier & Tarr, 1997; “Ziggerins”, Wong et al., 2009). As discussed extensively in previous reviews (McKone et al., 2007; Rossion, 2013), but also demonstrated with cases of reported prosopagnosia (Rezlescu et al., 2014), this latter view simply does not hold: one can learn explicitly to individuate exemplars of a nonface category such as “Greebles” of course, but it does not mean that after learning, old and new (unfamiliar) individual exemplars of that category are individually recognized accurately, rapidly and automatically (see Vuong et al., 2017; Lochy et al., 2018; for evidence that small learning effects attributed to visual expertise acquired in adulthood depend in fact on stimulus face-likeness). Moreover, there is no solid evidence that recognition of individual exemplars of these artificial categories learned at adulthood for a few hours relies on the same functional processes (as discussed in the next section) and neural substrates (as discussed in part II of the review on PS) as faces (McKone et al., 2007; Rossion, 2013)⁹.

Semantic knowledge vs. Visual expertise

Despite my criticism of the notion of visual expertise in human face recognition, whether the expert brain process that most humans associate only with faces could become also (partly) involved for other visual object categories if, say, from early in life and throughout development, one spends an enormous amount of time individuating exemplars of cars, or dogs, or birds of the same species (i.e., “natural expertise”; e.g., Diamond & Carey, 1986; Tanaka & Curran, 2001; Hagen et al., 2014) remains an outstanding issue. Yet, given that even experts in other domains than faces rarely learn to individuate exemplars, e.g., car experts learn to discriminate car models but not individual exemplars of the same car model (which are not supposed to differ beyond color anyway) or bird experts learn to discriminate bird species but not individual birds of the same species (although see Campbell & Tanaka, 2018), this possibility is questionable from the outset.

Yet, Barton and colleagues (2009) have claimed to provide evidence in favor of such a generic visual expertise account of prosopagnosia. These authors showed that five reported cases

⁹ Interestingly, PS was trained around 2002 at individuating Greebles as in the original training study of (Gauthier & Tarr, 1997) and was not highly successful, failing to reach the expertise criteria according to this study. However, none of the age-matched controls tested subsequently reached this expertise criteria. In addition, PS (and two other subjects) had more difficulties generalizing across families of individuals than individuating the Greebles, so that the outcome of the study was inconclusive and eventually not reported.

of prosopagnosia had an abnormal relationship between their high level of verbal semantic knowledge (finding the manufacturer from an index of their name, e.g., “450SL?”: “Mercedes”) with their low ability to provide semantic information about cars (model, year, manufacturer) from their pictures. In contrast, the two measures were highly correlated in typical participants. These observations were taken as evidence for a generic visual expertise account of prosopagnosia: according to these authors, in prosopagnosia, the recognition deficit would not concern faces *per se* but the objects for which there is a high level of visual expertise prior to brain damage (i.e., faces *and* cars for these patients) (Barton et al., 2009; Barton & Corrow, 2016). However, as I have argued elsewhere, semantic knowledge not an adequate measure of *visual* expertise (Rossion, 2018a). To make a parallel with faces, one is no considered as a “super recognizer” (Russell et al., 2009; Ramon et al., 2019) based only on their ability to provide a lot of semantic information about a large number of celebrities from their faces. Most importantly, Barton et al. (2009) have not shown that their patients do not have basic level object recognition problems, and in fact other reports of these patients suggest that they do (Barton, 2008). Therefore, it is not surprising that car enthusiasts suffering from visual object agnosia show a high verbal semantic score but a relatively low visual recognition score: their deficit appears relatively more severe for their objects of interest simply because they know more about them. That is, the generic visual expertise hypothesis could only be supported if a patient without basic level object recognition deficit would be impaired only for faces and for that other category of visual expertise (e.g., faces and cars only; faces and birds only ...). Unfortunately, PS did not develop a specific interest in cars or another nonface object category before her accident, so that her case could not be considered to test the hypothesis. However, interestingly, since her accident, she collects swan figurines, having hundreds of them at home and being able to recognize these exemplars without difficulty.

In summary, based on a series of behavioral studies, PS appears to present with a visual recognition impairment genuinely restricted to the category of faces, at least sparing visual object recognition. Her basic level object recognition ability is normal in real life environments and laboratory experiments. Moreover, her prosopagnosia cannot be accounted for by a difficulty at recognizing exemplars belonging to visually homogenous categories. Instead, PS’s deficit appears to concern an expert *process* that is *required* only for faces. What is therefore the nature of this process that PS, like typical human adults, was presumably able to apply automatically to individual faces before her accident, and which no longer works for her?

VII. Face identity is not in the eyes

It is common to reason about patients with prosopagnosia in terms of a deficit either in *perception* or *memory*. Or rather in terms of *perception vs. recognition*. This reasoning is based on the classic distinction of Lissauer (1890) between *apperceptive* and *associative* forms of visual (object) agnosia. In agreement with this distinction, patients with (*ap*)*perceptive prosopagnosia*¹⁰ are thought to present with a deficit in visual perception, whereas patients with *associative prosopagnosia*, would have preserved perceptual abilities but a deficit in recognition (Hécaen, 1981; De Renzi, 1986; Davies-Thompson et al., 2014).

If perception is defined as an *interpretation* of sensory inputs, then this distinction is difficult to understand because this interpretation, i.e., perception, depends on stored knowledge, usually derived from experience ('indirect perception'; Helmholtz, 1866; Gregory, 1980; 1997; Rock, 1997; Purves et al., 2015). That is, under this indirect empirical view, (visual) perception cannot, by definition, be separated from (memory) associations. On the contrary, if visual perception is defined, as more predominantly in cognitive (computational) (neuro)science, as a chain of (hierarchical) information processes leading to the construction of invariant visual representations independently of knowledge (Marr, 1982; Riesenhuber & Poggio, 1999; DiCarlo & Cox, 2007; Firestone & Scholl, 2016), then the distinction between apperceptive and associative prosopagnosia can be conceptualized. According to this latter view then, a patient with *apperceptive prosopagnosia* would not be able to correctly build a visual representation of an individual face and would therefore be impaired at FIR, operationalized as discriminating different facial identities and matching different instances of the same identity, irrespective of whether these faces are familiar or not. In contrast, a patient with *associative prosopagnosia* would be successful at these tasks but unable to associate a correctly built visual representation of a facial identity to a representation of a familiar face in memory (i.e., "a correct percept stripped of its meaning"; Teuber, 1968).

In line with studies of visual object agnosia (see e.g., Humphreys, 2000), this distinction between perception and recognition/memory stages has been advocated by many authors in prosopagnosia research (e.g., Hécaen, 1981; de Renzi, 1986; Sergent & Signoret, 1992; Schweich & Bruyer, 1993; Davies-Thompson et al., 2014). These authors consider that it is important, or at least useful, to distinguish these two putative types of prosopagnosia (see Barton & Corrow, 2016) and, accordingly, to distinguish between behavioral tests of perception *vs.* tests of recognition of

¹⁰ Technically, the terminology should be "perceptive agnosia" rather than "apperceptive agnosia".

face identity (e.g., simultaneous matching of unfamiliar faces *vs.* decision of short-term or long-term familiarity of a face identity; see e.g., Robotham & Starrfelt, 2018). It is completely in line with standard cognitive models of human face recognition, which draw a (hierarchical) border between processes leading to the construction of a view-invariant visual representation of someone's identity (i.e., a 'structural encoding stage') and a memory store of representations of familiar faces ('face recognition units', FRUs) (Bruce & Young, 1986; Young & Bruce, 2011; Young, 2021). Moreover, this distinction has been fully adopted in (neuro)computational analyses and models of FIR, which aim at describing and understanding how view-invariant representations of facial identities are built from the visual stimulus independently of memory processes/representations (e.g., Haxby et al., 2000; Jiang et al., 2006; DiCarlo & Cox, 2007; Gobbini & Haxby, 2007; Duchaine & Yovel, 2015; see also Chang & Tsao, 2017; Freiwald, 2020).

I do not subscribe to this hierarchical conceptual distinction between perception and recognition, not only because my conception and definition of (visual) perception aligns with a Helmholtzian view (Helmholtz, 1866; Gregory, 1980) rather than an objectivist cognitive/computational view, but also because I find it more problematic than useful for our understanding of prosopagnosia and the nature of FIR. This issue will be discussed more deeply in section X below. Regardless, in the case of PS, there was no need to ponder over this distinction very much anyway: it was clear from the outset that her deficit did not only concern the recognition of a face identity as being familiar. Indeed, PS is already impaired at matching pictures of *unfamiliar* faces for their identity (e.g., **Figures 4 & 6**), even when these pictures are presented *simultaneously* (e.g., in the BFRT-c or other individual face matching tasks) and even when the *exact same images of faces* have to be matched against distractors (e.g., Rossion et al., 2003; Schiltz et al., 2006; Busigny & Rossion, 2010). Hence, irrespective of the two accounts of (visual) perception mentioned above, PS does not appear to perceive an individual face as well as typical observers, although I consider that classifying her as a case of apperceptive prosopagnosia would not make us progress at all in our understanding of the nature of her disorder.

Note that PS's accuracy scores at such individual face matching tasks is far from being catastrophic. With pictures of unfamiliar faces that are not morphed with one another, she scores significantly below controls but reaches about 80% performance in the delayed face matching task illustrated in **Figures 5** and **7**. In such tasks however, as in other individual face matching tasks, she also takes much longer than typical observers (see also Fysh & Ramon, 2022), a slowing down that is also specific to faces (**Figures 5-7**).

What this tells us here is an important issue to understand the nature of FIR: successful (i.e., above chance level) matching of identical pictures of unfamiliar faces (or even pictures that differ slightly) presented simultaneously for their identity does not imply that one is *expert* at FIR. For instance, many nonhuman animal species such as sheep, archerfish or even bees can be trained to discriminate pictures of human faces above chance level (Knolle et al., 2017; Newport et al., 2016; Dyer et al., 2005; respectively), but that does not make them experts at FIR in any comparable sense to neurotypical human adults (Pascalis et al., 2006; Rossion & Taubert, 2019; Towler et al., 2019; Rossion, in press). Moreover, contrary to widespread misinterpretations, these observations do not allow to derive any conclusion about the nature of human expertise at FIR. Yet, providing that both accuracy and correct RTs are considered, a *real* expert at FIR, i.e., a neurotypical human adult in most cases, will do better *even* at this simple task than a non-expert (e.g., a case of prosopagnosia like PS, but also an infant, a young child, or other animal species, e.g., monkeys, sheep, fish, bees). Hence, contrary to yet another received idea in human face recognition research (Young & Burton, 2018), (pictures of) (upright) unfamiliar faces do call upon expert FIR processes (Rossion, 2018b) but one has to go beyond a simple can/can't do distinction at this task to identify the experts.

From a practical point of view, the fact that PS is still able to extract enough cues from an unfamiliar face stimulus to individuate it above chance level in a given task means that we can capitalize on her performance to physically manipulate unfamiliar face stimuli and test how these manipulations affect her performance. This logic forms the basis of the investigation carried out with PS for many years, as summarized in the next sections.

7.1. Bubbles on faces

Initially, I reasoned that PS can no longer recognize individual faces, and only faces, because she must have lost sensitivity to some specific *type of information* critical to individuate faces but no other visual shapes. However, rather than defining *a priori* this source of information on face stimuli, my colleagues and I first aimed at determining the missing piece of information in a more open and objective way by using a response classification technique (Ahumada & Lovell, 1971) in which PS had to recognize face identities as revealed through apertures varying in number, size and location at every trial. This kind of response classification approach was developed in human face recognition research by Dennis Haig (“random apertures”; Haig, 1985; Haig, 1986) and adapted later under the name *Bubbles* (Gosselin & Schyns, 2001). Under specific stimulus conditions, this Bubbles technique or similar other response classification techniques (Sekuler et al., 2004) can reveal the specific facial features diagnostic for a given task (Schyns et

al., 2002). Since PS was willing to perform such a tedious experiment, we applied the Bubbles approach with her during months of testing – the leading author on this project was my colleague Roberto Caldara.

To start, we asked PS to associate 10 unfamiliar facial identities with different names, with 2 full-front greyscale pictures per identity and a non-diagnostic hairline. Pictures were presented in full view, and PS and the control participants in the study were not aware that they would be shown these faces at a later stage only through limited random apertures. While typical observers could learn the faces in a few minutes, obviously, PS had more difficulties to learn the 10 face identities. Yet, after 2-3 hours of training in different sessions, she was flawless: she could associate each identity to a specific key of the keyboard, corresponding to the first name of the face. Note that this successful learning of pictures of face identities is not surprising, as shown in other studies with reported prosopagnosic patients (e.g., Sergent & Signoret, 1992; Dixon et al., 1998).

Following learning, PS had to recognize each facial identity as revealed only by random apertures at each trial (**Figure 8A**). Percent accuracy at the task was maintained at 75% by increasing or decreasing the number of apertures in a staircase procedure. Therefore, PS's performance was matched to typical observers. We were interested in two other variables: (1) the number of apertures needed to perform the task at 75% and (2), most importantly, the location of the apertures associated with correct responses for PS versus typical observers.

First, we found that PS needed many more (i.e., about 4 to 6 times) apertures than all typical observers to achieve the same 75% percent accuracy (**Figure 8B**). To ensure that she was not just a bit slower to reach the same low number of apertures as controls, we tested her for many more sessions than typical observers. However, despite a significant decrease over sessions – PS performed 31 sessions of 300 trials in total (i.e., 9300 trials), she still needed a much higher number of apertures to achieve successful recognition of the faces than typical observers (**Figure 8B**). This observation simply reflects her severe FIR impairment.

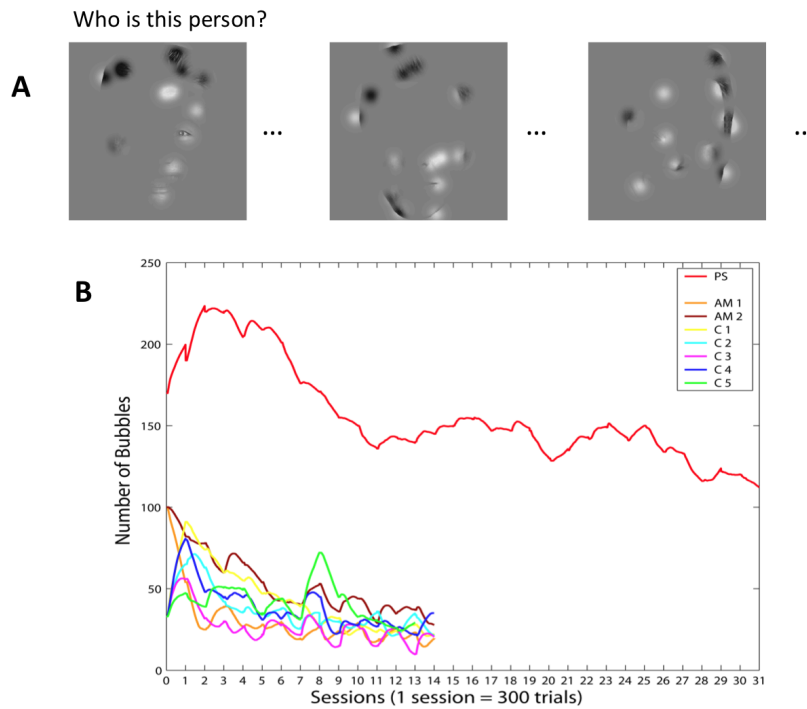


Figure 8. *The Bubbles experiment with prosopagnosic patient PS (from Caldara et al., 2005). A.* After learning 10 facial identities (two images/identity), PS had to identify each face covered with random apertures (“bubbles”) for thousands of trials. **B.** Number of Bubbles per session to maintain performance at 75%. PS (data in red) performed 31 sessions of 300 trials over several weeks of testing (i.e., 9300 trials), while 7 typical observers (two age-matched, AM1 & AM2) did the same experiment but stopped after 14 sessions, when the number of bubbles was stable. Note that PS requires many more bubbles on the faces to achieve the same level of performance as the typical observers, even after many extra sessions.

Second, most importantly, the classification images obtained by subtracting an average image of all bubble images associated with correct responses to an average of all bubble images associated with incorrect responses (Gosselin & Schyns, 2001 for details) revealed that PS relied on a *different* type of cues than typical observers: while they all predominantly used cues from the *eye* region, as in other studies with this kind of approach (Haig, 1985; Gosselin et al., 2002; Sekuler et al., 2004), PS mainly relied on the *mouth* to recognize the facial identities (**Figure 9**).

To be honest, this was quite an unexpected result, which revealed a *qualitative* difference between PS and typical observers, offering potentially important information to understand the nature of (her) prosopagnosia and FIR.

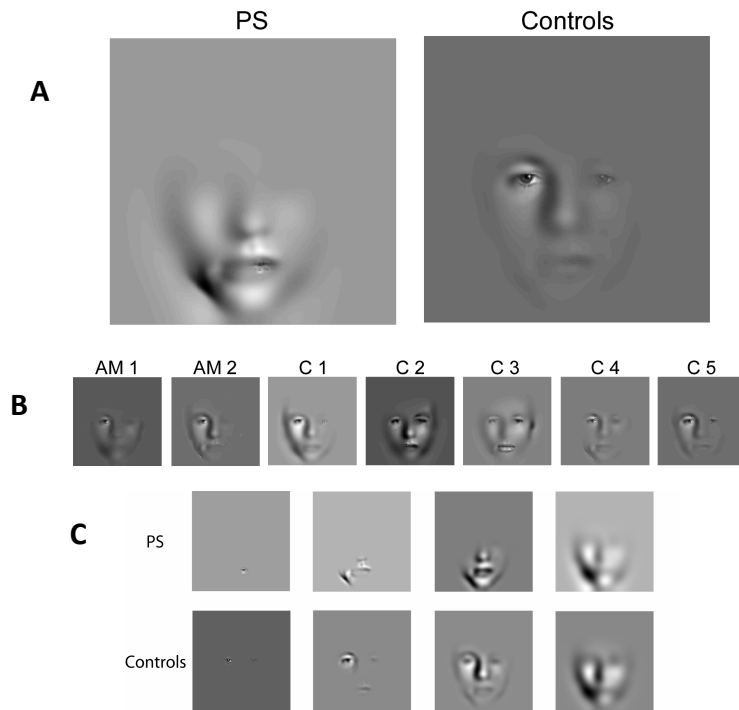


Figure 9. *A. Classification images for the prosopagnosic patient PS and (averaged) normal controls, revealing the respective diagnostic information to recognize face identities (from Caldara et al., 2005). While typical observers rely more on the eye region (see also Gosselin et al., 2002), PS essentially uses the lower part of the face, and the mouth in particular. B. Classification images for each typical observer separately, showing that information at the level of the mouth is also used by typical observers, but not with a relative dominance of the mouth as for PS. Note also the lack of obvious difference between age-matched controls (AM1 & AM2) and younger controls. C. Classification images at four levels of spatial resolution, from high to low spatial frequencies, showing that PS underuses the eyes at all spatial scale levels.*

7.2. Why (not) the eyes?

The important observation here is not so much that PS relies on the mouth to recognize facial identities in this study; after all, most typical observers also use cues at the level of the mouth, in addition to the eyes (**Figure 9**). What is striking is that the patient barely uses the eyes, despite the fact that this region of the face contains diagnostic cues to distinguish the face identities. Hence, PS differs from typical observers in her relative use of the eye region versus the mouth. Note that the outcome of this specific experiment, i.e., the striking contrast between PS and typical observers in classification images, depends on the type of the specific stimuli used. Typical observers rely primarily on the eye region because this region carries the most diagnostic cues for them. However, there are also enough diagnostic cues at the level of the mouth, i.e., enough differences between these individual face mouths, to successfully differentiate them in the task with 75% accuracy, otherwise PS would not be able to reach this level of performance.

Had we used another set of face stimuli, for instance faces differing only at the level of the mouth *or* the eyes, we might have found similar classification images for PS and typical observers, and interpreted that as a *quantitative* difference. To make a parenthesis, this is exactly what happened with another study performed at about the same time, which used response classification in typical observers having to match upright and inverted faces covered with noise (Sekuler et al., 2004). Since observers relied on the same features, the eye region, for both orientations, the authors of that study concluded that “*face inversion leads to quantitative, not qualitative, changes in face processing*”. However, in reality, there was a limited set of stimuli (2 face pairs) in the response classification task of that study, with these stimuli differing essentially at the level of the eyes/eyebrows. Hence, there was no other option for observers than to rely on the eyes, for both orientations (Rossion, 2008). In short, the strong bias in the choice of the face stimuli, which is more likely to occur when a small set is used, completely oriented the results of Sekuler et al. (2004)’s face recognition experiment. As often, this study’s conclusions were unfortunately overgeneralized, i.e., it should have been that “*face inversion leads to quantitative, not qualitative, changes in face processing when discriminating the same 2 pairs of faces differing most significantly at the level of the eye/eyebrow with random noise*” (see Rossion, 2008).

I make this parenthesis here to remind the reader to remain careful in overinterpreting the findings made with PS in the Bubbles experiment described above. If we had tested PS with faces differing only or even mainly at the level of the eyes, she would have been forced to use the eyes, and therefore also rely essentially on the same type of cues as typical observers. Due to a highly constrained stimulus set, we would have therefore concluded that there is only a *quantitative* difference between prosopagnosia and typical observers¹¹. This could be relatively easily tested by asking PS to match full pictures of faces differing only in terms of the eyes, experiments that will be described in section 6.4 below. Before that, let me address another important issue, concerning the *ecological validity* of our observations.

7.3. In the kindergarten

In the Bubbles experiment, PS learned 20 images, with only two images per identity. She was exposed tens of time to each image during training, and during thousands of trials during the Bubbles experiment. This amounts to about 500 exposures to each face image, a huge number.

¹¹ See for instance the recent observations of Abudarham et al. (2021) in which the same diagnostic facial features for FIR are used by people classified as developmental prosopagnosics as by normal observers, a lack of difference which may be due to the lack of qualitative difference between the two populations or to the highly constrained stimulus set used in the study.

Moreover, in order to build classification images across the different facial identities, these images had to be transformed, i.e., normalized in size and distances between features, to overlap in their features (Gosselin & Schyns, 2001). These methodological aspects certainly question the validity of the observations made with the Bubbles technique with respect to how observers, including PS, make use of facial cues to recognize people in real life.

To address this issue, we were able to take advantage of PS's natural exposure to numerous face identities, not only in her rich social life in general, but specifically in her profession. Two years after her spectacular accident, in 1994, PS started to work again as a teacher in the same kindergarten as she used to work before her accident in Geneva. She was perfectly able to do her job as before, even though recognition of the children's identity was not natural anymore because she struggled to recognize them from their faces alone. Therefore, she had to develop a number of strategies to recognize them accurately, and because of that, she felt that her job was much more tiring, requiring constant concentration. This is the reason why she requested to work only half time since 1994, until her retirement a few years ago. Nevertheless, this meant that she was repeatedly exposed to the new facial identities of 20 to 35 children in her class every schoolyear, and she had to learn to identify them (Mayer et al., 1999). This ecological experience provided us with a fantastic and unique opportunity to study the nature of PS's prosopagnosia.

One of these schoolyears (2006-2007), we took pictures of the children of the kindergarten and tested PS in a series of experiment using photographs of these faces. These experiments have been reported in various papers (Orban de Xivry et al., 2008; Busigny & Rossion, 2010; and Ramon et al., 2017 for an extensive report). In one of the first tests, we presented PS with either the two eyes or the mouth in isolation, told her that these features belonged to children of the kindergarten only, and asked her to identify (i.e., name) each child. Strikingly, PS identified only 4 of the 27 children from the isolated pair of eyes, but about half (14) of them from the mouth only. In contrast, her colleagues in the kindergarten, including one (C3) who was much less familiar with the children, performed all above 70% for the eyes, better and faster than for the isolated mouths (**Figure 10A**; Ramon et al., 2017). In fact, for identifying the children from the mouth only, PS matched her colleagues' performance.

In a subsequent experiment, we increased PS's performance with the eyes only by using an easier 2-alternative forced choice task. While PS was now about 75% correct with the eyes only, there was still a 10% increase with the children's mouths only. Moreover, while this task was now too easy for the controls - they were virtually at ceiling for both the isolated eyes and mouth - they were all significantly faster for the eyes than the mouths, contrary to PS (**Figure 10B**; Ramon et al., 2016). Finally, we also ran a full Bubbles experiment with the children's faces,

with more than 20.000 trials with PS – this took several months of testing. Despite an increased reliance on the eye region as compared to the original study, perhaps due to the use of naturally familiar stimuli (Butler et al., 2010), PS still used the mouth significantly more than the eyes on these naturally learned faces. Again, the contrast to her colleague, who relied much more on the eyes than the mouth, was striking (**Figure 10C**; Ramon et al., 2016).

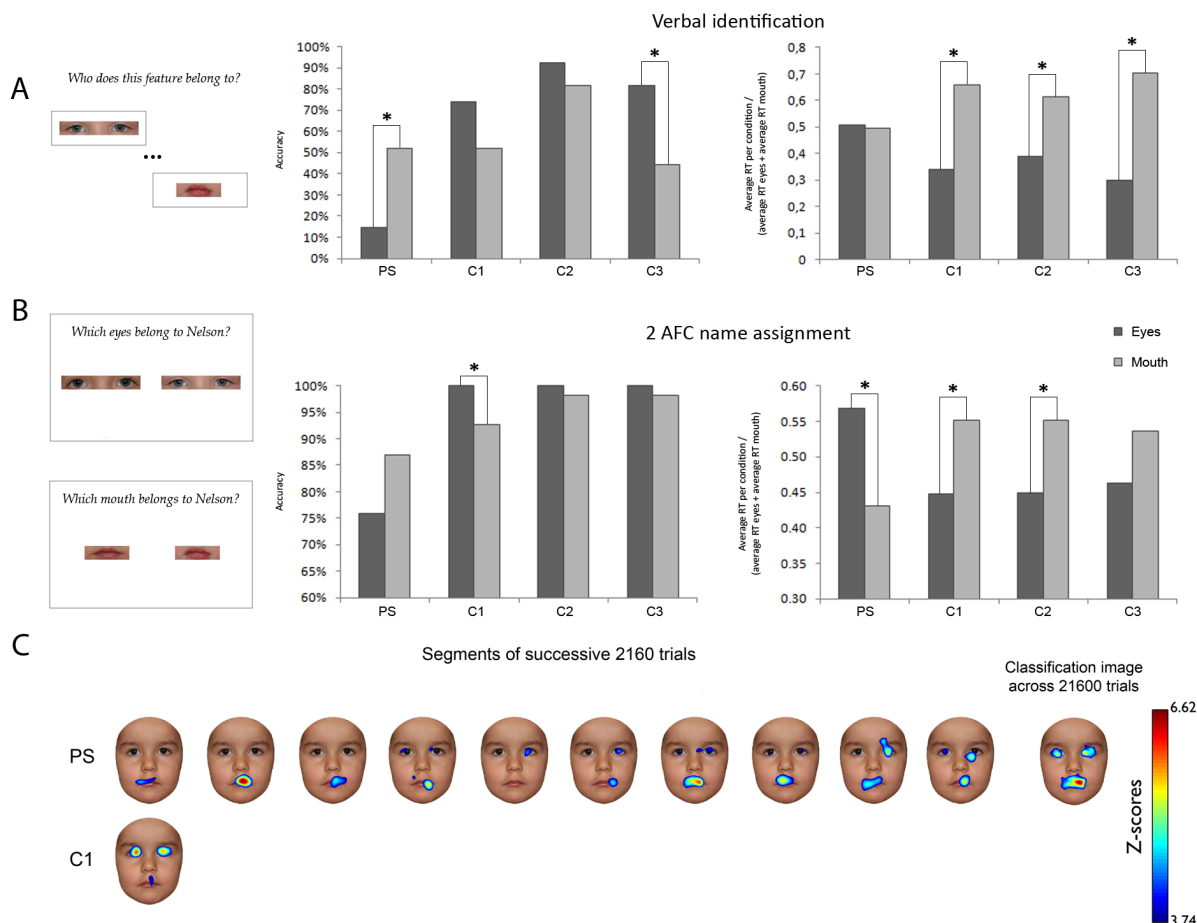


Figure 10. *A. Identification of the children from either the eyes or the mouth (in different trials) (from Ramon et al., 2017). PS’s performance is compared to three controls familiar with the children of the kindergarten (C3 with little exposure to the faces). PS performed much better with the mouth than the eyes, contrary to all controls. She did not differ in terms of speed for correct responses for the two features, while normal controls were all faster for the eyes. B. Results obtained in a 2AFC task with the same stimuli. C. Classification images of a Bubbles experiment with familiar faces (children of the kindergarten), contrasting PS and her age- and gender-matched colleague C1: for PS, 10 images based on 2160 trials each, and on the right the final classification image. Note that the first three images indicate a reliance on the mouth only for PS (i.e., for 3 times 2160 trials).*

7.4. Eyes, mouth, relative interfeature distances and uncertainty

In summary, whether facial identities have been learned experimentally (without instructions about which features should be encoded) or naturally, the prosopagnosic patient PS is able to recognize identity better from cues provided by the mouth than the eyes of these faces.

Why is that? Why does PS show reduced sensitivity to diagnostic cues for face identity at the level of the eye region? Obviously, this has nothing to do with a social disorder of some sort, as observed in some individuals with Autism Spectrum Disorder (ASD) for instance, who tend to avoid paying attention to the face, and to the eyes in particular (Klin et al., 2002; Moriuchi et al., 2017). Indeed, PS always had a very rich social life, and although her prosopagnosia has caused her social difficulties, she has never been shy about interacting with people, quite the contrary. Moreover, the Bubbles experiment tells us that PS does not rely (much) on diagnostic cues from the eyes to identify faces, but it does not tell us that PS does not *attempt* to extract diagnostic cues from the eyes or not, nor does it tell us whether PS *fixates* the eyes or not. Importantly, in the Bubbles experiment, and in other experiments in which we systematically replicate this observation of an overreliance on the mouth, PS is actively involved in the FIR task. However, in real life circumstances, in a conversation for instance, PS does not avoid looking in the eyes of the person she is interacting with: since she knows already who the person is, there is no reason for her to focus on the mouth.

Would PS improve her FIR performance in the task if she was explicitly told to use the eyes of the faces? Although a patient with amygdala damage may improve at judging fearful expressions when instructed explicitly to use and look at the eyes (Adolphs et al., 2005), it does not work this way with prosopagnosia, or at least with PS: again, she uses the mouth because it is the most diagnostic source of information *for her*. Otherwise, when she was presented with the eyes of the children in isolation (**Figure 9**), she would have performed better, not worse. In addition, a series of studies summarized below (section 7.4) show that PS does not even avoid fixating the eyes in a full face, and in fact she even spontaneously attempts to use the eyes when it is the only region containing diagnostic information for identity recognition. However, as we shall see, having to rely on the eyes always comes at a cost for her performance.

Could the reduced diagnosticity of the eyes be due to low-level visual problems, i.e., as if extracting diagnostic cues at the level of the eyes was affected more by her scotoma, and/or she needed higher spatial resolution, or higher sensitivity to color/contrast information, to extract diagnostic information from this region? The scotoma would only be a problem if faces were small in size and presented briefly for instance, perhaps masking the right eye (in the left visual field) if PS was fixating in the center of the face (**Figure 3**). However, in the experiments that

identified the lack of sensitivity to the eye region, face stimuli are not only presented at a relatively large sizes, but PS is free to move her eyes and explore the faces for almost as long as she wants. Moreover, when the eyes are presented in isolation (**Figure 10**), if she fixates in between the two eyes, the scotoma falls above the stimulus. The results of the Bubbles experiment also show that PS differs from typical observers in terms of using the eyes *vs.* the mouth *at all spatial scales* sampled (**Figure 9C**), ruling out an issue of spatial resolution/visual acuity. Color information does not seem to be an issue either: PS's color vision is largely good enough to tell people's eye color correctly, and she was able to tell the color of the eyes of a number of children of the kindergarten, which may have increased her reliance on this region with children faces as compared to the grayscale faces learned in the original Bubbles study. In another study, we found that PS was better at matching whole individual faces based on color and texture information only than on shape information only (Jiang et al., 2011).

If we can exclude a high-level social disorder or a low-level sensory account of PS's behavior during FIR, then why this decreased reliance on the eye region of the face? As far as I know, before this observation on PS in the Bubbles experiment, there was only one early paper of two reported patients with prosopagnosia having difficulties at putting together facial parts to create facial identities, particularly for the ocular region (Gloning & Quatember, 1966; see also Gloning et al., 1966). When we made the first observations on PS, I was unfortunately not aware of this finding, published in German and rarely cited. At about the same time as our first report, (Caldara et al., 2005), Bukach and colleagues (2006) independently reported a defect in discriminating individual faces differing on the basis of cues at the level of the eyes in a patient with prosopagnosia following a traumatic injury to the right anterior temporal lobe, a case that will be discussed below (section XII). However, there was no clear theoretical interpretation of these observations.

My initial feeling about PS's lack of sensitivity to the eye region of faces was in line with a then influential view of human face recognition, which emphasized the importance of the *relative distances between features*, such as the interocular distance, or the distance between the nose and the mouth (Carey, 1992; Leder & Bruce, 2000; Maurer et al., 2002). These relative distances between features, which can vary substantially between individual faces of given "racial" groups (Farkas, 1994; Sheehan & Nachman, 2014) and can be detected very well on facial images (Haig, 1984) have been usually referred to as "second-order relational" or "configural/configurational" cues in the field (Carey, 1992; Rhodes et al., 1993; Leder & Bruce, 2000; Maurer et al., 2002). Moreover, Barton and colleagues (2002) showed that reported cases of prosopagnosia following midfusiform damage had increased difficulties at discriminating

individual faces differing at the level of these relative distances between features. Based on this, I initially reasoned that PS might have increased difficulties with the eye region of the face because its diagnosticity may depend relatively more on the perception of relational/configural cues than other regions of the face: compared to the mouth, which varies in terms of its relative distance to the nose, the eyes of faces can vary in terms of their distance with the nose but also in terms of interocular distance, or eye-eyebrow distance. This is the account emphasized in the discussion of the Bubbles study report (Caldara et al., 2005), even though all co-authors certainly did not agree with it at the time.

To test this hypothesis more directly, I first asked PS to perform a simple same/different matching task with unfamiliar face stimuli developed by my colleague Valérie Goffaux for experiments with typical observers: faces differing in terms of the nose and mouth region, or the identity of the eyes, or their interocular distance, or their vertical position in the face (**Figure 11**). In each case, the differences between the two faces of a pair were striking, with the changes in interocular distance and eye-nose distance being grossly exaggerated to equate performance across conditions for typical observers when these stimuli were presented at the upright orientation (Goffaux & Rossion, 2007).

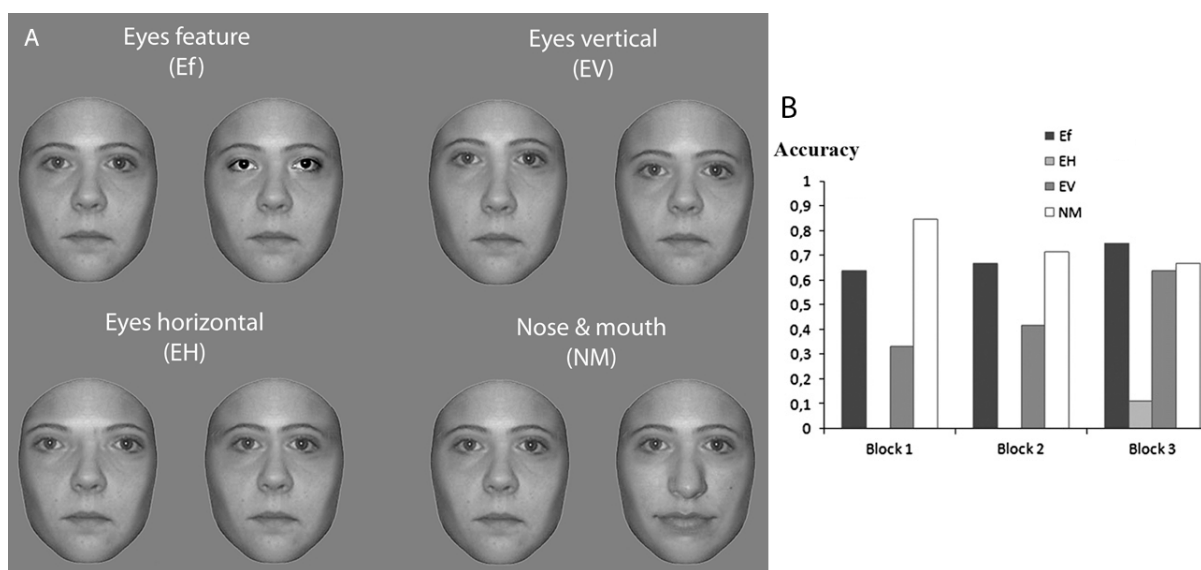


Figure 11. *A. Examples of stimuli used in the pilot experiment reported in Ramon & Rossion (2010), which were developed originally by V. Goffaux (Goffaux & Rossion, 2007; 20 different identities used, stimuli presented at 4x5° of visual angle). The differences between individual faces in terms of relative distances at the level of the eye region (Eyes horizontal and Eyes Vertical) were grossly exaggerated to equate performance across conditions in typical observers. Despite the striking differences, PS was initially able only to detect the changes at the level of the nose&mouth (NM condition, right bottom corner) in a same/different task. However, as shown in B, PS's performance in the study progressively increased for the other conditions when she started to realize the nature of the changes on the faces.*

Note the slight decrease of performance in the nose&mouth (NM) condition across blocks as performance for detecting changes at the level of the eyes increased. Some trials are not shown here (i.e., accuracy at 0 for EH in block 1 means that PS does not detect any difference and considers these faces as being the same).

Sitting in the room with PS to monitor her responses, as often, I was of course not surprised when she started to respond very well for trials in which the distractor differed at the level of the nose&mouth (NM), but struggled with the other three conditions, i.e., responding “same” even though it was obvious that the two faces differed at the level of the eyes. However, suddenly, she started to improve and to respond “different” to a number of trials in which the difference was at the level of the eyes. At the end of the block of trials, I asked her for her impressions about the experiment and she told me: “*At first I did not notice that something was changing in the eyes, but now I am getting it*”. Interestingly, her performance increased essentially for the condition in which the identity of the eyes was different but their position within the face did not change, suggesting indeed a specific impairment with this type of “relational” cues, as hypothesized.

However, two aspects of her performance qualified this hypothesis. First, in subsequent blocks, PS progressively improved also for detecting at least one type of relative change, i.e., when the distance between the eyes and the nose increased between faces (**Figure 11B**). Second, as her performance for discriminating faces based on information at the level of the eyes increased, it started to slightly *decrease* for nose&mouth trials (**Figure 11B**)! Thus, it seemed that there was a trade-off between the types of differences that PS was able to detect, and she had to pay attention to one region of the face at a time to find the difference between faces. Although she was also extremely slow, the real problem for her did not seem to be so much about the *nature* of the diagnostic cues for discriminating face identities, but the *uncertainty*: contrary to typical observers, the differences between individual faces, even when they were grossly exaggerated as in **Figure 10**, were not striking for PS: she had to search region by region of the face for what defined the identity of each face.

With Meike Ramon, we then tested PS more systematically in such experiments, presenting her with a 2AFC task (simultaneous presentation of a triplet of faces), with 6 types of stimulus manipulations (**Figure 12**). Since we did not want PS to detect changes in relative distances between internal features by using a local cue such as the distance between one eye and the contour of the face, we used schematic stimuli constituted only by the main internal features of the faces (eyes, eyebrows, mouth, nose), i.e., without contour (**Figure 12**).

The critical manipulation, however, was elsewhere. In one version of the experiment, all 6 types of trials were presented in random order, so that the specific diagnostic cues could be one

of 6 types of changes at each trial, i.e., maximizing uncertainty. In the other version, the 6 types of manipulations were presented in separate blocks, so that participants could focus throughout the whole block on that specific cue, i.e., reducing uncertainty. At a quantitative level, PS performed lower (by about 8%) than typical observers in the face identity discrimination task, and both improved by about 8% with blocked as compared to random trials. However, although PS was much slower than controls in both conditions, she was much faster when removing uncertainty.

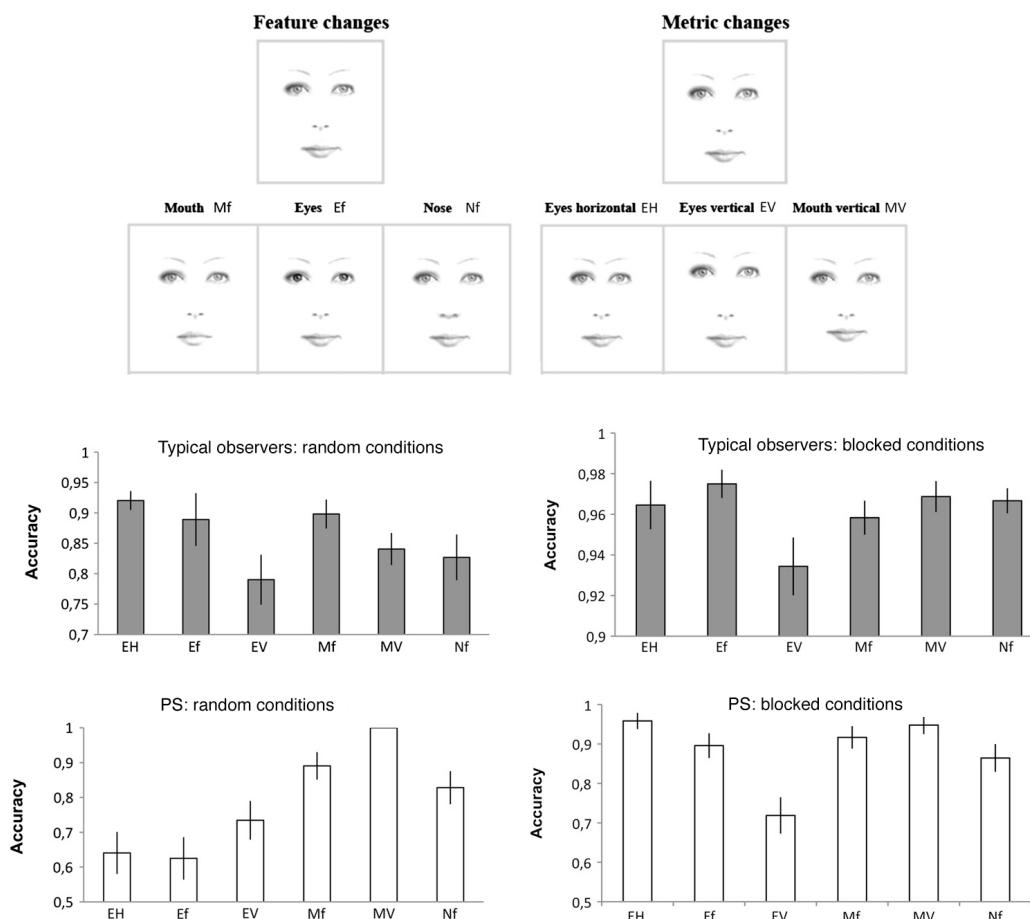


Figure 12. Examples of stimuli and results obtained in the study of Ramon and Rossion (2010). PS had to discriminate one of 6 types of distractors from a target face, with the changes concerning (on the left) the identity of the mouth, eyes or nose, or the relative distances between these features. When all types of trials were presented in random order, PS presented with a completely different response profile than typical observers, in particular showing reduced performance for diagnostic information at the level of the eyes. However, when the trials of the different conditions were blocked, her profile of response was similar to normal controls, even though she still performed lower, and was much slower (see Ramon & Rossion, 2010 for RT measures). These results suggest that PS is able to extract information from each region of the face, but that she needs to focus on one region at a time to resolve the task.

Most interestingly, at a qualitative level, she performed particularly poorly at detecting differences in the eyes in conditions of uncertainty, presenting with a very different pattern of

response as compared to typical observers (**Figure 12**; Ramon & Rossion, 2010). In contrast, when blocking the types of stimulus manipulations, PS was still impaired, but improved dramatically in two conditions in which the difference was at the level of the eyes, showing now a similar *pattern* of performance as typical observers (**Figure 12**). In fact, in the block condition, the only types of trials for which she still scored well below controls was for the change in vertical position of the eyes, arguably the most difficult conditions for controls also. Hence, even though PS remained significantly slowed down in all conditions relative to normal observers in these challenging experiments, performed with highly artificial stimuli, what they reveal is that it is not so much in terms of the nature of the information (i.e., the cues that allows distinguishing facial identities) *per se* that PS differs qualitatively from typical observers. Instead, she differs most from typical observers in conditions of *uncertainty*, i.e., when the nature of the most diagnostic difference between face identities is unknown and variable from trial to trial. In such conditions, she tends to rely more on the mouth region of the face which, with stimuli that differ naturally, i.e., across all features, remains the most diagnostic for her.

Although these observations could be interpreted as a visual attentional defect, the fact that her identity recognition impairment is specific to faces, as described in the first part of the present review, rules out any general visual attentional account. Moreover, her behavior rather reflects the opposite of a selective attention deficit: a hyper focalization, an increase in selective attention, which becomes so focused on a single cue/region of the face that PS fails to notice obvious differences in other cues/facial regions. That is, while the (exaggerated) differences between the two faces of a pair are obvious for everyone to see, at a glance (**Figures 11 & 12**), PS seems to have to pay attention to each part of the face, including the eye region, in turn, as if she was unable to *grasp a global impression of the face so as to immediately capture its individuality*.

VIII. The dual approach in human face recognition research

When I realized the nature of PS's difficulties in these simple experiments about 15 years ago, it was straightforward to relate to the notion of *holistic or configural processing*, as already used in human face recognition research for many years (Sergent, 1984; Young et al., 1987; Tanaka & Farah, 1993) and even hypothesized as a key defect in prosopagnosia by a number of authors (Levine & Calvanio, 1989; Sergent & Villemure, 1989; Sergent & Signoret, 1992; Saumier et al., 2001; Boutsen & Humphreys, 2002). To understand what this holistic/configural view is, let me first contrast it with its rival, the analytic view of human face recognition.

8.1. The analytic view of face recognition

Human face recognition research 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 recognition tasks (Ellis, 1975; Ellis et al., 1986). These early studies invariably revealed the dominance of the eye region (eye/eyebrow combination) for FIR (e.g., Davies et al., 1977; Sheperd et al., 1981; Walker-Smith et al., 1977). This cue saliency approach is still very well alive today (e.g., Abudarham & Yovel, 2016; Abudarham et al., 2021) and associated with three different approaches (**Figure 13**).

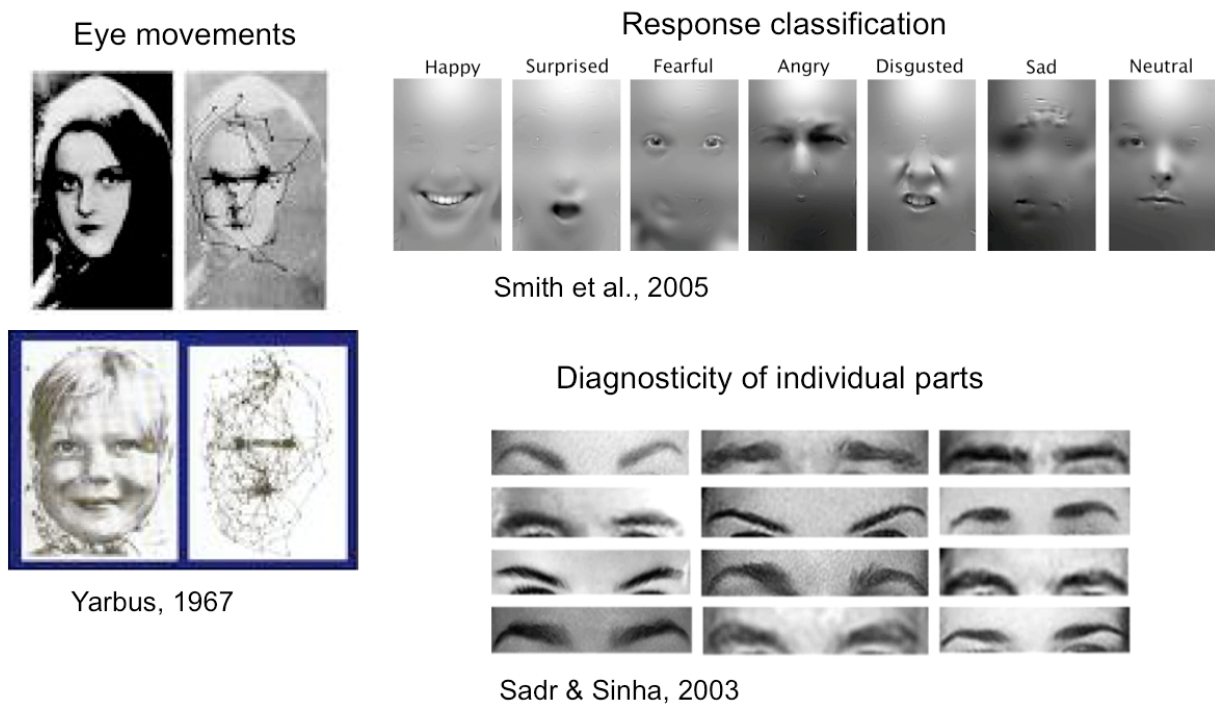


Figure 13. *The cue saliency approach in human face recognition research: three different approaches under the framework of part-based analysis of faces. Left: **Eye movements** during exploration of faces (from Yarbus, 1967) focus on specific parts of the face (right eye, left eye, mouth). Above, right: The approach of **response classification**, initiated by Haig (1985), objectively extracts the local diagnostic information for various face categorization tasks (here the categorization of facial expressions using “Bubbles”, Smith et al., 2005). Below, right: **Diagnosticity of individual parts**: recognition of individual faces can be performed on the basis of local parts presented in isolation (here from Sadr et al., 2003).*

The first approach consists in selectively revealing, masking or exchanging experimentally-defined pieces of information of the face (e.g., the eyes or the nose only) and measuring human observers’ performance at a given FIR task in these conditions (e.g., Sadr et al., 2003; Abudarham & Yovel, 2016). The second approach consists in the analysis of eye gaze fixations on the face, following Yarbus (1967); 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.,

Henderson et al., 2005; Williams & Henderson, 2007) although more recent approaches derive pixelwise statistical maps of fixations across the face (e.g., Caldara & Miellet, 2011; Peterson & Eckstein, 2012; Lao et al., 2017). The third approach is the *response classification* or *classification images* that we have described (Haig 1985; Haig, 1986, Gosselin & Schyns, 2001; Sekuler et al., 2004; Butler et al., 2010; see also Gold et al., 2004). This is the approach that revealed the reduced sensitivity to this eye region in patient PS (**Figure 9**).

In general, this cue saliency approach is associated with an *analytical view* of face recognition, according to which a face stimulus is processed part-by-part, with the goal of extracting its most diagnostic piece of information. Studies performed under this framework are often considered as providing evidence for a part-based analysis and representation of faces (e.g., Schyns et al., 2003; Sekuler et al., 2004; Smith et al., 2005; Butler et al., 2010; Issa & DiCarlo, 2012) and are generally associated with the view that recognition of the whole face is no more than the recognition of the sum of its parts (Gold et al., 2012). This does not imply that there is no global representation of the face that integrates all parts. However, this global representation is thought to *follow* an independent process/representation of the parts, and to be built hierarchically by combining these parts (**Figure 14**).

This view is generally favored by computational approaches and models of human face recognition (e.g., Jiang et al., 2006; Ullmann, 2007; **Figure 14**) and visual object recognition in general (e.g., Riesenhuber & Poggio, 1999; Serre et al., 2007). It is also largely advocated by neuroscientists working on the visual system, inspired by the view of a strict processing hierarchy from simple to complex (i.e., progressive increase in response latencies, receptive field size and complexity of representation), as proposed originally by Hubel and Wiesel (1962) for the organization of the (cat and monkey) visual system for instance. In line with this view, researchers have attempted to describe face-selective neurons in the monkey temporal cortex in terms of their responses to single features such as the eyes (Issa & Di Carlo, 2012; see also Freiwald et al., 2009), and neurofunctional models explicitly include a part-based face-selective representation at an early stage of human face processing in the inferior occipital gyrus (Haxby et al., 2000; Pitcher et al., 2011; Duchaine & Yovel, 2015; see also Zhang et al., 2021; see Review on PS part II).

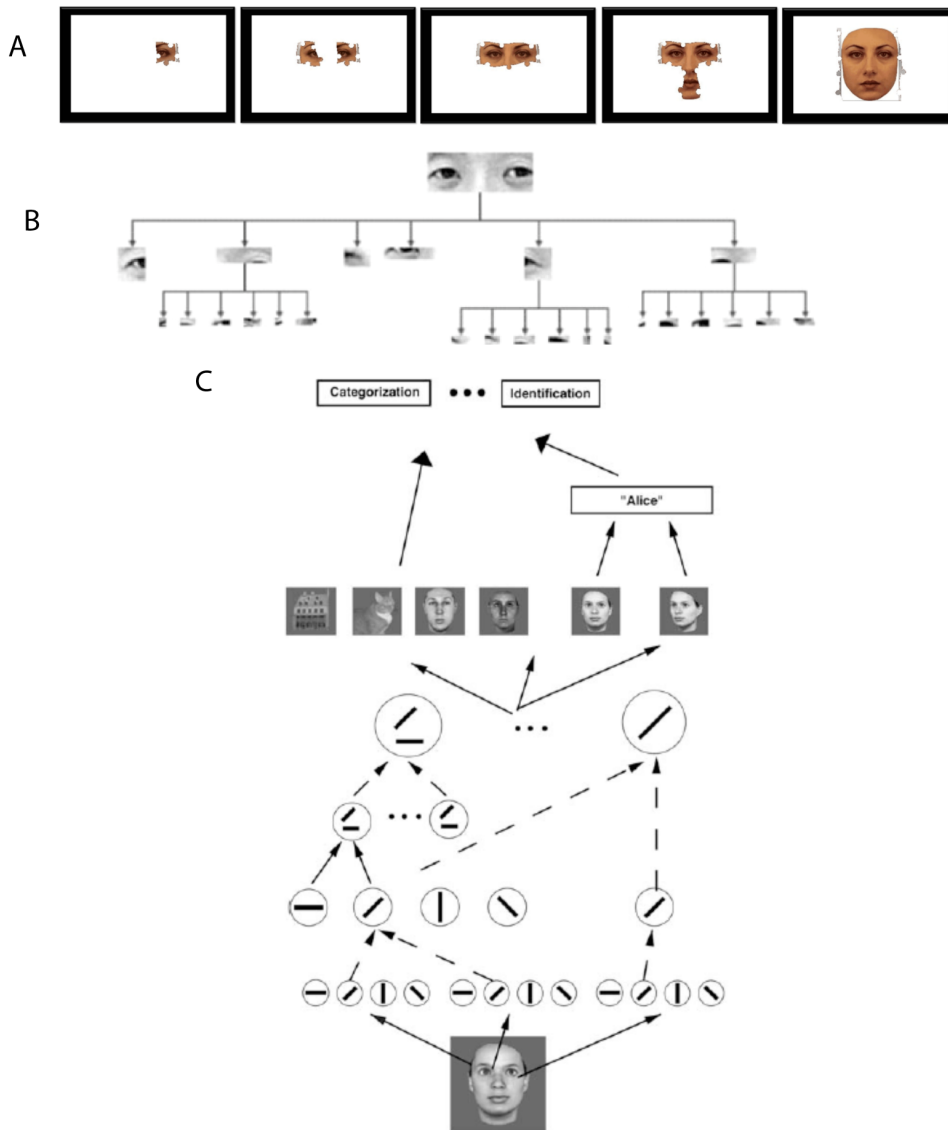


Figure 14. *A. Schematic illustration of the analytical/atomistic view of human face recognition, according to which a face is processed part-by-part, these parts having to be integrated progressively, like the pieces of a puzzle, in order to derive a representation of the whole face. B & C: Two prominent hierarchical/featural conceptions of how faces are processed in the human brain: B. The fragment model proposed by Ullman (2007) in which visual objects are represented by a hierarchy of fragments that are extracted during learning from observed examples. The fragments are thought to be class-specific (here face-specific) features selected to deliver a high amount of information for recognition. C. The H-Max feature-based hierarchical model of Riesenhuber and colleagues (here from Jiang et al., 2006).*

8.2. The holistic/configural human face recognition

According to a fundamentally different tradition of research, the face is instead perceived as a whole unit or a *Gestalt*, along the lines of the Gestalist view of visual perception (Wertheimer, 1925/1967; for reviews, see Wagemans et al., 2012a; 2012b). This view is primarily based on

visual illusions or 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 15A**; or Arcimboldo paintings, see Hulten, 1987). One reason for which the human face is often considered as the quintessential whole, or Gestalt (Pomerantz & Kubovy, 1986; Palmer, 1999), is because faces are perceived more easily than objects in such Mooney pictures (Moore & Cavanagh, 1998).

The most compelling illustration of this holistic/configural view is arguably the composite face illusion, an illusion named after the composite face effect reported by Young and colleagues (1987; see also Hole, 1994). It shows that the identity of the top half of a face cannot be recognized without being influenced by the identity of its bottom half (Rossion & Boremanse, 2008; see Rossion, 2013 and Murphy et al., 2016 for reviews). Or, to put it more exactly, even if this bottom half is not fixated, its alignment with the top half creates the perception, i.e., the subjective phenomenological experience, of a whole new face (**Figure 15B**).

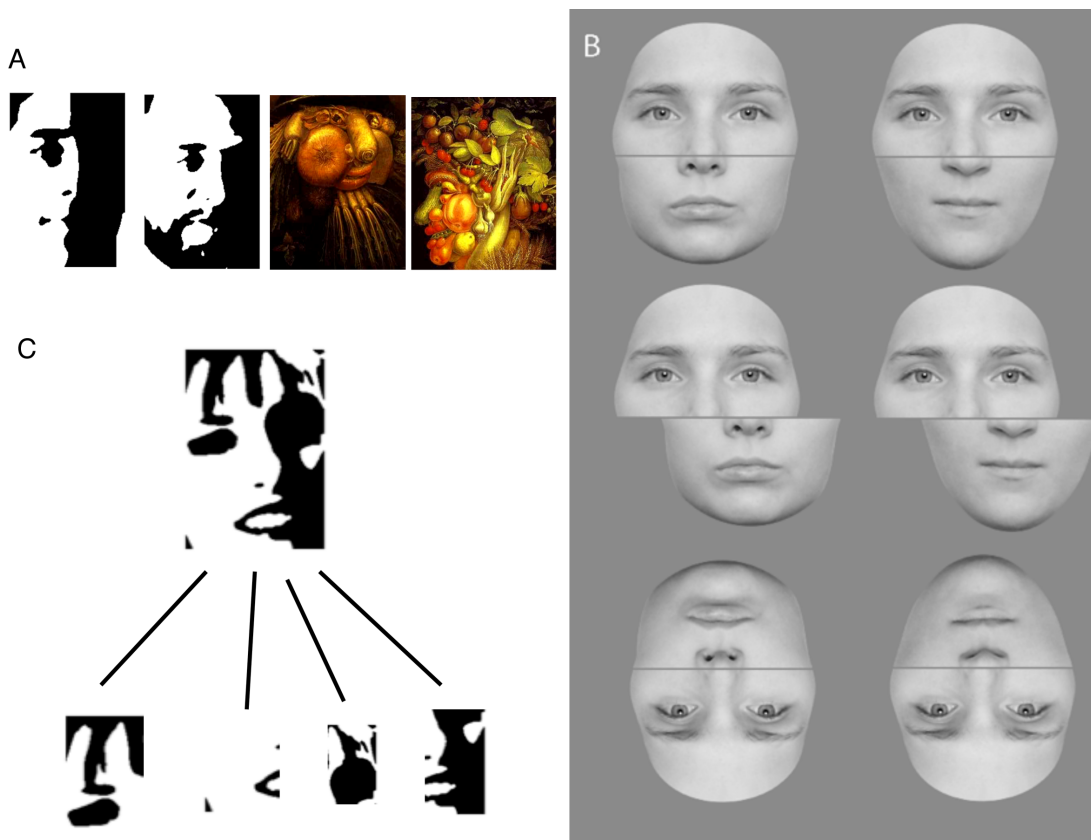


Figure 15. *A. Examples of stimuli that are readily recognized as faces despite no clear representation of facial parts: (left) binarized images known as Mooney stimuli (Mooney, 1957), (right) Arcimboldo paintings. In both cases, a face is readily perceived even though the parts are not face-like. B. The composite face illusion (Figure from Rossion, 2013). Top row. The two identical top halves are perceived as being different because they are aligned with different bottom halves. Misaligning the bottom halves as in the middle row breaks the illusion, which also vanishes when faces are presented*

upside-down (bottom row). This powerful visual illusion indicates that the visual system automatically glues the two halves of a face into an integrated configuration. C. In isolation, the parts or fragments of a Mooney stimulus are meaningless, and it is difficult to understand how they would be logically combined to form a whole face in a hierarchical, part-based representation system.

At the empirical level, many behavioral studies have used such phenomena to show that the processing of a facial “part” (e.g., eyes, nose, mouth, or half of a face) is mandatorily affected by alterations to the identity or the position of one or several other parts of the face (e.g., Homa et al., 1976; Mermelstein et al., 1979; Sergent, 1984; Young et al., 1987; Hole, 1994; Suzuki & Cavanagh, 1995; Tanaka & Farah, 1993; Tanaka & Sengco, 1997; Farah et al., 1998; see Rossion, 2013 for review). Collectively, these studies are taken as evidence in favor of a holistic/configural view of human face (identity) recognition.

8.3. Coarse-to-fine holistic perception

It is important to understand that the holistic view of human face recognition is fundamentally opposed to an analytical view of 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, an eye for instance (**Figure 15C**). Yet, the whole stimulus is recognized as a face. This observation is fundamentally incompatible with a hierarchical view according to which the (category) identity of parts is initially coded and then these parts are combined to form a whole face (Jiang et al., 2006; Ullman, 2007; Pitcher et al., 2011; Issa & Di Carlo, 2012; **Figure 14**).

The holistic/configural view does not state that the whole stimulus is represented before its parts during visual processing, but that there is no independent *category-selective* (i.e., face-selective) representation of parts, at any processing stage. That is, according to the holistic/configural view, the parts of a face do not even have an independent category-selective representation (Tanaka & Farah, 2003; Rossion, 2013): instead, non-face sensory parts of a visual stimulus co-activate (simultaneously or within a short time-frame) a (memory-based) holistic (i.e., unified) face representation. This activation/matching corresponds to the recognition of the stimulus as a face.

This holistic/configural view of human face recognition is compatible with a coarse-to-fine process, according to which the initial representation of the whole face is very coarse, allowing to categorize the stimulus as a face, but no more (Sergent, 1986). This representation then refines, rapidly providing sufficient cues to individuate the face (i.e., discriminate it from other face identities, familiar or unfamiliar; Sergent, 1986; **Figure 16**). Importantly, throughout

this coarse-to-fine process, which would last between 80-200ms following stimulus onset, the representation of the stimulus is always holistic, i.e., *never* decomposed in parts (Rossion, 2013; Yan et al., 2021).



Figure 16. *Two illustrations of the coarse-to-fine view of face recognition, 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 (filtering parameters as in Yan, Goffaux & Rossion, 2021; full view images under creative commons license). Note that with natural views of faces including hairstyle, highly fine-grained representations are not needed for optimal FIR performance, with spatial frequencies below 8.7 cycles/head (step 5 here for the 2 examples) being sufficient.*

Understanding how such a dynamic coarse-to-fine holistic process could be implemented in the human brain, and modeling it, is particularly challenging. Hence, it is not surprising that neuroscientific and computational models of human face recognition favor the opposite analytical/hierarchical view of human face recognition (**Figure 14**). Moreover, the holistic/configural view of face recognition lacks formalism and has been the source of numerous confusions in the scientific literature. One such confusion arose when scientists attempted to define “many faces of configural processing”, in particular referring to the relative distance between features as “configural” or “configurational” features (Carey, 1992; Haig, 1984; Maurer et al., 2002; Mondloch et al., 2002) as opposed to “local” features or “featural information” such as the shape of the mouth or the color of the eyes. As I argued in previous theoretical reviews, attributing the “configural” label solely to relative distances between facial features is profoundly misleading (Rossion, 2008; 2009; 2013; see also McKone & Yovel, 2009). The term “configural” or “holistic”, which should be synonyms in human face recognition research for sake of clarity, both refer to a *process*, according to which *the parts of a face are necessarily integrated into a single representation of the whole face*. When this process is applied to a face stimulus, every feature of the face is therefore “configural/holistic” in some sense. Another source of confusion come from the misconception that holistic processing requires the *presentation* of a whole face stimulus (e.g., Leder & Bruce, 2000; Leder et al., 2001). However, there is no reason for this to be the case: if a subregion of a face stimulus is presented, such as a well-segmented eye region

for instance, it may be sufficient to trigger a holistic/configural representation. For this reason, holistic/configural processing may even be crucial in recognizing faces which are partly occluded or presented in degraded conditions for instance (see Rossion, 2009; 2013 for discussion of this issue).

IX. PS's prosopagnosia: a defect in holistic finer-grained face perception

With a summary of these theoretical frameworks in hand, let me now come back to the case of prosopagnosia PS. Thanks to analytic methodological approaches, we found that PS has increased relative difficulties in extracting diagnostic cues from the eye region of the face. Importantly, this limitation is not absolute: PS is able to extract information from this region of the face if she focuses on it. However, it comes at a cost: she then fails to perceive diagnostic cues located elsewhere on the face. That is, a local difference between two facial identities is not automatically noticed: this diagnostic cue has to be searched for, selectively attended. Of course, her increased lack of sensitivity to the eye region and her difficulty in spontaneously detecting unattended local differences between faces could be unrelated: she could have two independent deficits due to extensive brain damage. However, there is a more parsimonious explanation: *PS' inability to represent a face identity holistically, i.e., as a single unit, could particularly affect the diagnosticity of the eye region. Indeed, this region of the face is constituted of many elements, which form a local configuration (e.g., pupils, eyelids, iris, eyebrows, distance between eyes, distance from nose and forehead). In comparison, the mouth is a relatively isolated element in the face. Hence, while the region of the eyes on a human face is highly diagnostic for facial identity, as demonstrated in many studies cited above, this advantage in diagnosticity might be particularly fragile: it may depend relatively more on the ability to process the multiple elements of the eye region as an integrated unit, i.e., holistically.*

This is the line of reasoning that I developed about PS's difficulties about 15 years ago: her core impairment in holistic recognition of a face identity *causes* a specific decrease of sensitivity to the eye region. Even in the experiment where the eyes of familiar children are presented in isolation (**Figure 10**), a difficulty in holistic recognition could be more problematic for that stimulus, made of several elements, than the mouth. Moreover, being aware of her difficulty at using the eye region to recognize people, PS is also likely to focus more on other parts such as the mouth in real life, thus encoding information predominantly at this level.

To test this hypothesis, we first had to show that PS indeed was impaired at holistic recognition of face identities and if so then best characterize this deficit.

9.1. Face inversion

One of the first tests that we applied in this context was to ask PS to recognize face identities presented upside-down (Busigny & Rossion, 2010). In typical human adults, this simple stimulus manipulation is known for decades for decreasing FIR performance in a variety of tasks and across a wide range of face stimuli, much more so than for the recognition of mono-oriented objects' identity (Yin, 1969; see Rossion, 2008 for review). In fact, this large decrease of performance for individuating inverted pictures of faces is probably the most robust experimental effect in human face recognition research. Picture-plane inversion is a great stimulus manipulation because the physical difference between face stimuli is strictly the same across the two orientations, upright or inverted. That is, for a machine or ideal observer, two face identities differ as much in terms of their diagnostic cues at upright or inverted orientation. However, thanks perhaps to biological constraints (i.e., the preference to visual patterns with more contrasted elements in the top half at birth; Turati et al., 2002) but most likely to our extensive life experience with upright faces¹², neurotypical adults are significantly better and faster to recognize the identity of upright as compared to inverted faces.

Although the recognition of local cues (e.g., the shape of the mouth) is affected by picture-plane inversion, the main effect of this manipulation is to disrupt holistic/configural face recognition as defined above. This is well illustrated in **Figure 15C** above, with the loss of the composite face illusion for stimuli presented upside-down. This disruption of holistic/configural FIR has been well documented across various tasks (Sergent, 1984; Young et al., 1987; Tanaka & Farah, 1993; Rhodes et al., 1993; Sekunova & Barton, 2008)¹³. Based on this, we tested PS in

¹² Although there are contradicting reports, a significant effect of inversion in FIR tasks does not appear before 6 years of age (see Hills & Lewis, 2018), indicating that biological constraints at birth (i.e., the preference for top-heavy patterns; Turati et al., 2002) can be overruled, and suggesting that the inversion effect is driven essentially by visual experience. However, visual experience with upright orientations is not enough: it has to take place in a biological system that is constrained - and develops a high ability - to individuate conspecifics. Adult macaque monkeys for instance, a species with little expertise in FIR (Parr et al., 2008; Rossion, & Taubert, 2019), do not show significant inversion effects in FIR tasks (Rosenfeld & Van Hoesen, 1979; Bruce, 1982; see Rossion, & Taubert, 2019 for review).

¹³ A few paradigms and measures in psychophysics fail to demonstrate qualitative differences between upright and inverted faces (Sekuler et al., 2004; Murphy et al., 2020), or suggest that irrespective of orientation faces are processed as a mere sum of their parts (Gold et al., 2012). However, as discussed above in the main text for the first study, they form an exception, which is essentially due to the lack of adequate paradigms and variables measured in these studies to properly capture holistic face identity recognition.

several face identity matching tasks, including the BFRT-c, with stimuli presented at upright and inverted orientations. While we expected PS to show a reduced face inversion effect compared to typical participants, the outcome was even more extreme than that: despite well above chance level performance, PS showed no advantage whatsoever at matching faces for their identity at upright as compared to inverted orientations (Busigny & Rossion, 2010; e.g., **Figure 17**).

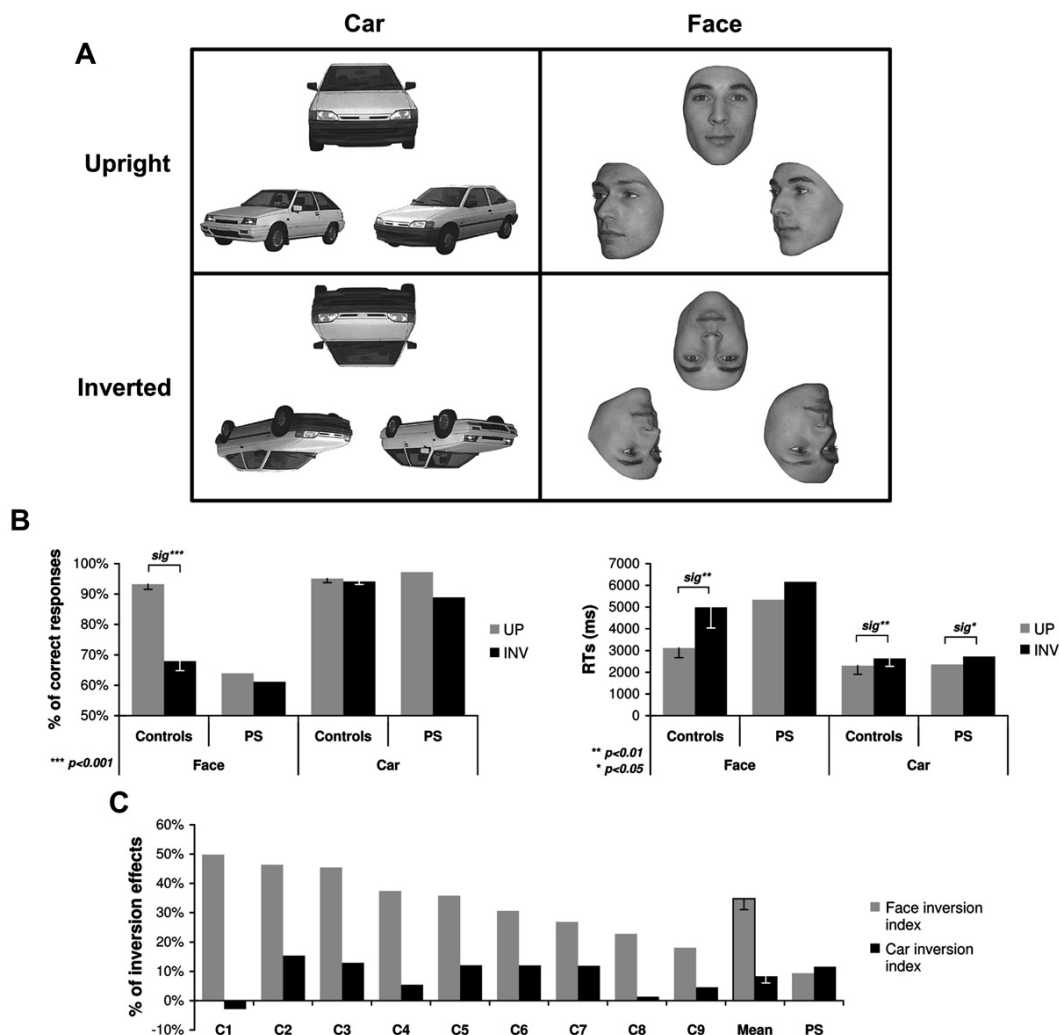


Figure 17. Face inversion (from Busigny & Rossion, 2010). **A.** Examples of stimuli (faces & cars) used in a simultaneous 2AFC matching task across views. **B.** Contrary to normal observers, PS shows no advantage for upright as compared to inverted faces. The small inversion effect for pictures of cars is in the normal range. **C.** The inversion index, taking into account both accuracy rates and correct RTs, for PS vs. age-matched controls. Other experiments reported in that paper did not require matching across depth-rotation of the stimuli, increasing PS's overall performance up to 75% for instance. However, contrary to all controls, she showed no difference in performance between upright and inverted faces.

This lack of face inversion effect was confirmed across 5 experiments, evaluating the matching of unfamiliar and familiar face identities presented under the same head orientation,

different head orientations, with or without delay between the stimuli to match (Busigny & Rossion, 2010). These observations indirectly point to PS's lack of holistic/configural recognition of faces, in line with the observations described above.

To make it clear, PS sees a face stimulus as being upside-down of course, and she can tell apart an upright from an inverted face straight away. However, when she has to *individuate* faces (i.e., recognize their identity), it does not matter if they are presented at an upright or inverted orientation. Note also that PS does not present an *advantage* at matching inverted as compared to upright faces, as previously found in some reported cases of prosopagnosia such as LH for instance (Farah et al., 1995). This latter effect is very rare and nonspecific to faces (Degelder et al., 1998), probably due to random fluctuations of poor performance levels (i.e., close to chance level) in visual recognition tasks combined with upper visual field defects common in such patients (see Busigny & Rossion, 2010).

9.2. Parts, wholes, composites

Searching for more direct evidence of impairment in holistic/configural face recognition, PS was tested in a series of behavioral studies with unfamiliar faces in which she had to match/discriminate facial parts that were either presented in isolation or in their whole facial context (Ramon et al., 2010). In the part/whole paradigm (Tanaka & Farah, 1993), participants encode a whole face stimulus and then have to determine which of two faces differing by one part (e.g., the eyes) is the same as the encoded stimulus. In half of the trials, the face parts are presented in isolation. Although the physical difference between the two items is the same in the two presentation conditions, participants usually perform better and faster with whole faces than isolated parts (Tanaka & Simonyi, 2016 for review). Across two paradigms, measuring both accuracy rates and correct RTs, PS did not show this whole/part advantage in FIR, as if she processed the stimuli part-by-part, without being influenced by the other parts of the face (Ramon et al., 2010).

PS was also tested in two different experiments with composite faces such as presented in **Figure 15C**, in which she had to match two identical top halves of faces spatially aligned or misaligned with different bottom halves. While neurotypical participants showed typical composite face effects in these tasks, i.e., they made more mistakes and took longer to match identical top face halves aligned as compared to misaligned with different bottom halves, PS's performance was not influenced by the irrelevant facial halves in the test (Ramon et al., 2010). Since this composite face effect is widely considered as providing the strongest evidence for holistic recognition of face identity (Rossion, 2013; Murphy et al., 2016 for reviews), the outcome

of these studies suggests that PS indeed fails to recognize a face identity holistically/configurally, having to analyze it part-by-part.

While these studies were performed with pictures of unfamiliar faces, we also took the unique opportunity of PS's work at the kindergarten to test whether these observations were valid for pictures of (personally) familiar faces (**Figure 18**). Face identities learned – for months - in natural conditions are not only more ecologically valid, but they allow avoiding to present a stimulus at an encoding stage as with unfamiliar faces. This project, led by Meike Ramon, required an enormous amount of work, organization and good will, with pictures of the kindergarten children carefully edited and transformed, and all participants (i.e., PS and her colleagues) subsequently tested on a laptop computer in the kindergarten during several sessions. In total, PS and her colleagues took part in 13 behavioral experiments with the familiar children faces (grouped in 9 studies; see Ramon et al., 2017). Here I will just summarize and illustrate a few results.

In some of these experiments, PS and her colleagues had to determine which isolated part (either the eyes or the mouth) of a pair belonged to a given child's identity (i.e., “*Which one is Nelson?*”). In half of the trial of this 2AFC task, the parts were inserted into the whole face of this child. Although we were able to test only 2 or 3 controls in these studies (PS's colleagues), the effects with familiar faces were consistent and spectacularly large: they performed much better and faster with whole faces than with isolated parts, noticing immediately when a mismatching face identity part was inserted into a given child's face (think of how easily and quickly you would notice if your child's eyes were replaced by those of another child). In contrast, in that experiment, PS performed *worse* with whole faces than isolated parts (**Figure 18a**)! Although some would interpret this effect as sort of interference of holistic face representation on the analysis of facial parts (e.g., Farah et al., 1995b), there is a much simpler account: in the context of the whole face, PS does not know in advance where the diagnostic cue is, and has to search for it. Once again, having to deal with a whole face stimulus increases the uncertainty of the recognition process for her. In contrast, typical observers do not have to search for the incorrect part inserted in the face: at a glance, they notice that the whole face suddenly appears incongruent, making it much more salient than when the part is isolated.

In a composite face task with familiar faces, similar to the original demonstration of Young et al. (1987) with pictures of celebrities, PS and her colleagues had to determine which top half of two different faces belonged to a given child's identity (i.e., “*Which one is Nelson?*”) (**Figure 18b**). The top halves were either aligned or misaligned with bottom halves of a different face identity. This arrangement led to large composite face effects in neurotypical participants: they

performed better and faster with misaligned than aligned stimuli. In contrast, PS's judgment was uninfluenced by the spatial alignment between facial halves (Ramon et al., 2017). Both the whole/part advantage and the composite face effects were also replicated with a simpler task, requiring making only familiarity judgments (see Ramon et al., 2017).

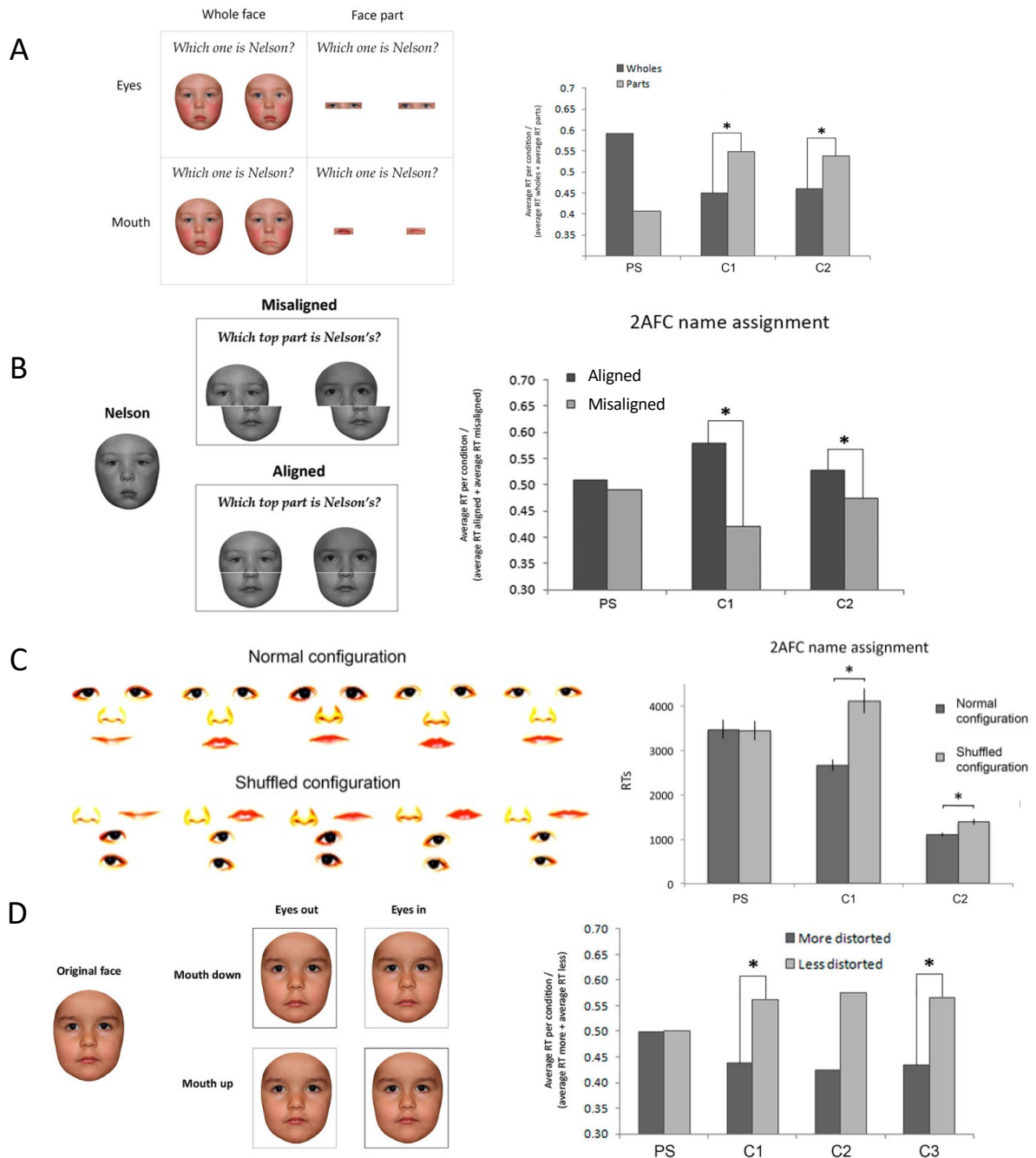


Figure 18. Examples of experiments and results obtained with PS and two colleagues of the kindergarten tested with manipulated versions of the familiar children's faces (Ramon et al., 2017). **A.** Whole-part advantage. In one version of that experiment, PS had to choose which of the 2 full faces or the two isolated parts (eyes or mouths) belonged to a familiar child of the kindergarten. She performed the task well above chance level (about 80%, see Table 5 in Ramon et al., 2017) but taking much more time than

her colleagues (C1 and C2) and, most importantly, much more time for whole faces than isolated parts. In contrast, her colleagues showed the typical advantage for whole faces over isolated parts. The results are shown here for the eyes trials, but were similar for the mouths trials. B. Composite face effect. In one experiment, participants had to choose which of the two top halves presented was the face of a familiar child (here “Nelson”, with his full face picture shown on the left but not in the experiment). Neurotypical individuals scored at ceiling but found it significantly harder (i.e., increased RTs) when the top halves were aligned with a bottom half face belonging to a third child than when the two halves were misaligned, a typical composite face effect with familiar faces (Young et al., 1987). In contrast, PS, while performing at about 70% accuracy, showed no advantage whatsoever for misaligned faces, as if her judgment of the top halves were not influenced at all by the bottom halves making a full face picture. C. While PS’s colleagues performed significantly faster at a 2AFC name-face identity assignment task with facial parts arranged in a normal as compared to a shuffled configuration, PS showed no such advantage, as if she recognized a facial identity part-by-part without any influence of the other parts arranged in a typical whole configuration. D. PS and her colleagues had to decide which of 2 face pictures was the real child, with the distractor being more (eyes closer/mouth down; eyes further apart/mouth up) or less (eyes closer/mouth up; eyes further apart/mouth down) distorted. While they all performed faster for less distorted faces (a facial geometry effect), PS, who performed the task above chance level, was insensitive to the ratio between distances of facial parts.

In all of these experiments with various stimuli, paradigms and tasks, participants have to focus and use a specific part of a face stimulus (i.e., a subregion of a face, whether it is defined as the eyes or mouth, or a half face). However, their judgment is automatically (i.e., without volitional control) influenced, positively or negatively depending on the paradigm, by the other parts of the face presented in a normal configuration. In contrast, when she is engaged in a FIR task, PS can analyze each part of a face stimulus as if the other parts did not even exist: the presence, correct organization and position of these latter parts have no influence whatsoever on her judgments. Two other experiments performed with pictures of the familiar face children devoid of any external cues illustrates this point very well. First, contrary to her colleagues, PS showed no disadvantage at recognizing the identity of the children faces when their internal parts were shuffled in position (**Figure 18c**; Ramon et al., 2017). Second, while PS’s colleagues recognized a veridical child face identity more easily when contrasted with an incongruently distorted distractor (e.g., eyes closer and mouth further down from the nose) than a congruent (e.g., eyes further apart and mouth further down from the nose) distractor (a “facial geometry effect”, Barton et al., 2003), PS showed no advantage in rejecting the incongruent distractor, indicating that she was not sensitive to this overall facial geometry of the face identity (**Figure 18D**; Ramon et al., 2017).

9.3. A facial map of prosopagnosia

If PS recognizes a face identity part-by-part, how does this translate into her pattern of eye gaze fixations on that face? Does she look at a whole face differently than normal observers when she attempts to recognize its identity? Since the location of eye movements does not necessarily reflect the focus of attention, this is not a given, and it may be one of the reasons why studies of eye movement patterns in reported cases of (prosop)agnosia have generally provided equivocal results (Lê et al., 2003; Barton et al., 2007). Being aware of this issue, my colleagues and I nevertheless analyzed PS's eye movements during her recognition of the identities of the kindergarten's children's pictures, presented one by one at conversational distance (12° x 16° visual angle).

Knowing in advance that only children of the kindergarten were presented, PS scored at 61% in a task where she had one chance out of 27 at each trial, and took 12.5 seconds on average to provide a response. Irrespective of her performance, she fixated on 3 main spots on the face: the mouth (about 60% of fixations and fixation duration), but also the left and the right eye (about 30% of fixations), with only a negligible fraction of fixations outside of these three facial parts (**Figure 19**; Orban de Xivry et al., 2008). PS's pattern of fixations thus resembled typical patterns of explorations of faces as described initially by Yarbus (1967; **Figure 19**), with the exception that the mouth – as hypothesized – was fixated more and longer than any other face parts, and was also systematically fixated first (Orban de Xivry et al., 2008). However, much to our surprise, we found a radically different pattern of fixation for her kindergarten colleague tested in the same task. Indeed, this neurotypical individual almost made no fixation to the mouth or on the eyes themselves but fixated centrally, just below the eyes, on the upper part of the nose. In fact, the pattern of fixations was strikingly different than PS's fixation pattern: there was almost no overlap between the location of the eye gaze fixations between the two (**Figure 19**).

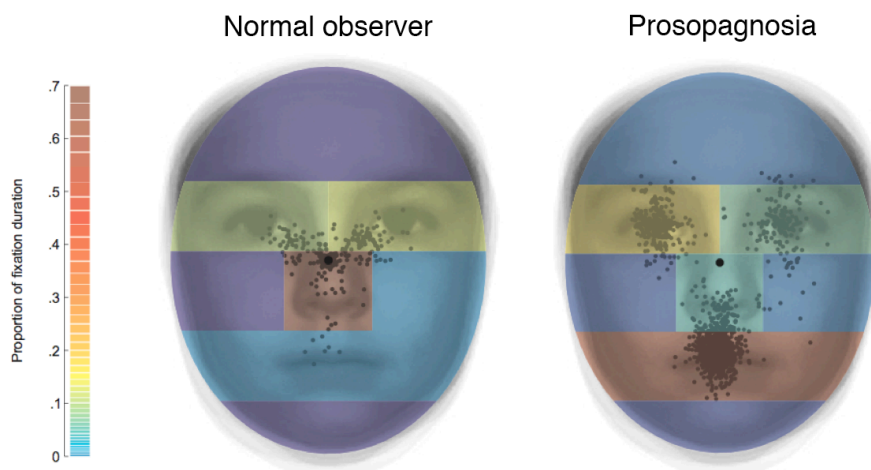


Figure 19. A. *Distribution of gaze fixations during a FIR task for PS and a neurotypical observer who was also personally familiar with the faces shown (Figure adapted from Orban de Xivry et al., 2008). During FIR, PS fixates exactly on each internal part of the face, with a large proportion of fixations on the mouth (here 60%), but also exactly on each eye. In contrast, the typical observer tends to fixate on the center of the face, slightly below the eyes, rather than on any of the specific parts of the face (see also Hsiao & Cottrell, 2008; Peterson & Eckstein, 2012). This featureless fixation location is biased towards the superior half of the face, probably because of the larger number of diagnostic cues in the top half of the face. It may reflect the center of gravity, or center of mass, for FIR, being optimal for holistic face identity recognition (Orban de Xivry et al., 2008; Rossion, 2014). This figure offers perhaps one of the clearest illustrations of the contrast between an analytic (PS) and a holistic/configural (typical observer) way of recognizing face identity.*

At first glance, given previous reports of typical eye gaze fixations on faces (e.g., Yarbus, 1967; Henderson et al., 2005), our most unexpected observation was for the neurotypical observer, not for PS. However, at second glance, this observation made complete sense. In these studies, eye movement patterns during spontaneous explorations of faces, for relatively long durations, were analyzed, and quantified in large regions of interest without displaying the individual fixation points (e.g., Henderson et al., 2005). Here the neurotypical participant, who was flawless at the task, answered within 1-2 fixations, which were all located *outside* of the main diagnostic parts of the face (i.e., a featureless location; **Figure 19**, left).

While this featureless fixation location? Presumably because it is optimal to extract *diagnostic cues across the whole face, at a glance*, as a typical holistic processor would do (**Figure 19**). Inspired by a developmental study that had shown such patterns of fixations in between the eyes in children classified as configural processors in a behavioral task (Schwarzer et al., 2005), this is exactly how we interpreted our observations (Orban de Xivry et al., 2008).

Note that the optimal fixation point is not on the tip of the nose – corresponding roughly to the geometric center of the face image - but slightly above it, as if this location was weighted by the number of diagnostic facial parts to take into account, these parts being more numerous in the top half of the face. That is, this location appears to correspond to the *center of mass*, or *center of gravity*, of the face (Orban de Xivry et al., 2008; see also Jeffreys et al., 1992¹⁴). Interestingly,

¹⁴ Jeffreys et al. (1992) showed that this fixation point on the nasion also leads, in most observers, to the largest amplitude of a well-documented early face-selective event-related potentials in EEG, the vertex positive potential. According to more recent evidence, this optimal location, which can nevertheless vary across individuals, is associated with the largest electrophysiological measures of unfamiliar face identity discrimination (Stacchi et al., 2019).

our paper came out at the same time as a study showing that typical observers indeed fixate at this central location just below the eyes when having to individuate learned faces (Hsiao & Cottrell, 2008). Such findings have since then been widely reported and extended, indicating that the initial featureless fixation point between the eyes and the nose is indeed optimal for face identity recognition in (most) typical observers (Peterson & Eckstein, 2012; Or et al., 2015; see also Blais et al., 2008 for cultural variations of subsequent eye fixations).

This finding obviously raises the issue of whether PS's abnormal fixation strategy is suboptimal for her (and thus could be modified), or if she really *needs* to fixate each local part of the face to have the best chance to recognize its identity.

9.4. Holistic face perception probed with gaze-contingency

An opportunity to answer this question arose when Goedele Van Belle and I designed probably the most elegant experiment performed with the case of prosopagnosia PS, an experiment for which we made clear hypotheses and obtained a striking double dissociation of performance between her and typical observers. The experiment was based on *gaze contingency*, a technique in which the observer is presented with a visual stimulus constrained by their own gaze fixation(s). This approach had long been used with written words in order to determine the reading span (Rayner, 1975; Rayner, 1988) but later adapted with an on-line control of moving masks and windows (van Diepen et al., 1994) to be introduced in human face recognition research.

To test directly the hypothesis of PS's defect in holistic FIR, we first constrained her view of a face stimulus to one major part at a time, by presenting her with a *gaze-contingent window* of about the size of an eye (+eyebrow) *or* the nose *or* the mouth (depending on where *she* chooses to fixate) (**Figure 20A**). That is, if PS fixates the mouth, she would be presented with the mouth only. We reasoned that if PS recognizes a face identity part-by-part, i.e., analytically, her performance should not deteriorate much in this gaze-contingent window condition. In contrast, typical observers –assumed to rely on holistic recognition – should be impaired in this viewing condition (think of having to recognize people's identity by seeing only one of their facial part at a time). We designed a 2AFC task which was easy enough for PS to perform well with faces presented at full view: a first unfamiliar face identity presented for 4 seconds then replaced by the exact same image of that face side by side with a distractor face, asking PS to select the target face as accurately and fast as possible (**Figure 20A**).

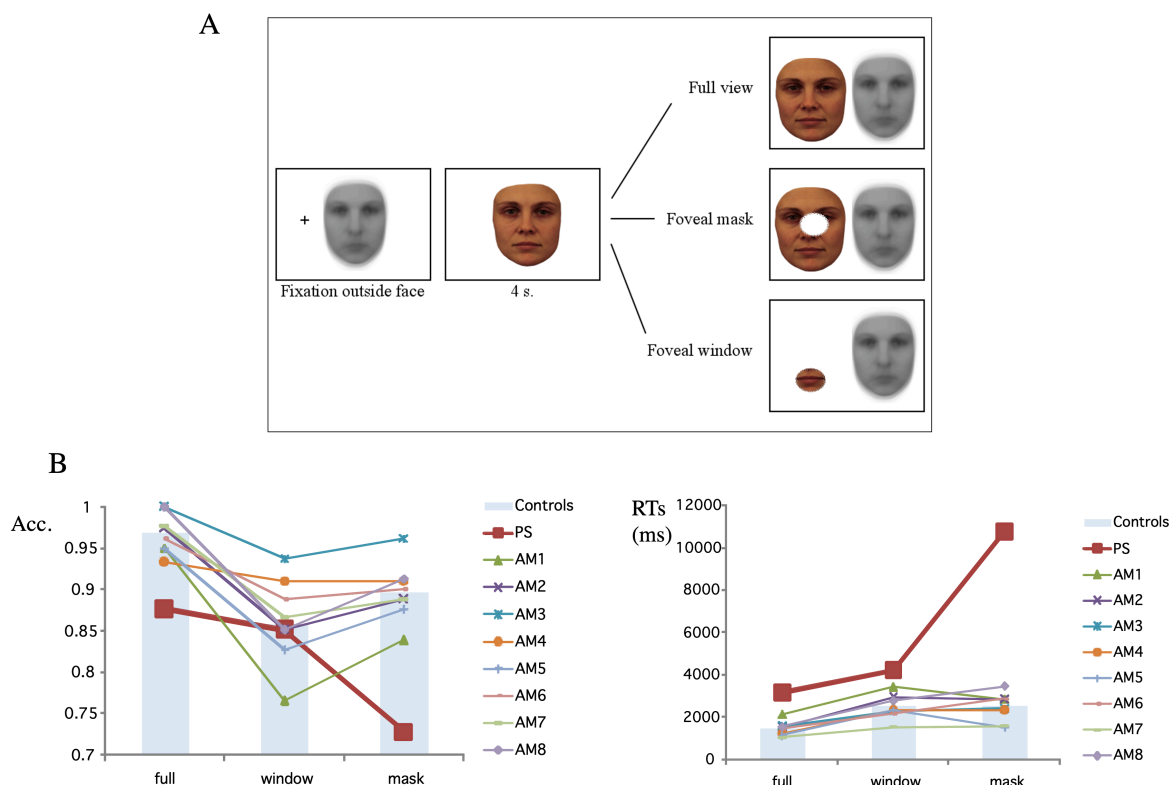


Figure 20. The first application of gaze-contingency to human face recognition research (Van Belle et al., 2010a). When PS fixates the cross on the left, an unfamiliar face identity appears on the screen for 4s to be freely explored. Then, one of three conditions (random order) is displayed, in which she has to choose which of two displayed identities corresponds to the first presented face (i.e., a delayed face identity matching task). Only the fixated face is revealed, while the other one is covered by a neutral greyscale face template (identical for all trials of the experiment). The target and the distractor are either: 1) viewed in full; 2) through a gaze-contingent window revealing only the fixated part (“window” condition) or 3) a gaze-contingent mask of the fixated part. The task was easy enough for PS for faces at full view, providing room to test the effect of the gaze-contingent mask and window. **B.** Contrary to normal observers, PS performed much worse in the mask than in the window condition, as if she could not discriminate face identities based on cues outside of her fixation. The exact same pattern was found when PS and controls were moved further away from the display, showing that it is the relative rather than the absolute size of the window/mask to the face that matters (Van Belle et al., 2010a; experiment 2). Videos of PS performing the task in these two conditions are available at <http://face-categorization-lab.webnode.com/pictures/>.

While typical observers’ performance dropped significantly with the gaze-contingent window relative to faces presented at full view, PS did not feel more uncomfortable in that situation, and her well above chance level performance was virtually unaffected (**Figure 20B**; Van Belle et al., 2010a). This observation is again consistent with the view that PS relies on a part-by-part analysis of the face in a FIR task. Unsurprisingly, and while this was not a major interest in this study, observers focused relatively more on the eye region (i.e., one eye at a time)

of the faces, whereas PS focused essentially on the mouth, though she also sometimes tried to use the eyes to collect more evidence to support her decision (Van Belle et al., 2010a). Hence, it appears as if focusing on the mouth of the faces is truly the most efficient way for PS to individuate faces.

However, is it mandatory for PS to focus on the mouth and on each facial part at a time, or is it simply a strategy that she got used to and could modify to improve her performance? To test that, we included another condition in which the fixated face part is selectively *masked* (i.e., gaze-contingent mask). With this manipulation, PS is forced to use cues *outside* of her fixation. Note that this does not mean that holistic recognition is strictly necessary to perform the task – the mask could be put on the nose and the discrimination task performed using a single part outside of fixation, e.g., the mouth only. However, if this part-based approach is used, performance must deteriorate in the gaze-contingent mask (with the used part outside of fixation) as compared to the gaze-contingent window (with the used part at fixation). In contrast, the ability to recognize a face identity holistically, i.e., from *all* (unmasked) parts of the face into a single representation, should facilitate FIR in the gaze-contingent mask condition, overcoming the lack of cues at fixation.

As often, I was observing PS participating in that experiment, and I rapidly realized that there was almost no need to analyze the data: contrary to trials of the gaze-contingent window condition, PS's difficulties in trials of the gaze contingent mask condition was plain to see. While typical observers found it relatively easier in the gaze-contingent mask condition, PS's performance dropped significantly, and she took an extremely long time to perform these trials. In fact, after a few blocks of trials (of all three conditions in random order), she literally said "*This experiment is horrible, can I have a break?*". In 20 years of testing her, this is perhaps the only time that PS asked me to take a break during an experiment! Of course, we gave her a deserved break, but asked her to perform more blocks of trials and do her best, collecting a substantial amount of data. As illustrated on **Figure 20**, both for accuracy rates and correct RTs, there was a clear double dissociation between PS and typical observers across the two gaze contingent conditions (Van Belle et al., 2010a).

Although this publication and the approach have not been as influential as I would have liked in human face recognition research, this was a real turning point for me in understanding the nature of PS's deficit. Here, contrary to the Bubbles study, the manipulations of different cues on face identities or the eye movement recording study, we had a very clear prediction, and the data turned out even better than what we hoped for. We nevertheless complemented this dataset in three ways. First, we extended it to the recognition of personally familiar faces (Van Belle et al., 2010b). Second, we showed that the pattern of performance for PS relative to typical observers

was independent of the relative size of the stimuli. To do that, we simply moved the participants two meters away from the screen, and replicated the original results (Van Belle et al., 2010a, experiment 2). This manipulation helps understanding PS's deficit, which is not due to an *absolute* constriction of the size of her visual field (as in neurological patients with tubular vision for instance). Instead, her part-based perception of the face flexibly adapts to the size of the face stimulus, indicating a defect of central origin. In other words, PS's impairment concerns the *perceptual field* rather than a (sensory) visual field (Rossion, 2014)¹⁵.

Finally, Goedele Van Belle suggested an interesting extension in which, rather than selectively revealing or masking a fixated part and measuring FIR performance, the patient was presented with a target face constituted of two conflicting identities: identity A at the level of the fixated part (gaze-contingent window) and identity B for the rest of the face, outside of fixation. PS had to choose whether the target face looked more like face A or face B, these pictures being presented below the target face. Thus, there was no correct response in this paradigm, but simply a preference judgment based on what observers were seeing. The size of the gaze-contingent window was adjusted so that across a group of control participants, the two identities were selected equally often. In contrast, as predicted, and systematically, across all trials, PS selected the identity A, corresponding to the information displayed in the gaze-contingent window, as if she was not even perceiving the facial identity presented outside of fixation (Van Belle et al., 2015).

9.5. Summary: a face-selective holistic recognition impairment

The extensive set of experiments summarized above and reported in a series of publications (Orban de Xivry et al., 2008; Busigny & Rossion, 2010; Ramon & Rossion, 2010; Ramon et al., 2010a; Van Belle et al., 2010a; Van Belle et al., 2015; Ramon et al., 2017) show that a patient with an acquired selective deficit at FIR – i.e., prosopagnosia – recognizes a face identity part-by-part, as if her judgment was not influenced by the other parts of the face in any positive or negative way. It is as if PS lost her ability to recognize a face identity holistically, i.e., as an integrated representation. When her part-based analysis is made very difficult by gaze-contingently masking the fixated part, trying to force her to rely on holistic recognition, her

¹⁵ Also, the pattern of results of PS cannot be explained at all by her scotoma, which is central and in fact falls entirely (or almost entirely in experiment 2 in the study of Va Belle et al., 2010a) in the window/mask surface. Hence, it should not affect performance in the foveal mask condition and, if anything, could even have contributed to decreasing slightly her performance in the window condition. In other words, any putative contribution of the scotoma runs contrary to our hypotheses.

performance deteriorates substantially, and her above-chance performance in the task is presumably driven by analyzing one part at a time outside of fixation. Indeed, PS is not blind in the periphery: it is not her visual field that is limited, but her *functional visual field*, or *perceptual field*, that shrinks to the fixated facial part. This shrinking is not absolute but *relative* to the size of the face stimulus (Rossion, 2014).

Instead of calling upon several independent functional impairments, PS's lack of holistic FIR may account for her increased difficulties at extracting so-called "configural" or "configurational" cues of face identities, i.e., relative distance between facial features, as compared to local featural cues, as discussed above. Of course, if the location of a single diagnostic cue for FIR is unknown, PS is in trouble in the task. However, once she detects that local cue, she can focus on it to reliably discriminate faces for their identity, although ignoring potential diagnostic cues anywhere else on the face (Ramon & Rossion, 2010; **Figures 11 & 12**). However, in general, PS fails to detect changes of relative distances between facial parts more than changes occurring locally (e.g., eye color) because, by definition, the former involve *several* parts across the face stimulus. This does not mean that PS has several functional deficits in FIR, or that there are "*many faces of configural processing*" (Maurer et al., 2002): the loss of holistic/configural recognition easily accounts for PS's increased difficulty at recognizing relative distances between facial parts.

The loss of holistic/configural recognition can also account for PS's increased difficulties at extracting cues from the eye region of a face as compared to the mouth, as conjectured above. Indeed, the eye region of the face contains many different elements or parts, close to each other, which makes it particularly diagnostic for neurotypical observers. However, without holistic recognition, each part of the eye region taken in isolation conveys only little information, and the region as a whole is overwhelming. Interestingly, although she does not read our scientific papers and is happy to remain naïve to the goal(s) of our experiments, PS is in fact very aware of that: one day, I asked her why she does not use the eyes to recognize people's faces and her answer was clear: "*there is just too much stuff in the eyes*". Indeed, while her colleagues in the kindergarten recognize children better with an intact pair of eyes (without eyebrows) than with an isolated eye or spatially misaligned, her performance is unaffected, as if adding another eye in an intact local configuration provided no advantage whatsoever (Ramon et al., 2017, experiment 9).

As acknowledged and discussed in all of our publications, difficulties or loss of holistic/configural face recognition have regularly been associated with prosopagnosia in the scientific literature, well before the first reports on the patient PS (e.g., Sergent & Villemure, 1989; Levine & Calvanio, 1989; Sergent & Signoret, 1992; Saumier et al., 2001; Boutsen &

Humphreys, 2002; Barton et al., 2002). However, these reports often concerned a single test, in patients whose recognition impairment was not selective to faces (i.e., cases of visual object agnosia). This – as well as a limited understanding of the nature of holistic/configural recognition - has often led to a great deal of confusion, as if the impairment concerned a generic holistic process applicable to a wide variety of stimuli with different configurations (e.g., Levine & Calvanio, 1989; Tanzer et al., 2013; Avidan & Behrmann, 2021). However, if PS is impaired at recognition of faces *only*, and if her deficit concerns holistic recognition, then surely she should be able to still recognize *nonface objects* holistically? Translated into an experimental design, this means that when having to recognize a local element of a global nonface visual configuration, her performance should be influenced by the nature of this global configuration.

This hypothesis was tested by Thomas Busigny and me, using hierarchical “Navon” stimuli (Navon, 2003). PS was presented with large letters (e.g., an H or a S) formed of small letters (e.g., Hs or Ss). Critically, her recognition of the identity of the small letters was influenced by the congruent relationship with the large letters, just like normal observers (Busigny & Rossion, 2011; **Figure 21A**). Thus, for nonface stimuli, PS is influenced by cues that are distributed over a large visual space and make sense only as an integrated unit.

Note that this observation of a dissociation between holistic recognition of face and nonface stimuli in a single case does not contradict the *association* that can sometimes be observed between the two functions in neuropsychological (e.g., Levine & Calvanio, 1989) or neurodevelopmental (Tanzer et al., 2013; Avidan & Behrmann, 2021) disorders of FIR. However, such associations occur in the absence of a *face-selective* recognition disorder, i.e., in cases of visual object agnosia (Levine & Calvanio, 1989) or visual dysgnosia (Tanzer et al., 2013; Avidan & Behrmann, 2021) and may therefore be due to damaged generic processes. The contrast between PS’s performance and such cases clearly illustrates the importance of isolating the category-selectivity of the recognition disorder to understand its nature.

While a wider range of experiments on holistic recognition of nonface object categories could have been documented with the patient PS, the following section, demonstrating intact holistic recognition of visual stimuli as faces, provided advantageous and inspiring replacements.

9.6. Intact holistic generic face recognition

The extensive series of studies summarized above have established that PS analyzes a face part-by-part to recognize its identity, an inefficient and time-consuming strategy. The gaze-contingency experiments further show that PS has no other option than to resort to this part-based process: gaze-contingently masking her fixated facial part causes profound difficulties for her,

even in simple face identity matching tasks. However, does PS has to rely on this part-based process for all types of recognition functions on faces or just to recognize a face *identity*? As far as we know, PS never complained of any difficulty at recognizing a visual stimulus as a face, i.e., *generic face recognition* (GFR). For instance, she is flawless and fast at classifying rapidly presented natural images containing a face against natural images containing various nonface distractors (Schiltz et al., 2006). More recent studies using electroencephalography (EEG) show that her brain readily categorizes a visual stimulus as a face even under severe stimulation constraints, i.e., highly variable unsegmented face images appearing briefly (166 ms SOA) in a rapid periodic stream of variable nonface object images (Liu-Shuang et al., 2016).

How is it possible if PS recognizes a face part-by-part? Admittedly, full pictures of real faces, such as in photographs, can be readily classified as faces based on the presence of one or two diagnostic parts alone (see e.g., Scheirer et al., 2014). However, certain types of visual stimuli *require* a holistic process to be recognized as faces. A notable example is provided by Giuseppe Arcimboldo's 16th century paintings, which are made of nonfacial parts (e.g., fruits, vegetables, books, flowers, etc.; **Figure 15**; see Hulten, 1987). To recognize these paintings as faces, one cannot rely on a part-by-part analysis. That is, recognizing an Arcimboldo painting as a face requires integrating the different parts of the stimulus into a unified visual representation, i.e., holistic recognition. Indeed, when the paintings are presented upside-down, they are usually not recognized as faces, as designed purposefully by Arcimboldo.

For this reason, it is generally believed that “*prosopagnosics can see the vegetables (i.e., the parts), but not the face (i.e., the whole) in Giuseppe Arcimboldo's The Vegetable Gardener (Natura)*” (Harris & Aguirre, 2007)”. Is this true? No: PS recognizes Arcimboldo paintings as faces readily, just like neurotypical observers. We first showed her informally a few pictures on postcards, and she spontaneously said they were faces. Then, we tested her with many Arcimboldo painting presented one by one, contrasted with the same images inverted and slightly rearranged, asking her to classify them as “face/noface” stimuli. PS was flawless at this task and performed as fast as normal observers (Rossion et al., 2011). Impressed by her performance, we invited her with the lab members to the 2007-2008 exhibition of Arcimboldo's paintings, temporary assembled from various collections at the Musée du Luxembourg in Paris (**Figure 21**). To strengthen these observations, we also replicated them with Mooney faces, such as illustrated in **Figure 15**. Again, despite the requirement to use holistic representation to perceive these stimuli as faces, PS performed just as normal observers (Rossion et al., 2011; **Figure 21**).

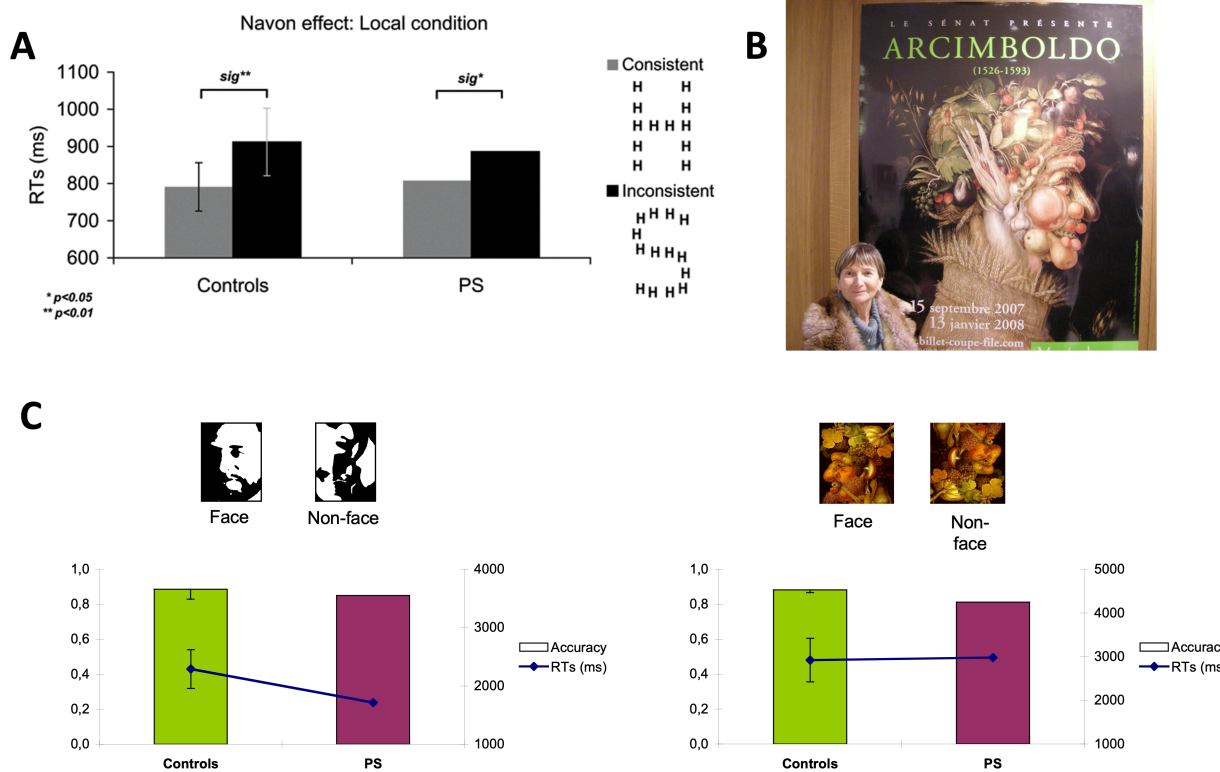


Figure 21. *A. Due to her loss of holistic recognition of a facial identity, when PS fixates a local facial feature, her performance is not affected by the identity of the features of the face outside the area of fixation. Yet, when she has to judge the identity of a small letter (H), her performance is worse if the large letter is inconsistent than if it is consistent, just like normal observers (Busigny & Rossion, 2011). Thus, her deficit cannot be explained in terms of a general loss of visual holistic recognition. B. Despite her domain-specific holistic recognition impairment, PS, photographed here at the entrance of the Arcimboldo exhibition in 2007 in Paris, recognizes an Arcimboldo painting as a face readily. C. This was tested systematically by asking her to classify Arcimboldo or Mooney stimuli as faces, two tasks that she performed as well and as rapidly as normal observers.*

9.7. Impaired holistic fine-grained perception of faces

Altogether, these observations indicate that PS recognizes a stimulus as a face holistically, just like neurotypical observers. Yet, she cannot recognize a *facial identity* holistically. How is it possible? How can we resolve this apparent paradox? The typical way to account for such functional dissociations in cognitive neuropsychology is by postulating that there are two separate subsystems or modules: one to recognize a stimulus as a face (‘face detection system’) and a second one, involved afterwards, for recognizing its identity (‘face identity recognition system’). Only the second system would be impaired due to PS’s brain damage. Starting with Hay & Young (1982), a number of functional, neurofunctional and computational models of human face recognition have indeed proposed such a two-stages distinction (e.g., Haxby et al., 2000; Degelder

& Rouw, 2001; Tsao & Livingstone, 2008). This distinction, which was not implemented in Bruce and Young (1986)'s influential model, is nevertheless also very much present in more recent neurofunctional architectures of human face recognition (Haxby et al., 2000; Pitcher et al., 2011; Duchaine & Yovel, 2015; see also Schweinberger & Neumann, 2016). According to this view, PS's deficit, similarly to many cases of prosopagnosia, would concern only the second system, involved in face individuation.

It is not the place here to go into detailed arguments, but suffice to say that such a theoretical view – distinguishing subsystems for generic face recognition and face identity recognition – does not only lack parsimony, but is also at odd with many observations. For instance, as extensively discussed in part II of this review, all face-selective regions of the human brain, including the most posterior regions in the lateral inferior occipital gyrus, show sensitivity to differences between (unfamiliar) face identities (e.g., Gauthier et al., 2000; Rossion, 2014 for review; see also Kovacs, 2020; Jacques et al., 2020). Moreover, PS's key lesion in the right hemisphere precisely concerns the most posterior region of the right inferior occipital gyrus, which is hypothesized as a 'face detection stage' in these models (Haxby et al., 2000; Pitcher et al., 2011; Duchaine & Yovel, 2015; see the accompanying paper on PS, part II). In reality, the proposal of a 'face detection' subsystem independent from and preceding a 'face individuation' system is only based on indirect evidence, i.e., the effect of brain damage sparing face detection, the fact that face detection (or GFR) is performed faster than FIR (unless one uses very specific label-to-picture matching tasks with few repeated face identities and strong expectations; Tanaka, 2001), that face detection requires less evidence than face individuation, etc. (see Quek et al., 2021). Yet, these observations do not imply that there are two subsystems: simply, recognizing a visual stimulus as a face is easier and faster than recognizing the identity of the person for his/her face, for many reasons as presented at the beginning of the paper. In the same vein, accounting for PS's deficit at holistic face identity recognition by postulating a dissociation between a part-based module and a holistic processing module (e.g., Moscovitch et al., 1997; Rivest et al., 2009; see also Farah et al., 1995) cannot explain why a case like PS recognizes a stimulus as a face, but not its individuality, holistically (i.e., one would have to consider that there are 4 subsystems...).

A more parsimonious alternative account of the pattern of preserved and impaired functions in patient PS is provided by the coarse-to-fine framework described above: just like neurotypical observers', PS's initial percept of an encountered face stimulus is holistic (i.e., a single representation, undecomposable in parts). However, it is very coarse, usually preventing face individuation (unless the head is extremely distinctive in terms of its global shape, e.g., PS usually recognizes the French actor Gerard Depardieu on most pictures ...). While, in neurotypical

brains, this percept is rapidly and automatically refined holistically (i.e., simultaneously across the whole face, with no decomposition in parts), this holistic process no longer works for PS. Instead, her percept can be refined only locally, on each fixated part independently (**Figure 22**). Consequently, while PS recognizes both the overall shape of a face (e.g., “a round or oval head”, “long curly hair”) and each of its detailed parts one by one, she is unable to derive a finer-grained holistic percept of a face (**Figure 22**), struggling to recognize a given facial identity.

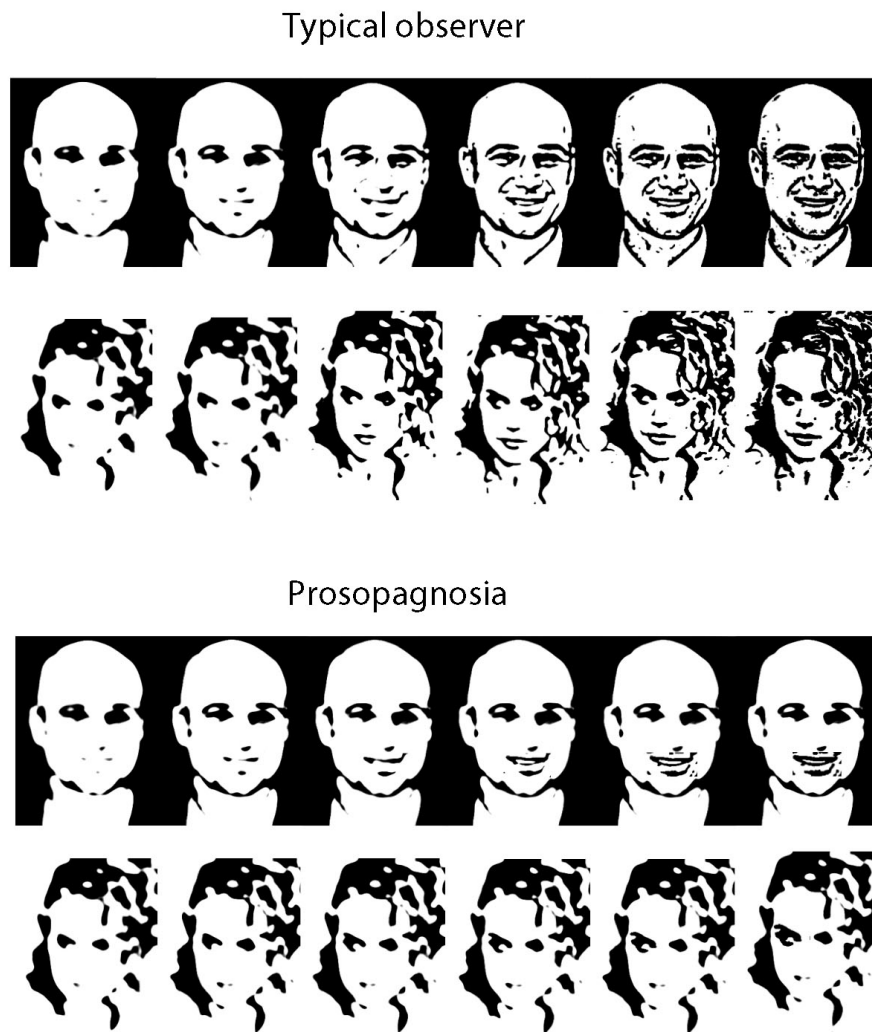


Figure 22. Above, schematic representation of the hypothetical perception of a face by a typical observer, for whom the initial global face percept is refined simultaneously (from left to right) across the whole face, in order to be able to recognize the person’s identity (here Andre Agassi and Nicole Kidman). Below, PS can see the whole face initially at a coarse level, and is thus able to perform face detection. 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.

In the second part of the current review on PS, I will make a proposal regarding the neural underpinnings of this holistic, category-selective, coarse-to-fine deficient process. Here, to end

this section, let me make three further remarks. First, a deficit restricted to a fine-grained holistic (FGH) process/representation explains why PS's visual recognition deficit is restricted to faces (i.e., domain-specific): while the recognition of nonface objects, including their individuality, can always be based either on their overall shape at a coarse level of resolution *or* on their specific parts, the efficient identity recognition of a face requires both together, i.e., a fine(r)-grained holistic representation. That is, due to a number of factors (e.g., high visual homogeneity of face stimuli, a requirement to rapidly individuate them, extensive and active natural experience with numerous faces throughout life ...), only the category of face signals is associated to, and requires, integrity of this FGH process. Hence, a selectively impaired FGH process in adulthood, which occurs extremely rarely, can lead to a category-selective impairment in FIR, i.e., prosopagnosia. There is therefore no opposition between a theoretical account of prosopagnosia in terms of a *domain* or in terms of a *process*: because of biological factors, and through extensive active experience, most neurotypical adults in the human species have an astonishing ability to individuate faces of conspecifics based on a FGH process. In rare cases, this FGH process is selectively impaired by brain damage, leading to a category-selective disorder as in PS.

This account also enables an understanding of why PS can sometimes describe faces based on their global shape ("a big round head"), using a very coarse holistic representation, or their local details (blue eyes, thin lips, a nose piercing, etc.). She is able to mentally verbalize and store this information in memory (e.g., she knows that G. Depardieu has a very big head, that Michel Cymes' mouth is asymmetrical, with one corner higher than the other, etc.). then confront it with verbal information derived from the current percept and guess whose face is presented ("*This atypical mouth, it must be M. Cymes*"). Unfortunately for PS, a FGH representation of a face cannot be (easily) described and verbalized. In neurotypical observers, FIR using such a FGH representation/process is automatic and fast. While we are conscious of the outcome, i.e., the recognition of a given identity, this process is unconscious and cannot be forced through: studies have shown that in neurotypical observers verbalizing features of faces can be detrimental to their subsequent face identity recognition (i.e., the "verbal overshadowing effect", Schooler and Engstler-Schooler, 1990; Meissner and Brigham, 2001).

Third, as mentioned above, and further discussed below in the conclusion section, a defect of holistic/configural face recognition in prosopagnosia is not an original proposal: several reported cases of prosopagnosia have been interpreted this way (e.g., Levine & Calvanio 1989; Sergent & Villemure, 1989; Sergent & Signoret, 1992; Saumier et al., 2001; Boutsen & Humphreys, 2002; Barton 2002; Delvenne et al., 2004; see also Tanzer et al., 2013; Avidan & Behrmann, 2021). However, as I have discussed elsewhere (Rossion, 2018a), these reports

typically concern cases of *visual (object) agnosia*, in which the impairment goes beyond FGH and may concern holistic/configural visual recognition *in general* (see Levine & Calvanio 1989; Boutsen & Humphreys, 2002; Delvenne et al., 2004 in particular for evidence of generic holistic/configural visual defects). Unfortunately, this has led to a great deal of confusion in the scientific literature.

In addition, many researchers in human face recognition have lost interest in the notion of holistic/configural face recognition, for two reasons at least. First, contrary to a feature-based analysis approach, holistic/configural recognition is difficult to formalize and to quantify in terms of information. The holistic view of human face recognition is thus often seen as being “vague” or just descriptive, in comparison to approaches that attempt to quantify information provided by specific features of faces (e.g., Schyns et al., 2002; Sekuler et al., 2004; Abudarham & Yovel, 2016; Abudarham et al., 2019). Yet, these approaches are highly dependent on constrained stimulus sets and may spectacularly fail in revealing any difference in the use of facial features between typical and atypical observers (Abudarham et al., 2021) or in providing any valid interpretation of such differences. Second, correlations between FIR performance and holistic face recognition measures across individuals are rather weak or inconsistent in the scientific literature (Wang et al., 2012; Verhallen et al., 2017; although see DeGutis et al., 2013 and the discussion in Rossion, 2013). This is not surprising since, as I have also argued elsewhere, performance at a given behavioral FIR task reflects many general processes beyond FGH, and these processes vary substantially across the normal population. Hence, a lack of correlation between behavioral performance at FIR and independently collected FGH measures – which also vary across individuals for various reasons that may have nothing to do with the core FGH process - does not imply at all that this FGH process is not key for FIR (Rossion, 2013). Moreover, let me state again, that there is no opposition between holistic/configural face recognition and a key role of features or parts in face (identity) recognition, as often misinterpreted (e.g., Cabeza & Kato, 2000). According to the holistic/configural account of face identity recognition, the parts/features of a face are very important, and in fact their importance is magnified by the ability to process a face holistically (Rossion, 2008; Rossion, 2009).

Last, the theoretical interpretation of PS’s prosopagnosia in terms of a deficient FGH process is not only there to make predictions and testable hypotheses, but to account for apparently disparate empirical facts in a coherent framework. If we had made this interpretation earlier, we would have predicted PS’s increased difficulties at extracting cues from the crowded eye region of the face as compared to the mouth. As it turned out, our finding of an increased recognition defect at the level of the eyes was an empirical observation made at a time when we did not have

enough knowledge to propose this framework. Notwithstanding which came first, the coherent framework has allowed to make other predictions with the patient PS. For instance, since surface (color and texture) information about face identity can be resolved locally, 3D shape involves relatively more interactions between different parts of the face and is associated with larger inversion and composite face effects (Jiang et al., 2011). Thus, we hypothesized that PS would have relatively more difficulties individuating faces differing in terms of their 3D shape than of surface (color and texture) cues. This is exactly what we found (Jiang et al., 2011). As discussed in the next section, this framework also allows conceptualizing spared and impaired associated face recognition processes under a new light.

X. A functional account of PS's prosopagnosia

Now that the key functional impairment of PS has been identified, I could stop here, as in the discussion of previous studies, or previous reviews based substantially on her case (Rossion, 2014). However, (and I apologize for the tired reader), this whole survey of her behavioral abilities and impairments gives me an opportunity to go a step further at the theoretical level. To do so, in the present section, I go back to the key issue of perception and memory of faces, as mentioned at the beginning of section V, regarding prosopagnosia and FIR in general.

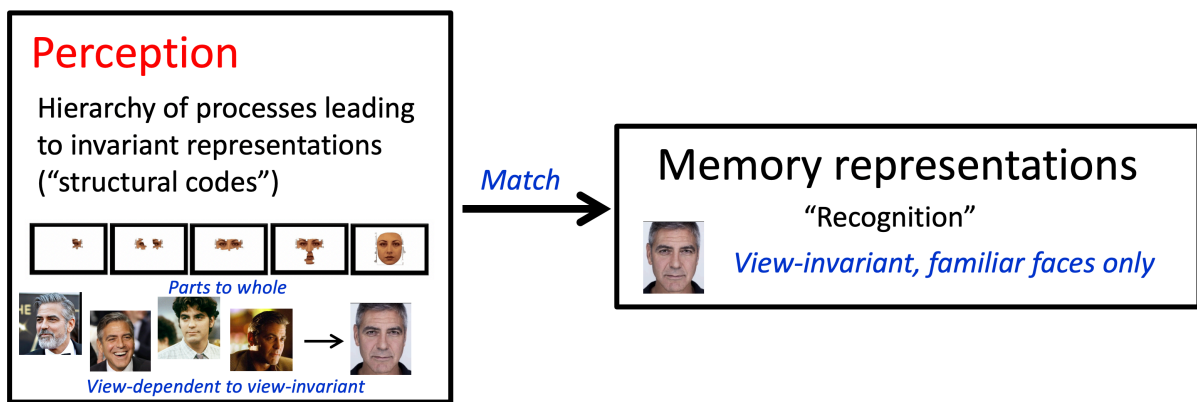
10.1. Standard models: a causal perceptual account

PS's defective fine-grained holistic process (FGH) prevents her from *perceiving* a face holistically at the fine-grained level required for individuation. Is this the *cause* of her prosopagnosia? In a standard theoretical framework of how faces are functionally processed in the human brain, the answer to this question would be positive. The reasoning would be the following: since PS cannot build a proper holistic visual representation of face identity, her memories of individual faces cannot be selected/contacted/associated correctly, preventing FIR. That is, her deficit would lie at the level of perception, not memory. PS would be classified as a case of "apperceptive prosopagnosia", following the terminology of Lissauer (1890) for visual agnosia, and extended to prosopagnosia (Hécaen, 1981; de Renzi, 1986; de Renzi et al., 1991; Sergent & Signoret, 1992; Davies-Thompson et al., 2014; Barton & Corrow, 2016). This (ap)perceptive deficit would explain why PS shows the same kinds of problems at individuating familiar or unfamiliar faces, as illustrated throughout the present review.

In Bruce and Young (1986)'s cognitive architecture of face processing, perhaps the greatest theoretical influence on human face recognition research for the last four decades, PS's deficit would therefore correspond to a defective "structural encoding stage", i.e., "*the stage which*

capture those aspects of the structure of a face essential to distinguish it from other faces” (Bruce & Young, 1986, p.307). This visual processing stage is thought to occur irrespective of, i.e., prior to, *recognition* (as classically defined; Mandler, 1980) of the face as being familiar. Once the visual representation of a face identity has been derived, only those corresponding to familiar faces can match representations of familiar face identities stored in memory (“*Face Recognition Units*”, FRUs; Bruce & Young, 1986, p.307; see also Young & Bruce, 2011 for a more recent version of the model) (**Figure 23A**). This successful association leads to recognition of a familiar face identity, and to further associations with semantic and lexical information further along in the system.

A Standard view



B Novel framework

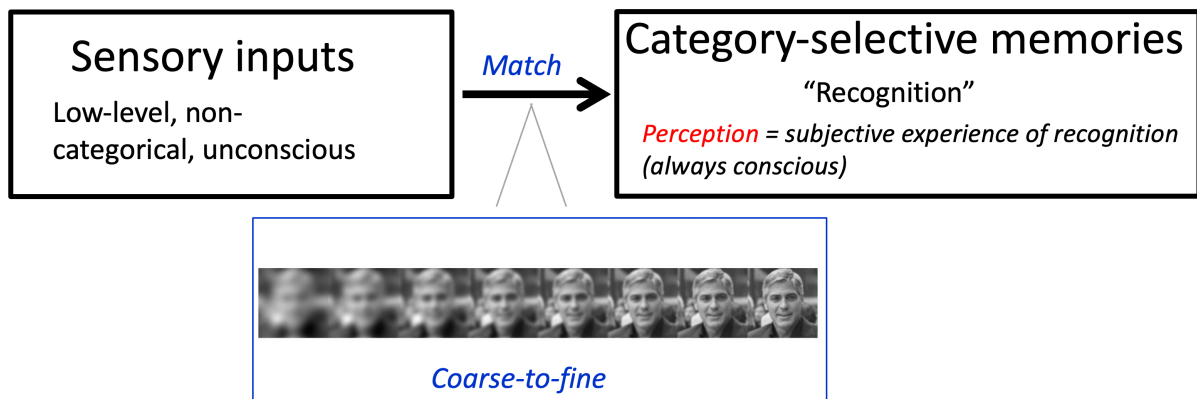


Figure 23. *Two different theoretical frameworks for human face identity recognition to provide alternative interpretations of PS's prosopagnosia. A. In a standard theoretical framework, perceptual processes leading to identity-specific representations are completed before (only) familiar faces can match stored representations of these face identities in memory. For PS, these perceptual processes would be dysfunctional, so that the association of representations of (familiar) faces with memory cannot be made (i.e., PS would be a case of "apperceptive prosopagnosia"). B. In an alternative framework, low-level sensory inputs that successfully match with (cortical) memories of faces lead to the initial (holistic) recognition of the stimulus as a face. The phenomenological experience associated with this successful recognition is called 'perception' (which is always conscious). Thanks to view-dependent unimodal memories of facial identities, the percept is rapidly and holistically refined within the same system. In PS's case, (access to) this memory system – constituted of a network of ventral occipito-temporal category-selective cortical regions – is damaged, so that holistic refinement of facial identity cannot take place. PS therefore perceives a face holistically, but not its identity (Figure 22). Note that in the alternative framework, for a neurotypical human adult, both familiar and unfamiliar face inputs match category-selective memories. The successful matching, or triggering of these memories through inputs conveyed by white matter fibers, constitutes the function. There is no view-invariant representation independently of (multimodal) semantic memory, which provide the superiority for generalization of familiar faces across views.*

Pretty much all functional and neurofunctional models of human face recognition proposed over the past four decades, often inspired by Bruce and Young (1986)'s original proposal, follow this logic, distinguishing between perception and recognition/memory stages for faces (e.g., Tovée, & Tovée, 1993; Haxby et al., 2000; Calder & Young, 2005; Jiang et al., 2006; Pitcher et al., 2011; Duchaine & Yovel, 2015). While Bruce and Young (1986)' model does not differentiate holistic/configural vs. part-based processes, current neurofunctional models conceptualize a part-based process preceding holistic integration of the facial parts (Haxby et al., 2000; Pitcher et al., 2011; Duchaine & Yovel, 2015). An interpretation of PS's prosopagnosia in this framework would be that she has a perceptual deficit: she would not be able to assemble facial parts (that she perceives very well) into a holistic visual representation of a face identity, this latter representation being necessary to build a structural encoding code/an invariant facial identity representation.

For a number of reasons, I would like to argue that this standard theoretical framework attributing PS's impairment to a deficient perceptual process preceding recognition is not adequate, paving the way for an alternative account (**Figure 23B**).

First, this standard theoretical framework is, again, not parsimonious. According to this framework, a view-invariant percept/visual representation of a facial identity is derived from the sensory input, presumably through a series of computational stages in the visual cortex (DiCarlo & Cox, 2007), before connecting to another view-invariant representation of an individual face stored in memory. Thus, the brain would hold (at least) two visual representations of any familiar

face identity. While many researchers seem comfortable with this idea, even searching for distinct neural seats of ‘perceptual’ and ‘memory’ representations of faces, this “dual copy” account of FIR seems highly implausible, and not supported by consistent evidence.

The second reason is that this theoretical framework struggles to deal with processing differences between familiar and unfamiliar faces. We (humans) are significantly better at matching pictures of faces for their identity when these faces are familiar, i.e., when they have been encoded in memory from past experience. This has been demonstrated with a wide variety of stimuli and tasks, originally old/new recognition tasks (Bruce, 1982) and even in simple simultaneous matching tasks (e.g., Bruce et al., 2001; Megreya & Burton, 2006). This is an important observation, both for fundamental and applied research perspectives (Bruce et al., 2001). Unfortunately, this difference between familiar and unfamiliar faces has led researchers to make the claim that unfamiliar faces are not processed like faces but more like objects or inverted faces (Megreya & Burton, 2006), using low-level, iconic, image-based visual processes only (Hancock et al., 2000; Megreya & Burton, 2006; Jenkins et al., 2011). In short, that humans would be expert only at recognizing the identity of familiar faces, not unfamiliar faces (Young & Burton, 2018).

If this is the case, then how is a structural encoding stage in standard models (e.g., Bruce and Young, 1986 and all other derived models) achieved for unfamiliar faces then? Isn’t this structural encoding stage supposed to be completed for both familiar and unfamiliar faces *before* accessing representations in memory only for familiar faces? How could we explain the advantage at matching familiar over unfamiliar faces for their identity in such a framework? Perhaps in terms of “feedback” from memory (“facial recognition units”) to give an advantage to invariant representations for familiar faces? This does not seem to be very compatible with the high speed at which faces can be matched for their identity or judged as being familiar (e.g., Barragan-Jason et al., 2013; Wiese et al., 2019; Zimmermann et al., 2019). Moreover, decades of neuroimaging studies have shown that pictures of unfamiliar faces selectively activate high-level (i.e., non-retinotopic, category-selective) regions in the human VOTC and STS (Grill-Spector et al., 2017 for review), in fact with little or no consistent difference with pictures of familiar faces (e.g., Natu & O’Toole, 2011; Ramon et al., 2015; Weibert et al., 2016; Kovacs, 2020).

Last but not least, this standard account rests on the assumption that there are cases of prosopagnosia with (ap)perceptive disorders, and other cases with purely associative disorders (De Renzi, 1986; De Renzi et al., 1991; Barton & Corrow, 2016; Barton et al., 2021). However, despite decades of clinical observations and research on brain-damaged patients with FIR deficits, convincing cases of prosopagnosia who have a normal percept of an individual face “stripped of

its meaning”, have never been reported. On the one hand, a number of patients classified as cases of associative prosopagnosia have not been tested thoroughly for their ability to match/discriminate pictures of unfamiliar faces, in particular failing to take into account response time measures (e.g., De Renzi, 1986; see Farah, 1990/2004). Over the years, several authors have emphasized this limitation, and showed that when response times (RTs) are taken into account, putative cases of associative prosopagnosia in fact have objective difficulties at matching/discriminating pictures of unfamiliar faces (Davidoff & Landis, 1990; Farah, 1990; Delvenne et al., 2004). As a matter of fact, if RTs were not taken into account and a single test of face identity matching considered, PS could also be considered as a case of “associative prosopagnosia” (e.g., her performance at the BFRT, 39/54, was borderline, but she took 30 minutes to perform that test; see also Delvenne et al., 2004 for another case, NS). On the other hand, the very few patients classified as cases of associative prosopagnosia who indeed appear to perform identity matching tasks with pictures of unfamiliar faces both correctly and rapidly, either present with recognition deficits in other channels and modalities, or have patterns of brain damage which suggest such deficits (i.e., in anterior temporal lobe regions which are severely atrophied in cases of semantic dementia; e.g., Busigny et al., 2009; see Ding et al., 2020). One such case who is often cited as a case of associative prosopagnosia, the patient PV, studied by Sergent and Poncet (1990), suffered in reality of a multimodal semantic recognition impairment following (right dominant) bilateral anterior temporal lobe damage (Boudouresques et al., 1979; see also Sergent & Signoret, 1992). In recent years, Guido Gainotti has written reviews on this latter issue, analyzing reported cases of associative prosopagnosia in the literature and arguing against pure deficits of visual recognition (i.e., without either perceptual or multimodal semantic impairments) (Gainotti, 2010; Gainotti, 2013). I generally agree with this colleague’s arguments and conclusion, and I would go as far as to claim that associative prosopagnosia – as defined classically – has never been demonstrated.

Note that even if this apperceptive-associative distinction of prosopagnosia is not supported by consistent empirical data, most authors find it useful (e.g., Tranel & Damasio, 2001; Barton & Corrow, 2016). Here again I disagree, rather finding this distinction profoundly misleading. That is, if we still cannot identify clear cases of associative prosopagnosia after decades of research, and in particular if the initial “evidence” was particularly weak (de Renzi, 1986), we should do better than call upon vague ad-hoc explanations for the lack of clear-cut evidence such as “*the continuum between perception and memory*” or the fact that “*brain lesions do not respect clear-cut anatomico-functional borders*” (e.g., Damasio 1982; Davies-Thompson et al., 2014). Rather, I argue that a theoretical framework that separates ‘perception’ from

‘memory’ of faces should be fundamentally questioned and revised. This is what I propose to interpret (PS’s case of) prosopagnosia.

10.2. An alternative account: perception emerges from recognition

Based on this extensive research of PS, I propose that the inability to efficiently *perceive* faces for their individuation is *caused* by the selective and substantial loss of (access to) cortical face *memories* (through brain damage, as will be addressed in detail in Part 2 of this review).

In this alternative account, for neurotypical human adults, face *recognition* occurs when sensory, low-level, non-categorical patterns of visual inputs (coming from low-level, i.e., retinotopic, visual regions) successfully match memories of faces in the cortex (e.g., in the middle fusiform gyrus) (**Figure 22B**). Perception is just the *phenomenological experience* that accompanies this successful match. Hence there is no perceptual stage, or set of processes, to build putative invariant visual representations¹⁶ before an association of sensory inputs with memory traces in the cortex. Importantly, these memory traces of faces are holistic, i.e., there is no independent category-selective representation of an eye, a mouth, etc. A single face feature presented as input may be insufficient (e.g., part of a binarized Mooney stimulus; **Figure 15C**) to trigger memories of faces so the stimulus is not at all recognized (i.e., perceived) as a face. Alternatively, if the face part is sufficient (e.g., an image of a well segmented human eye), it automatically triggers a holistic face representation in memory and the stimulus is recognized as a face. The more diagnostic features, arranged in the most experienced configuration, the faster activation of the face memory trace.

In (neuro)typical observers, a continuous accumulation of sensory inputs *within the same cortical memory system* rapidly leads to the recognition of a familiar identity (**Figure 22B**). However, in the case of PS, while there is still a large amount of intact cortex selectively tuned to readily recognize sensory stimuli as faces, (access to) the face-selective network’s internal structure has been disrupted by brain damage, preventing a full, memory-guided completion of the visual representation. This *causes* PS’s recognition deficit: she cannot use memories of facial identities to complete an individuated face percept.

¹⁶ In fact, according to the alternative view proposed here, there are no invariant visual representation of face identities in the system, at any stage of processing. The notion of an invariant visual representation is not a fact to explain but a theoretical construct (Marr, 1982). The goal of face recognition and visual object recognition research is to understand how we can generalize so efficiently across various views of faces and objects, not how putative invariant representations are built.

Thus, due to her memory deficit, according to the standard terminology, PS could be defined as a case of *associative prosopagnosia*. However, in the alternative framework, this necessarily *implies* a perceptual defect (**Figure 22B**): she cannot even discriminate unfamiliar face identities using these holistic cortical memory traces. Instead, she has to rely *either* on differences between facial identities at a very coarse level (e.g., two faces differing by their hair, overall shape, skin tone, etc.) or on a time-consuming, inefficient, local part-based analysis.

Where does this theoretical framework come from and how does it differ from other frameworks? I will not go into detail here, in this already long review, but its sources are from Hermann von Helmholtz (1866)'s first theory of (visual) perception (as re-actualized by Gregory, 1980; also Gregory, 1997). According to Helmholtz, perception is defined as an *interpretation* of sensory information, this interpretation, i.e., perception, depending on stored knowledge, usually derived from experience (Helmholtz, 1866; Gregory, 1980; Rock, 1997; Purves et al., 2015). That is, under this conception, (visual) perception cannot, by definition, be separated from (memory) associations. Because memory content is thought to be derived from experience, Helmholtz (1866) defined this view as empiricist, but it may as well be called a constructivist view of perception; the terminology does not matter much¹⁷.

Another source of inspiration from the present framework is the work of Lissauer (1890), particularly his landmark article on 'mind blindness' (partly translated from German to English in Lissauer & Jackson, 1988; commented by Shallice and Jackson, 1988). As mentioned above, Lissauer (1890) is usually credited as a major figure in the neat distinction made between (visual) perception and memory. However, this is not a fair reflection of his view, which is highly relevant for FIR. The end of his famous paper, translated in English, tells its own story: "*We have now arrived at the possibility that there may exist both an associative and an apperceptive form of visual agnosia. I do not expect to find clinical cases representing pure examples of these two forms of agnosia. In particular, 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 apperceptive and associative functions. We have defined apperception as that function which enables us to give information about the differences between sensory impressions. When simple*

¹⁷ In recent years, there has been a growing popularity of related Bayesian views (Knill & Richards, 1996; Kersten et al., 2004) and predictive coding theories in visual perception (Rao & Ballard, 1999; Friston, 2005), the latter having become increasingly influential. However, these computational frameworks usually preserve the hierarchical distinction between perception and memory, and call upon notions of feedback, error corrections, etc., which are not necessary (e.g., it is not because PS would not get an error detection signal somewhere at a higher stage of processing that she would not recognize facial identities ...).

*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 (Lissauer, 1890/1988, p.184-185).*

Remarkably, Lissauer goes further, using faces as a key example: “*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.*” (Lissauer, 1890/1988, p.184-185).

I find it particularly interesting that, a century later, the authors who commented Lissauer’s seminal paper, well versed in the tradition of cognitive neuropsychology, considered that he refuted an absolute distinction between apperceptive and associative agnosia simply because he had been unable to isolate a clear-cut clinical case (Shallice and Jackson, 1988). In reality, Lissauer (1890) could not be more explicit: since the (full) perception of a face *requires* memory (‘associations’), he did not think that a clear-cut dissociation between perception and memory for visual entities, in particular faces, could ever be drawn. While more contemporary authors have also emphasized that decades of neuropsychological observations have failed to provide clear-cut distinctions between apperceptive and associative forms of prosopagnosia (or visual object agnosia), they have interpreted these observations in terms of *causal perceptual* defects (e.g., Farah, 1990/2004; Davidoff & Landis, 1990; Delvenne et al., 2004). Here, along the lines of Lissauer (1890) the case of prosopagnosia PS, supported by a large amount of empirical observations, is instead interpreted in terms of a defect of (access to) memory representations *causing* a perceptual impairment.

Further, in this framework, *both* familiar and unfamiliar face inputs trigger facial memories in the cortex, both being initially categorized as faces when sufficient evidence has been accumulated. In a neurotypical human brain, both types of sensory inputs are holistically refined to a level that is sufficient for rapid individuation. An unfamiliar face input recruits the same population of face-selective neurons as a familiar face input in the cortex, and its recognition as an unfamiliar face is helped by the comparison of its pattern of activation to familiar patterns. However, unlike unfamiliar faces, familiar faces are automatically and rapidly associated (due to strengthened neural connections) to a rich set of previously associated visual and nonvisual

representations (“semantics”), greatly expanding the range of generalization for identity recognition of these faces. Hence, this provides a substantial advantage in face identity matching tasks for familiar over unfamiliar faces (Bruce et al., 2001), which is lost in cases of prosopagnosia such as PS (see e.g., section XIII below).

At the neural level, I argue that PS has a recognition deficit because brain damage partly - but substantially - destroyed (access to) her (access to) memories of faces in the VOTC (see review part 2). More specifically, these memories are populations of VOTC neurons that have learned to fire selectively to face inputs across a wide variety of formats, and selectively to certain faces over other, also across a wide variety of formats. These populations of neurons in PS’s VOTC have been selected to respond to faces rather than other visual entities following years of active experience at FIR during development and throughout life. The same system, a set of neuronal populations, serves as memories for faces at both generic and identity levels. However, when it is only partially destroyed, as in the case of PS, generic face recognition, which relies on much coarser inputs, can be functionally spared (we will see in the review part II that PS’s brain still holds a substantial number of face-selective regions, even if they do not show sensitivity to differences between facial identities; Rossion et al., 2003; Schiltz et al., 2006). Thus, despite her intact bilateral medial temporal lobe (see Rossion, submitted, review part II), PS’s prosopagnosia is due to a *memory* impairment, which leaves her with an inability to rely on cortical traces of faces encoded before brain damage to recognize these faces, derive a holistic fine-grained percept of a face, strengthen /consolidate these memories and form new memories of faces in the VOTC.

Obviously, I am fully aware that this is only a functional theoretical account, which is speculative and vague at this stage of our knowledge (**Figure 22b**). However, this account is no more speculative and imprecise than the standard account outlined above, and more parsimonious since it requires only one key system to recognize faces (in the face-selective ventral occipito-temporal cortex; albeit as a widely distributed network, as we shall see in part 2) and a single representation or “stage” at which this visual representation of a face stimulus is extracted. Although it is inspired by a single case study, this model is more coherent in terms of integrating disparate observations into a unified framework. Ultimately, the evaluation of this framework will have to be based on the full range of available relevant evidence, including performance of other (properly defined) cases of prosopagnosia, visual object agnosia¹⁸, and normal individuals (Caramazza, 1986) as well as neural evidence (see part 2 of the review on PS).

¹⁸ In patients with “associative” visual object agnosia, who are also rare, (bilateral) lesions extending more widely in the VOTC (e.g., Humphreys & Riddoch, 1987; Levine & Calvanio, 1989; Delvenne et al., 2004) concern

XI. Implications for other face recognition processes

Humans do not only recognize faces as faces, or faces of specific identities, but recognize them also in terms of their emotional expressions, sex, ethnical origin (“race”), head or gaze orientation as cues of attention, etc. We also recognize people’s faces as being of a certain age – relatively young or old - attractive, dominant, trustworthy etc., with evidence showing that neurotypical human adults tend to agree on the outcome of these recognition functions (Perrett, 2010; Todorov, 2017). The range and diversity of recognition functions that our brain performs on faces of conspecifics, most of the time rapidly and automatically (Todorov, 2017), is astonishing and unparalleled in the animal world.

Interestingly, the term “recognition” is often reserved in the scientific literature for the recognition of a specific (familiar) identity (i.e., FIR; see the beginning of section 2), and researchers usually use the terms “categorization” or “judgement” to refer to these other functions. This is due again to this artificial - but firmly rooted in the minds of cognitive scientists - distinction between perception and memory, and also because we tend to think that some of these functions (i.e., recognizing a face as a face, or its identity) are based on *objective* features of the stimuli, whereas others (i.e., recognizing someone’s age or physical attractiveness) would be (more) subjective¹⁹. Yet, in all of these cases, what the brain does is to produce a *selective* response that can be *generalized* across different instances, i.e., a recognition function. Moreover, *all* these types of face recognition functions are based on a mixture of objective sensory features and (subjective) knowledge derived from experience. In fact, even the recognition of a visual stimulus as a face is partly subjective and certainly not based on a list of sufficient and necessary features, as illustrated by the Arcimboldo painting described above (section IX) and numerous instances of face pareidolia (Takahashi & Watanabe, 2012; Omer et al., 2019; Rekow et al., 2022). Hence, in a coherent framework it is certainly not helpful to use different terms, and this is why the term recognition (as a synonym of categorization) is used here to define these functions (see also Rossion & Retter, 2020).

both faces and non-category-selective visual memory representations, causing their perceptual deficit (Farah, 1990). If properly evaluated, these patients should be clearly impaired at recognizing a stimulus as a face, e.g., in an Arcimboldo painting or a Mooney face image.

¹⁹ Yet another trendy term to refer to these recognition functions is “decoding”, as if our brain was only an information-processing device.

13.1. PS's other face recognition functions

How good is PS, whose deficit at FIR is clearly established but with preserved GFR, at recognizing sex, ethnicity, emotional expressions, etc., from faces? As far as I know, she never complained of any difficulty at this level in real life, and was never caught mistaking a male for a female face, or incorrectly interpreting someone's emotional expression from his/her face. She spontaneously recognizes people from their faces as males or females, reports their emotional expression, "race", and even make spontaneous judgments of attractiveness on faces that seem to agree with other people's judgements. In fact, she sometimes even relies on her ability to recognize faces' gender or ethnicity to help her guess their identity. In the kindergarten, for instance, among the vast majority of children of Caucasian origin, she would easily recognize the child with East Asian or African facial traits. She also used to recognize easily Fang Jiang, the only researcher of East Asian origin in my laboratory at the time, often joking about it ("*at least with you it's easy, I cannot not recognize you*") ... until there were more East Asians in the lab and it became more difficult again for her to guess Fang's identity from her face.

In the initial report of PS, she was described as performing in the normal range at various face recognition functions (face sex, age, emotional expression) only 6 months after her brain injury (Mayer et al., 1999). However, there were no RT measures, and the stimuli used in the battery of face recognition functions (Bruyer & Schweich, 1991) contained highly salient cues. While PS's ability to characterize faces according to their ethnical origin has not been formally evaluated to my knowledge, we measured her ability to classify hairless faces as males or females as part of our initial assessment of her visual recognition functions (Rossion et al., 2003). She performed relatively well and rapidly at this task – compared to her profound difficulties at discriminating faces for their identity even in simple 2 AFC tasks - but nevertheless made more mistakes and answered more slowly than neurotypical observers. She also scored well but below normal controls at a task requiring classification of faces according to three emotional expressions (Rossion et al., 2003). In another study, we asked her to classify faces according to trustworthiness or dominance, or other social categories. Her categorizations were generally in agreement with other observers, but with small differences for specific ones such as dominance (which depends relatively more on the eye region of the face) for instance (Quadflieg et al., 2012).

Thus, although PS's difficulties at these other face recognition functions are very modest, they can be captured in experimental settings. Why is she then unaware of these difficulties, and why do they not translate into incorrect recognitions in real life? One possibility is that these difficulties are compensated by the numerous sources of facial and nonfacial cues simultaneously available when recognizing emotional expressions, gender, age or ethnicity in real life

circumstances. In particular, facial expressions are inherently dynamic, i.e., evolving rapidly over various regions of the face differently for different expressions, a rich source of diagnostic cues that is not available from static images. In line with this suggestion, systematic investigations showed that PS performs below typical observers to recognize static images of expressions (Richoz et al., 2015), also relying more on the mouth than the eyes (Fiset et al., 2017). However, with dynamic facial expressions, PS was comparable to controls, using all facial features to (de)code facial expressions (Richoz et al., 2015). A notable exception in this latter study was the expression of fear, which again depends relatively more on the region of the eyes than other facial expressions (Smith et al., 2005).

Overall, these observations suggest this additional contribution of dynamic cues (both in terms of the order of changes of facial features for different expressions and their different speed; see Sowden et al., 2021) could well explain why PS does not suffer from difficulties in recognizing facial expressions in real life. In addition, in such real-life circumstances, many nonfacial static and dynamic cues at the level of the body or the voice are reliable and rapidly available for recognizing people's emotional expression or gender (e.g., Johnson et al., 1986; Atkinson et al., 2004; Sowden et al., 2021).

13.2. The outstanding challenge of face identity recognition

Why are other cues than faces insufficient to compensate for PS's FIR impairment in real life then? Here a key factor to consider is the inherent difficulty of FIR relative to all other human face recognition functions. In our human species, FIR is in fact extremely difficult, and constitutes arguably the most challenging (visual) recognition function. Let me briefly mention six potential reasons for that.

First, while individual faces most likely differ more in humans than in other animal species (Sheehan & Nachman, 2014), all human faces, in particular within a genetically homogenous group, share similar features and their overall configuration. Thus, FIR may require relatively finer-grained visual discrimination processes than, say, the recognition of people's sex from their face or their "race". Yet, other face recognition functions may also require relatively fine-grained visual discrimination ability, e.g., to distinguish between the facial expressions of surprise or fear for instance (which are often confounded) or to recognize subtle expressions such as irony in someone's face, or else to recognize at a distance from a person's eye gaze direction that he/she is looking at me rather than the person sitting next to me.

Second, the same face identity can vary substantially under different viewing conditions and over time, to the point where two views of the same face identity often differ physically to a

larger extent than two different facial identities (i.e., ‘within-person variability’ could be greater than ‘between-person variability’; e.g., Burton et al., 2016; White et al., 2022). This is why recognition of several instances of a facial identity as belonging to the same person does not obey classical rules of categorization, i.e., it cannot be based on merely counting (“computing”) sufficient and/or necessary features (Smith & Medin, 1981; Murphy, 2002), and FIR requires a high-level of *generalization* of a specific response across different facial views. However, here again, other face recognition functions may face the same challenge, e.g., when having to generalize across widely variable exemplars of male faces despite their physical differences (Rekow et al., 2020).

The third reason behind the extreme difficulty of FIR is that in most modern societies, the number of facial identities to recognize, i.e., the number of face categories, is very large, usually from several hundreds to thousands of individual faces (Jenkins et al., 2018). In comparison, other face recognition functions are based on a limited, albeit sometimes also flexible, number of categories (e.g., male or female faces, 6 basic facial expressions, etc.). I think that this is a major reason why FIR is extremely challenging as compared to other recognition functions and thus easily disrupted not only following selective brain damage as in the case of (prosopagnosia) PS, but in many neurological, neurodevelopmental and psychiatric disorders (Barton et al., 2021). This is also why humans who have been living in largely populated urban areas may show - on average - better FIR performance than those living in small cities or rural areas (Balas & Saville, 2017), and larger face-selective neural activity (Dehaene et al., 2010; Balas & Saville, 2015; see Rossion & Lochy, 2022).

Fourth, the number of identities to recognize is often *undetermined*, i.e., changes across different contexts and over time, with familiar faces mixed up among an undefined number of unfamiliar faces in various contexts. This is often neglected in human face recognition research, yet natural observations and experimental investigations of a case of prosopagnosia like PS show this factor is fundamental to explain the challenge of FIR. When PS knows that she only has to recognize the members of her family in the same constrained space, a birthday party or a barbecue in her garden for instance, she is not impaired at all and does not even need to rely on nonfacial cues to identify each person. However, mix the very same people in a large crowd of individuals, as when her daughter is among a group of friends at the theatre, and PS is suddenly lost (despite having the same “information” available from the familiar faces). In experiments, when PS was asked to identify each face of the 27 children of the kindergarten one by one, being aware that the set is limited to this children group, she could reach a decent score (e.g., about 60% identification, well above chance level; Ramon et al., 2017; section XII). Yet, when the same faces were mixed

up with faces of children unfamiliar to her, she was even unable to determine who was a child from the kindergarten or not, scoring just above chance level (Busigny et al., 2010).

Fifth, contrary to gender or emotional expression for instance, other cues of people's identity are not highly diagnostic, or convey diagnostic information at a too slow rate to compensate the absence of a rapidly derived FGH visual representation of a face. Compared with faces, body shape or body posture for instance, which can rapidly signal someone's gender and emotional state, convey relatively little diagnostic cues regarding specific identity (Sheehan & Nachman, 2014). Despite valuable parallels made between the recognition of faces and voices in the human brain (but also differences; Von Kriegstein et al., 2005; Yovel & Belin, 2013; Johnson et al., 2020; Young et al., 2020), people's voices are also largely insufficient and inefficient cues of identity compared to faces. Indeed, in many social circumstances, we (have to) recognize the identity of people well before they articulate or we can hear their voices. And while a few vocal excerpts may suffice to distinguish a male from a female face, or different accents or emotional tones, identifying specific people by their voice takes time and is much more difficult (see the review of Barsics, 2014). While neurotypical observers generally excel at telling apart familiar from unfamiliar people from faces, they have much more difficulties at doing so from voices (Barsics, 2014). This is both because different individual voices may not be distinguishable enough, and because someone's voice can also change very rapidly under different circumstances (Lavan et al., 2018). Most importantly, identifying someone by their voice only takes too much time for adequate social interactions, while the development and selection of an efficient system for individuating people based on their face makes a voice identity recognition system secondary.

Finally, regarding dynamic cues, while different people undoubtedly express idiosyncratic facial motions, there is little if any evidence that motion cues contribute significantly to FIR in real life. Studies that have tested the contribution of idiosyncratic motion in FIR usually only report a small advantage when face identity is made artificially ambiguous (e.g., morphing; contrast reversal, blurring; Roark et al., 2003) or when people are particularly poor at FIR (Steede et al., 2007; Albonico et al., 2015). Rather, while dynamic cues are intrinsic components of emotional facial expressions and can greatly enrich their recognition (Krumhuber et al., 2013), they do not appear to bring much to our understanding of the fundamental mechanisms of FIR: unlike for patient PS, neurotypical human adults recognize face identity usually at a single glance, i.e., from a snapshot (**Figure 19**; see e.g., Hsiao & Cottrell, 2008; Orban de Xivry et al., 2008; Peterson & Eckstein, 2012; Zimmerman et al., 2019). This is not to say that PS would not benefit from dynamic cues in a challenging FIR task performed in an experimental setting, but simply

that such cues are of little benefit in real life and cannot help her overcome her severe FIR impairment.

These six reasons combine to make recognition of the identity of people based on their faces (i.e., FIR) by far the most challenging face recognition function, but also arguably the most challenging recognition function across the board for the human brain, explaining why there is so much natural interindividual variability in this ability the normal population (Wilmer, 2017). Despite this high challenge, in humans, identity recognition is primarily based on the face, which, among all body parts, carries by far the largest source of morphological and genetic diversity in a homogenous population (Sheehan & Nachman, 2014), and there is intense social pressure to recognize people's identity based on their face. Of course, the ability to extract a whole facial configuration at once at a relatively high level of resolution is key, as we saw with the experimental study of patient PS. However, if there were only 6 individual faces to recognize in our environment (in parallel to the widely described 6 basic emotional facial expressions; Eckman & Rosenberg, 1998), if these faces were always encountered under contextually distinctive conditions, and if other cues were equally or more diagnostic than the face, this rapid automatic FGH process might not have been needed and might not have even developed in the human species.

13.3. Preserved and impaired face recognition functions in a memory-based framework

In short, all these reasons explain why following brain damage to (or access to) the cortical memory face system (see review part II), people will usually complain of FIR impairments, but not of difficulties at recognizing someone's facial expression, gender, age, eye gaze direction, or ethnical origin for instance. And this is why reported cases of prosopagnosia have sometimes been described as having completely normal recognition of face sex, expression, etc. (e.g., Bruyer et al., 1983; Tranel et al., 1988), while others such as PS, who have been more stringently tested, have been reported with impairments at these functions that remain relatively mild compared to the striking impairment in FIR (Rossion et al., 2003) (see also Young et al., 1993).

Importantly, besides supporting a (partial) neurofunctional dissociation between neural systems dealing with static *vs.* dynamic facial cues (Allison et al., 2002; Bernstein et al., 2018), this dissociation does not imply that FIR depends on a completely independent system compared to the recognition of facial expression for instance (Calder & Young, 2005). Instead, in the present framework, all kinds of facial recognition functions (emotional expression, gender, etc.) benefit from the ability to process the visual input holistically, based on memory representations, and are

all recognized holistically through the face-selective system (see e.g., Zhao & Hayward, 2010; Tanaka et al., 2012; for evidence of holistic recognition of face sex and facial expression, respectively). However, because of the high diagnosticity of other cues, the limited number of categories, etc. these other face recognition functions can be successfully achieved without a relatively fine-grained holistic representation in real life. In an experimental setting, the contribution of these cues can be limited, and it is not surprising that PS is slightly impaired at face sex or facial expression recognition for instance.

XII. A general account of prosopagnosia?

Assuming that the present theoretical account of PS's FIR impairment is correct, how about *other* cases of prosopagnosia? Even the reader convinced by the above proposed theory may be inclined to believe that this account is valid only for PS, or perhaps for a few other similar cases, but that it does not apply to (most) other patients with prosopagnosia. From my (current) perspective, to be honest, this is not the most interesting issue. I used to be interested in meeting potential new cases of prosopagnosia (only with brain damage, as neurodevelopmental disorders of FIR are an entirely different proposition and should not be called cases of prosopagnosia; see Rossion, 2018b) to study their deficit. Not anymore, and not only because PS, for many reasons including her availability, alertness, willingness to cooperate and her high social skills with a unique experience in learning new faces in the natural circumstance of the kindergarten, is probably the most informative case of prosopagnosia that one could find. More fundamentally, in line with the logic of the single case approach in cognitive neuropsychology (Shallice, 1979; Caramazza, 1986), I am *not* interested in developing a *theory of prosopagnosia* but to use a single neuropsychological case to inspire and constrain theories of normal human face (identity) recognition. This approach is similar to other single-case studies in neuropsychology, e.g., the study of the patient DF by David Milner and Mel Goodale. As far as I know, these researchers and their colleagues were never interested in developing a theory of DF's case, but instead to use the patient's performance to inspire and inform their influential theory of dissociation between the ventral and dorsal processing systems for visual object recognition, a theory that can then be evaluated with a wider range of evidence from multiple sources (Goodale & Milner, 2004).

So how about replication, which is thought to be the cornerstone of scientific research? And aren't there are other types of prosopagnosia that could provide a different light on our understanding of human face (identity) recognition?

12.1. Subcategories of prosopagnosia?

Like for all human beings, it's natural for scientists to create categories and put labels on them, as it often gives the impression of explaining phenomena. Yet, despite the description of potential cases of prosopagnosia for more than 150 years (Quaglino & Borelli, 1867), and decades of experimental research (since the 1960s) on such cases, it is striking that there is very little if any evidence for subtypes of prosopagnosia. The only systematic distinction between cases of prosopagnosia following brain damage that one can find in the scientific literature is the apperceptive/associative distinction, which, as I discussed above, is not supported by consistent evidence.

In this context, it is worth remembering that following Bodamer (1947)'s definition of prosopagnosia, clinicians and researchers used to consider this impairment as a single clinical disorder, searching for an impairment *either* in terms of (visual) perception (Hécaen & Angelergues, 1962) or memory (Benton, 1980; Damasio et al., 1982). In the mid-1980s, the view that there must be various types of prosopagnosia emerged with the cognitive (neuro)psychology framework, according to which the mind is conceptualized as a series of independent information processing modules, which can be potentially selectively disrupted by brain damage (Fodor, 1983; Shallice, 1988). Along the lines of this framework, researchers emphasized the variability of performance across various FIR tasks of different cases of reported prosopagnosia (De Renzi, 1986; Sergent & Signoret, 1992; Schweich & Bruyer, 1993; see also Barton, 2008 more recently) or the variety of face recognition impairments in clinical populations (Young, 2011; Barton et al., 2021).

This approach has certainly been informative in identifying functional differences between various recognition functions for faces (e.g., lip-reading *vs.* individuation, expression *vs.* identity, etc. see Young, 2011). However, while variability of behavioral performance at FIR tasks is genuine across reported cases of prosopagnosia, it can be due to many factors such as the severity of various associated impairments following brain damage and compensatory strategies developed by the patients, or even the premorbid ability at FIR, which we now know varies substantially also across neurotypical individuals (Wilmer, 2017). That is, variability of behavioral performance at FIR tasks across reported cases of prosopagnosia does not imply that there are deficits to fundamentally distinct functional components of the core FIR function in different patients. In fact, it is impressive that despite substantial efforts and decades of research under the cognitive neuropsychology framework, this variability never translated into well-defined functional subcategories of prosopagnosia. As for the famous apperceptive/associative distinction, it was not clear-cut originally (Lissauer, 1890) and it is not by chance that it reemerged

only in the 1980s with studies of both visual object agnosia (Riddoch & Humphreys, 1987) and prosopagnosia (Hécaen, 1981; De Renzi, 1986) under the umbrella of the cognitive (neuro)psychology framework. This revival was not due to the discovery of new clinical cases, but to the dominant theoretical framework at the time.

12.2. Generalization to two cases: GG and LR

Despite my reservations, following or in parallel to extensive behavioral studies on PS as described here, I nevertheless had the opportunity to evaluate the behavior of a number of other potential cases of prosopagnosia in my career. Yet, I have always been very selective: the visual recognition deficit must be specific to faces and occur at adulthood following sudden brain damage, in a patient with no neurological history or suspicion of premorbid impairments at FIR. Taking into account these criteria, my colleagues and I were able to apply a number of experiments as developed with PS and described in the present review to at least two other cases: patients GG and LR.

The patient GG sustained an ischemic infarct in the territory of the right posterior cerebral artery at the age of 60, which left him with a left hemianopsia, and a complaint of impairment at recognizing people's identities from their faces (which contrasted with his self-reported excellent ability prior to brain damage, as confirmed by his spouse). GG, who was initially identified by Olivier Felician and Sven Joubert at the hospital de la Timone in Marseille, had no prior history of neurological or vascular disease, and his structural lesion concerned the right hemisphere (occipito-temporal cortex) only (see Figure 1 in Busigny et al., 2010).

The patient LR, identified by Daniel Bub at Victoria and first reported in Bukach et al. (2006), suffered from a dramatic motor vehicle accident at the age of 19: he received a penetrating head wound when the hollow metal tube of an uncapped gearshift impaled his lower left cheek in front of the jaw, but piercing the temporal lobe of the opposite (right) hemisphere (see Bukach et al., 2006). For this reason, Daniel Bub called him "the modern Phineas Gage". LR's brain lesions are difficult to define precisely since he cannot be tested in a MRI scanner due to metal clips in his head, but they seem to encompass the whole right anterior temporal lobe; his low-level visual function appears completely preserved (Bukach et al., 2006).

Both of these patients did not report any visual nonface object recognition impairment. Despite GG suffering also of topographical disorientation, initial tests confirmed that basic level object recognition, as well as his recognition of famous monuments and places, was intact.

Both GG and LR vary in absolute performance and speed between themselves, and in comparison to PS, as tested with the same FIR tasks (e.g., see Rossion et al., 2009 for direct

comparison between the three cases). Again, this is in line with the known variability of performance of reported cases of prosopagnosia (Sergent & Signoret, 1992; Barton, 2008) and this variability supports a (multiple) single case approach rather than group studies (Shallice, 1979; Caramazza, 1986). Based on this functional variability, I was nevertheless hoping initially, and I expected, to find qualitatively different response profiles compared to PS and describe different types of prosopagnosia (which I thought would have been more exciting intellectually). However, across all experiments performed, both of these patients in fact showed exactly the same pattern of performance as summarized for PS in the present review: a category-selective visual recognition impairment for faces, i.e., with recognition of object identity preserved; relatively more difficulties for dissimilar than similar (morphed) faces; an impairment in FGH as evidenced by absent/reduced composite, whole/part and inversion face effects, increased difficulties with a gaze-contingent mask as compared to a gaze-contingent window, similar pattern of eye movements focusing on parts, overreliance on the mouth at the expense of the eye region of the face (as shown already by Bukach et al., 2006 for LR), and typical generic face recognition of Arcimboldo and Mooney faces (Rossion et al., 2009; Busigny et al., 2010; Van Belle et al., 2011; Busigny et al., 2014). Hence, despite differences in aetiology, brain localization of damage, age of onset, associated visual and nonvisual impairments, LR and GG showed the same qualitative functional profile of response as PS, suggesting a similar functional impairment in terms of FGH caused by a disruption of (access to) cortical face memories (**Figure 23B**).

12.3. Advocating a restrictive definition of prosopagnosia

Based on such similar observations in these two cases as for PS, I suggest a single type of prosopagnosia, providing that a restrictive definition of the condition is adopted (Rossion, 2018a). What should be the criteria? First and foremost, category-selectivity. As explained in detail above (section VI), if the patients have problems at visual object recognition, then they should be referred as cases of visual object agnosia (or multimodal semantic disorders), not prosopagnosia (even if they do not mistake their spouse for a hat). Trying to understand the nature of the FIR impairment, and the very nature of FIR for neurotypical individuals based on studies of such cases of visual agnosia, such as LH, can be problematic and lead to all sorts of incorrect ideas such as the view that prosopagnosia is about subordinate level categorization, or visual (semantic) expertise, or reflect a defect of “general holistic” processing (e.g., Levine & Calvanio, 1989, Gauthier et al., 1999; Barton et al., 2009). Moreover, including cases of multimodal semantic disorders following bilateral anterior temporal lobe damage (e.g., the patient PV; Sergent &

Signoret, 1990) can also lead to misleading views about the nature of human FIR (see Gainotti, 2010; Gainotti, 2013)

Besides category-specificity and the lack of causal low-level impairments and intellectual difficulties, I have advocated other criteria to define prosopagnosia: a causal brain damage that happens in a mature FIR system (i.e., at adulthood), suddenly rather than following neurodegenerative disorders, a massive impairment, and which is both retrograde and anterograde, i.e., concerns the failure to recognize faces learned before and after the accident (Rossion, 2018a). I also think that given our current knowledge about the neural basis of human face recognition (see Rossion, submitted review part II), the lesion(s) localization is not anecdotal and provides additional clues to diagnose a case of prosopagnosia.

Providing that these criteria are stringently adopted and that the nature of the impairment is characterized in depth, I claim that all cases of prosopagnosia – then a very rare deficit apparently specific to the human species (Heywood & Cowey, 1992; Rossion & Taubert, 2019) - can be accounted for a memory-based defect of FGH perception of faces.

If, however, a symptom-based definition of prosopagnosia is adopted, e.g., subjective complaints and /or objective difficulties at one or two behavioral FIR tests (e.g., Barton & Corrow, 2016), and the “prosopagnosic” impairment is described in the context of various neurological disorders such as semantic dementia, Alzheimer’s disease, temporal lobe epilepsy, or even psychiatric and neurodevelopmental disorders (‘developmental/congenital’ prosopagnosia), then the functional account proposed here does not apply. Indeed, beyond the core face-selective memory-based FGH process identified here from the study of PS, the ability to recognize people’s identity from their faces in an explicit behavioral task depends on various non-face-selective processes taking place in low-level visual circuits (retina, thalamus and retinotopic cortical areas), medial and anterior temporal brain regions, and even parietal and prefrontal networks (Tranel et al., 2009), with damage or dysfunction to these networks potentially leading to relatively severe FIR impairments.

XIII. Lessons from prosopagnosia: evaluation of face identity recognition

13.1. The problem of human FIR evaluation

Hundreds, if not thousands, of researchers around the world currently work on understanding human FIR, an important topic for fundamental research in cognitive neuroscience, but also for clinical evaluation and, evidently, for practical applications (i.e., automatic face

recognition devices; Christakis et al., 2021). At a fundamental level, researchers aim at answering questions such as *which stimulus cues form the basis of FIR?; how are facial cues/parts combined into holistic representations?; how fast is FIR, and how long does the process take?; how is it modulated by attentional processes and how?; where in the brain is this function instantiated and how is it achieved in terms of neural mechanisms? How does this function develop in the normal population?* Etc. At the clinical level, we want to know if, and if so how, FIR is affected in neurological and psychiatric conditions (e.g., Alzheimer's disease, semantic dementia, autism spectrum disorder, etc.) as well as how can we best use FIR measures to help the diagnosis and prognosis of these conditions. Over the past two decades, interindividual variability in human FIR has also been emphasized (Wilmer, 2017): while most people appear to perform around the population average (e.g., Bowles et al., 2009), some people appear to be very poor at this function and could even be defined as cases of prosopagnosia; in contrast, others excel at it ("Super (face identity) recognizers"; Russell et al., 2009; Ramon et al., 2019). At all levels, there are intense scientific debates, which lack resolution in part because the field lacks standard recognized measures of FIR.

Since the first use of face pictures and quantified measures of performance to test potential cases of prosopagnosia in the 1960s (de Renzi & Spinnler, 1966; Benton & Van Allen, 1968; Milner, 1968), and with computer developments in the 1980s, a large number of various behavioral FIR tasks have been proposed. While there were only two internationally recognized behavioral tests of FIR 20 years ago (the BFRT; Benton & Van Allen, 1968; and the Warrington Recognition Memory for Faces; WFMT; Warrington, 1984), there are currently more than 10 tests available, with most tests having appeared in recent years²⁰. These tests vary according to characteristics that reflect researchers' reflections, priorities, and disagreements about the type of stimuli to use (e.g., familiar or unfamiliar faces, controlled or natural (ecological) stimuli), the required tasks (e.g., old/new recognition, matching with or without delay, same/different task or

²⁰ Beyond the original BFRT and WFMT, a list of currently available FIR tests would include at least: the CFMT (Duchaine & Nakayama, 2006), which has a longer version (CFMT+; Russell et al., 2009) and various other versions to test children, or with faces of different ethnicities; the Cambridge Face Perception Test (CFPT; Duchaine et al., 2007); the Glasgow Face Matching Test (GFMT, Burton et al., 2010); the Caledonian Face Test (CFT; Logan et al., 2016); the Kent Face Matching Test (KFMT, Fysch & Bindemann, 2018); the computerized version of the Benton Face Recognition Test (BFRT-c, Rossion & Michel, 2018), the Crowds Matching or Models Memory Test (Bate et al., 2018); the 10-item version of the Yearbook Test (YBT-10; Fysh et al., 2020); the USC Face Perception Test (USCFPT; Margalit et al., 2016); and the Oxford Face Matching Test (OFMT; Stantic et al., 2021).

target matching of two alternatives, with two or more distractor faces, etc.) and the relevant measures (e.g., accuracy rates only, RTs, sensitivity measures).

Surprisingly, while the early tests in the field such as the BFRT or WFMT were based on clinical observations in reported cases of prosopagnosia, or brain-damaged patients with objective impairments in FIR (Benton & Van Allen, 1968), there is in fact very little connection nowadays with studies of (real) cases of prosopagnosia in terms of inspiration and constrain to develop all of these new FIR tests. This is unfortunate because *isolating* the key functional process that is deficient in a well-studied case of prosopagnosia, such as PS as illustrated here, could certainly tell us something relevant about how to build the most valid and diagnostic tests of FIR.

As a matter of fact, over the years, PS has also indirectly greatly contributed to methodological developments in my own research on FIR with neurotypical individuals. This is not so much because my colleagues and I had to develop FIR paradigms that would show her deficit against a group of normal controls – this is easy and works almost all the time, even for simultaneous matching of strictly identical pictures of faces. However, the single case approach in neuropsychology forces to develop experimental paradigms in which a significant effect is found in *every* single control, and to *maximize* the contrast between the patient and *each* control's performance. This constraint has constituted perhaps the main challenge for my research on PS over 20 years, and has forced me to constantly reflect on, and improve, the validity and sensitivity of behavioral paradigms to test neurotypical individuals (e.g., the composite face paradigm with unfamiliar faces; see Rossion, 2013).

Nevertheless, observing PS's behavior directly in various FIR tasks and real-life circumstances for more than 20 years has also provided a number of clues about the most valid and sensitive evaluation measures that I would like to share at the end of this review.

Familiar or unfamiliar faces?

Whether to use pictures of familiar or unfamiliar faces to evaluate prosopagnosia and FIR is an old debate (Benton & Van Allen, 1972). It has resurfaced over the past two decades with the claims by prominent researchers in the field that neurotypical human adults are generally “bad” or “poor” at recognizing the identity of unfamiliar faces (e.g., Hancock et al., 2000; White et al., 2010; Strathie et al., 2021), that they would essentially rely on low-level, “pictorial” cues of images (Hancock et al., 2000; Megreya & Burton, 2006; Jenkins et al., 2011) and thus would be experts at identity recognition only with familiar faces (Young & Burton, 2018). If this were true, then there would be no point in comparing a case of prosopagnosia to normal controls at a FIR task with pictures of unfamiliar faces (as in fact hinted at by Arthur Benton; see Benton & Van Allen, 1972; Benton, 1980): one should use pictures of familiar faces only.

Leaving aside the notion of expertise (as discussed above), defining neurotypical human adults' unfamiliar FIR as being "poor" or "bad" can only make sense in an applied research context (e.g., passport checks or eyewitness testimony), when below ceiling accuracy cannot be tolerated. If one designs an extremely difficult, highly artificial and ambiguous task requiring to match two very different pictures of the same identity among 9 similarly looking distractors, with a target that may or may not be present in the panel (Bruce et al., 2001; Megreya & Burton, 2006), then it is not surprising that FIR performance with unfamiliar faces can be indeed *relatively* poor (i.e., 20-30% mistakes). Indeed, to resolve such a task with very high accuracy, long-term familiarity and semantic knowledge about the faces is necessary. Thus, as used with familiar faces, such a task (or an inherently ambiguous card-sorting task; Jenkins et al., 2011) does not capture well the key FIR function, and instead largely reflects the contribution of higher level factors. Yet, even with unfamiliar faces, performance at this task is, on average, well beyond chance level (e.g., Megreya & Burton, 2006). Unfortunately, due to the ambiguity, artificial difficulty and complexity of this task, interindividual variability in performance is very high in the normal population, and one would never want to use such a task to compare a single case of prosopagnosia to normal controls (or to estimate interindividual variability at the core FIR function).

The claim that matching/discriminating pictures of unfamiliar faces for their identity would rely essentially on low-level visual, "pictorial" cues of images, is just plainly wrong. It is not because a task is (partly) resolvable using low-level visual cues – whatever they may be – that a neurotypical human adult proficient at FIR will use such cues in the task (Sergent, 1989). If it were the case, there would be no inversion effect in unfamiliar face matching tasks, and PS would have no *specific* recognition problems for (upright) faces at such tasks. Another key argument is that unfamiliar faces are typically discriminated for their identity in high-level cortical regions that respond specifically to faces, not low-level visual regions (see the review on PS part II).

As illustrated in the present review, when pictures of familiar faces have been used to test PS (Ramon et al., 2016; also Orban de Xivry et al., 2008; Busigny & Rossion, 2010; Van Belle et al., 2010b), the same effects were found and the exact same conclusions were reached as in the experiments using pictures of unfamiliar faces. Overall, most of the experiments that have identified PS's core impairment have used such pictures of unfamiliar faces, which offer substantial advantages in availability and stimulus control. The outcome of these experiments clearly supports the view that there is an expertise in (most) neurotypical human adults for identity recognition of pictures of unfamiliar faces, an expertise that is lost in prosopagnosia. Thus, it is highly recommended to use pictures of unfamiliar faces to evaluate FIR.

This does not mean that pictures of familiar faces (celebrities or personally familiar) cannot enrich the evaluation of FIR in neurotypical individuals, even though it is complicated because people have different degrees of semantic knowledge and experience with these faces. In fact, even if, as noted above, any advantage at FIR tasks with familiar as compared to unfamiliar faces is more likely due to semantic associations than to differences in terms of extraction of visual representations of identity (Rossion, 2018b), one could include a comparison of matching familiar and unfamiliar faces in a given test to provide additional information.

Controlled or natural stimuli?

Another recurrent issue in human face (identity) recognition research is whether to use maximally controlled stimuli or more natural, ecologically valid, stimuli. Early in my career, I used to think that highly controlled stimuli, most often devoid of external features, were necessary to isolate the nature of the key higher-level FIR function. However, in line with a (slow) progressive change in face stimuli used in human face recognition research over the past 20 years (see Dawel et al., 2021), my observations of PS's behavior have made me change my opinion over the years. I now think that it is often better to control for low-level visual cues by *varying* them between the face stimuli to match (e.g., **Figure 1**; or **Figure 24** below) rather than artificially homogenize the stimuli that need to be discriminated.

Indeed, many homogenization procedures in which the stimuli are strictly equalized for luminance, global contrast, amplitude spectrum (e.g., Rousselet et al., 2008), even feature position (Gosselin & Schyns, 2001) or surface cues (color and texture) (Logan et al., 2016) decrease ecological validity. This is because these cues, color and texture obviously, but even internal global contrast, naturally vary between facial identities and can therefore be valid to recognize one's identity based on their face. Moreover, when stimulus sets are artificially homogenized, this can paradoxically make low-level cues (e.g., the orientation of an eyebrow) particularly salient, potentially reducing the contrast in performance between a case of prosopagnosia and normal observers' performance.

In this context, a key observation from studies on PS is that artificially increasing similarity between face identities to discriminate, e.g., using morphing, is certainly not recommended if one wants to isolate the FIR function. Indeed, when using stimuli that were made highly similar through morphing, the contrast between PS and normal controls was reduced (**Figure 7**; Busigny et al., 2010), presumably because normal controls had to resort on a piecemeal analytic strategy similar to PS. This is corroborated by PS's real-life experience: she claims that the only time she was able to outperform her colleagues at recognizing children's identity in the kindergarten was for discriminating twin faces. Based on such observations, I would recommend against using

artificially similar faces through morphing (as in the CFPT; Duchaine et al., 2007) or other low-level controls (e.g., Caledonian Face test; Logan et al., 2016; USCFPT; Margalit et al., 2016) to evaluate the human FIR function.

Perception-based or Memory-based tasks?

The specificity of PS's deficit in recognizing upright face identities contrasts with the fact that she is impaired in all kinds of FIR tasks: identification, familiarity decision, old/new recognition, delayed or simultaneous matching, etc. as illustrated throughout the present review. In a standard framework of human face recognition, this generalization would be explained by a deficit of perceptual nature (i.e., apperceptive prosopagnosia). In the revised framework advocated here (section X), PS is impaired at these tasks because all of them, even the simplest simultaneous face matching task, require functional (cortical) memories of face identities. Regardless of which theoretical framework is correct or adopted, the common distinction in the scientific literature between "perception tests" or "memory tests" appears profoundly mistaken, if only because these functions (i.e., "perception", "memory") are not well defined. Instead, one should define what is required in a given FIR task, and perform an exhaustive *task analysis*. For instance, the CFMT (Duchaine & Nakayama, 2006) requires sufficiently high intellectual abilities to understand a relatively demanding task, low-level vision, face identity discrimination, face identity generalization across head orientation and noise levels, spatial and selective attention, temporary encoding and maintenance of face identities in memory, decision making, motor control, motivation, etc. For this reason, absolute performance at this test is only weakly related to one's core FIR ability, and it is not surprising that it is only weakly related to performance at other FIR tests (e.g., McCaffery et al., 2018).

Accuracy rates and RTs

Despite being computer-based, most if not all standardized current FIR tests rely only on accuracy rates (or derived measures, e.g., sensitivity) to evaluate this function, with RTs being generally neglected. As discussed elsewhere (Rossion & Michel, 2018) and illustrated throughout the present review on the case of prosopagnosia PS, this is a major limitation: FIR is naturally fast (i.e., achieved within a few hundreds of milliseconds at most) and if one takes several seconds to recognize people's identity in real life, there must be a problem. In the vast majority of experiments performed with PS, she was impaired relative to normal controls both in accuracy rates and (correct) RTs, but often with RTs showing the largest contrast with normal controls (e.g., **Figures 7; 18; 20**). This is not surprising because PS has to rely on a part-by-part analysis of the face picture to reach a decision about its identity and be able to match/discriminate it against other

pictures, such an inefficient procedure being particularly time-consuming (as revealed by her eye-gaze fixations for instance; Orban de Xivry et al., 2008; **Figure 19**).

Instead of using RT measures, one may want to apply time pressure during a task, e.g., forcing the participant to complete the task during a limited amount of time. However, time pressure to respond in an explicit unfamiliar FIR task can artificially deteriorate behavioral performance even in healthy adult participants (Bindemann et al., 2016; Fysh & Bindemann, 2017), could lead to unusual strategies, and would be particularly problematic when testing children or (some) clinical populations (e.g., Powell et al., 2019). We have not done that in studies on PS, always letting her take as much time as she wants to complete a task, albeit telling her that she should not wait to press a response key when she feels that she knows the answer or that she will not be able to do better with additional time. One thing that we have found very efficient is to limit the exploration time of a first stimulus, when there is no response to provide, and then present the second stimulus or pair of stimuli for as long as the patient wants to provide a response (e.g., Busigny et al., 2010; Van Belle et al., 2010; **Figure 20A**).

Of course, RT at a given task is only a limited proxy of *processing time*: ideally, we would want to isolate the time it takes to complete the core FIR process for an individual participant, independently of all other processes required to achieve the task. Indeed, there can also be many reasons beyond FIR for being slow at an explicit behavioral task, and this is one reason why researchers and clinicians are generally reluctant to include these RT measures in the evaluation. For instance, patients with temporal lobe epilepsy, particularly in the right hemisphere, are generally as accurate as normal controls but significantly slowed down at FIR tasks with unfamiliar faces (Volfart et al., 2020). However, these prolonged RTs are not specific to face stimuli. Moreover, contrary to PS, relative to normal controls, the relative slowing down of these patients for matching pictures of unfamiliar faces remains constant for upright and inverted faces (Volfart et al., 2020). In sum, the speed at which FIR is performed is a key element, which must be considered in a proper evaluation of the function, together with other qualitative measures.

Inversion

This last reflection leads to another surprising observation: to my knowledge, none of the currently available standardized FIR tests include a condition with pictures of faces presented upside-down. This is really astonishing because studies with PS (Busigny & Rossion, 2010) and of other cases of prosopagnosia as defined here (Busigny et al., 2010; Busigny et al., 2014) invariably show the high diagnosticity of such comparison: these patients do not show a (normal) face inversion effect (see Busigny & Rossion, 2010 for review). Moreover, this face inversion effect is absent or negligible in nonhuman animal species devoid of expertise at FIR such as

macaque monkeys (Rossion & Taubert, 2019; Griffin, 2020) and, in humans, takes years of development to appear and then reach adultlike level (Hills & Lewis, 2018). Thus, regardless of whether the face inversion effect is due to a specific loss of holistic perception, i.e., a qualitative effect, as advocated here (see Rossion, 2008), or to a simple quantitative (part-based or holistic) drop of efficiency in analysis of faces as claimed elsewhere (Sekuler et al., 2004; Murphy et al., 2020), comparing FIR performance for upright and inverted faces is potentially very informative: since the physical difference between two facial identities is identical regardless of their orientation, this comparison may reveal the extent to which the recognition system goes beyond the sensory information given (i.e., relies on high-level, knowledge-based, processes/representations).

Uncertainty

Another factor that is important to consider when evaluating the FIR function is *uncertainty*: we have seen that PS may be able to recognize the identity of a face if she knows or can reasonably guess that this identity is among the presented pictures (i.e., if the same celebrity or personally faces are presented to her all the time). However, if the exact same picture of that same face identity is mixed up with unfamiliar faces, she will certainly miss it (Busigny & Rossion, 2010). Uncertainty in the type of diagnostic cues to discriminate/match faces is also important (Ramon & Rossion; **Figure 12**), encouraging the use of a high number of variable face identities in a given test, these faces differing within or across trials from their distractors in terms of different diagnostic cues. However, uncertainty in the number of *responses* to provide in a given trial (e.g., target present or absent; Bruce et al., 2001; Jenkins et al., 2011) should be avoided because it can lead to substantial response biases (as in same/different tasks, e.g., the GFMT; Burton et al., 2010) and artificially inflate variability among neurotypical individuals.

13.2. A novel behavioral test of FIR

Based on all these considerations derived from studies on PS, we recently designed a novel FIR test that has not yet been reported in the literature (Volfart et al., in preparation). The test is based on a simple forced-choice face identity matching task with natural (unsegmented) images (**Figure 24**).

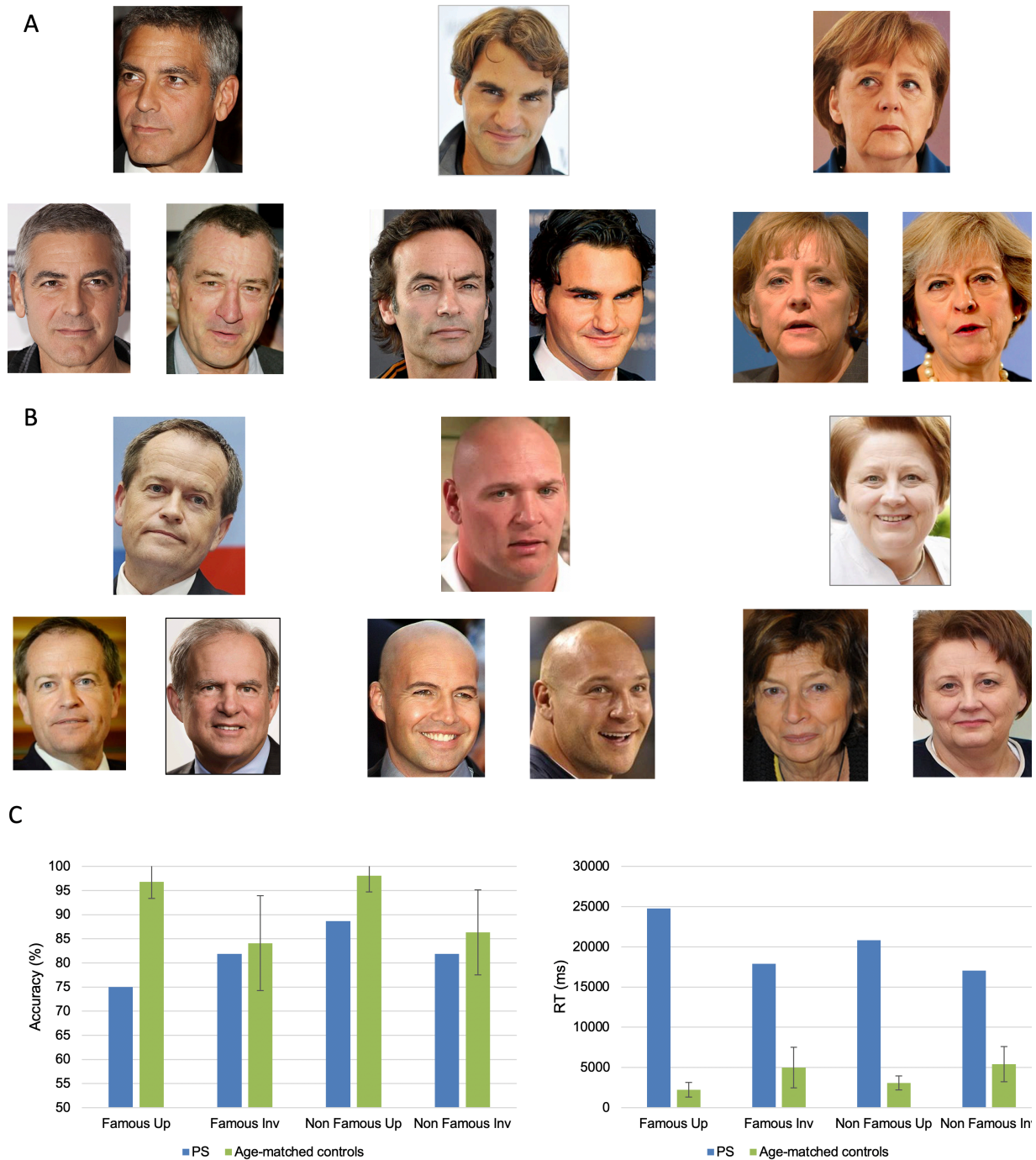


Figure 24. Matching natural variable images of faces for their identity. **A.** Examples of familiar faces (i.e., celebrities known by PS and age-matched controls). **B.** Examples of unfamiliar faces (i.e., foreign celebrities not known by PS and age-matched controls). **C.** Contrasted performance of PS and (7) age-matched controls, showing PS's impaired performance in accuracy rates and RTs relative to controls (only at upright orientation for accuracy rates), her lack of typical advantage at face identity matching for familiar faces and lack of inversion effect.

It includes 88 identities (44 celebrities, 44 non-famous faces; with 132 images in total). Half of the trials are with familiar faces and the other half with unfamiliar faces, but the trials are

presented in a fully randomized order and there is no explicit instruction regarding familiarity. In each trial, the two pictures of the same identity to match differ substantially from one another in terms of head orientation, lighting and background conditions, expression, size etc., and they are paired with a distractor who is matched for sex and (roughly) for age, and shares salient physical attributes with this identity (e.g., hair, glasses, beard, etc. **Figure 24**). All the trials of this task are presented with faces either at upright or inverted orientation, also presented in random order. Overall, the test therefore measures both discrimination/generalization ability, the effect of familiarity (i.e., advantage for familiar over unfamiliar faces in face identity matching), and inversion. Both accuracy and RTs are measured in the test, which is administered without time constraints. The results are shown on **Figure 24** for PS and age-matched controls. At upright face orientation, controls performed almost at ceiling (98%), although they took about 3 seconds on average for each trial (about twice the duration as for a group of younger participants of about 24 years old). Their performance dropped by about 16% for inverted faces (82%). In contrast, PS's performance was virtually the same for upright (80%) and inverted (82%) faces, in line with previous observations (Busigny & Rossion, 2010; **section IX** of the present review). Since they performed almost at ceiling, typical participants did not do better for familiar than unfamiliar faces in the matching task, but they were about 30% slower (i.e., from 2649 ms to 3450 ms) for unfamiliar faces, in line with the well-known advantage at generalizing across views for matching the identity of familiar faces (Bruce et al., 2001). In contrast, PS performed even worse (14% accuracy) and was 30% slower for "familiar" than unfamiliar faces²¹.

²¹ While one may be tempted to interpret PS's differential performance for unfamiliar as compared to "familiar" (faces) as evidence of implicit recognition ("covert prosopagnosia"; Bruyer et al., 1983; De Haan et al., 1991; de Haan, 1999), it is unlikely given that there was never any behavioral evidence of covert prosopagnosia in PS (e.g., Simon et al., 2011), and that she was better with unfamiliar faces in the task. Moreover, there is a much simpler account: since the two sets of images are different, the level of difficulty might be intrinsically higher for the images of familiar faces, independently of familiarity. If this is the case, the advantage provided by familiarity would in fact be underestimated in normal controls. Disentangling these possibilities would require testing participants who do not know any of the famous faces. An additional version of the test in which the two images to match were exactly identical showed that PS, who was still about 3-4 times slower than normal controls, did not show any advantage for unfamiliar over "familiar" faces either in accuracy or RTs in these conditions, suggesting that the difference observed in the main set of images is indeed likely to be due to different levels of difficulty for familiar and unfamiliar face stimuli rather than unconscious recognition of familiarity. PS's performance could thus also be equalized for the difficulty of matching familiar and unfamiliar faces in the main task (Volfart et al., in preparation).

In summary, this simple task, which took about 6 minutes (88 trials) without break in age-matched neurotypical individuals and is based on natural images of faces, shows maximal contrast between these participants and the prosopagnosic patient PS both at quantitative (i.e., absolute performance) and qualitative (effect of familiarity, inversion effect) levels. For all the reasons discussed above (section 13.1), it may well prove to be an invaluable neuropsychological test for FIR evaluation both for research and clinical purposes in the years to come.

13.3. Measuring FIR with fast periodic visual stimulation EEG

Even if the recently developed neuropsychological test presented above incorporates a lot of the key aspects of FIR, it is explicit and therefore depends on understanding task instructions and motivation, requires spatial and selective attention abilities, decision making, motor execution, etc. Moreover, stimuli are presented for an unlimited time, so that the test does not capture speed and automaticity, two key aspects of FIR. To deal with this issue, one could use EEG recordings during fast periodic visual stimulation (FPVS-EEG). This approach, also called “frequency-tagging” or “steady-state evoked potentials” is based on the old observation that a visual stimulus presented at a relatively fast periodic rate (e.g., a blinking light) leads to an EEG response exactly at that rate (Adrian & Matthews, 1934), which can be expressed in the frequency spectrum of the EEG following Fourier Transform (Regan, 1966; for review, see Norcia et al., 2015). Since 2011, my colleagues and I have applied this approach with various paradigms to implicitly measure human face recognition, in particular FIR, providing highly sensitive, objective and reliable measures of this function (Rossion, 2014; Rossion et al., 2020 for reviews).

The most common paradigm is based on stimulation sequences of about 60 seconds in which a single unfamiliar face identity is repeated (across substantial changes of size) at a fast 5.88 Hz rate, with a different unfamiliar face identity appearing every 5 stimuli, i.e., 1.18 Hz (**Figure 25**; original paradigm as in Liu-Shuang et al., 2014). In this simple ‘oddball’ paradigm, validated now by more than 20 published studies (Rossion et al., 2020 for reviews), an EEG peak exactly at 5.88 Hz (and harmonics: 11.76 Hz, etc.) reflects the common neural response to all face stimuli, while an EEG peak at 1.18 Hz (and harmonics, 2.36 Hz, etc.) reveals an *automatic* discrimination of facial identities (across changes of stimulus size, and variable changes of identities in the sequence). Indeed, there is no explicit FIR task: PS and other participants simply have to detect brief nonperiodic changes of color of the fixation cross. Besides the implicit measure, significant advantages of this approach are its high sensitivity, allowing to record significant responses virtually in every individual (neurotypical) brain within a few minutes (see e.g., Xu et al., 2017; Rossion et al., 2020), its objectivity, i.e., the EEG response is identified only

at a pre-defined frequency and quantified in a straightforward manner as a sum of the relevant baseline-corrected harmonics (Retter & Rossion, 2016; Retter et al., 2021), and its high test-retest reliability (Dzhelyova et al., 2019; Stacchi et al., 2019).

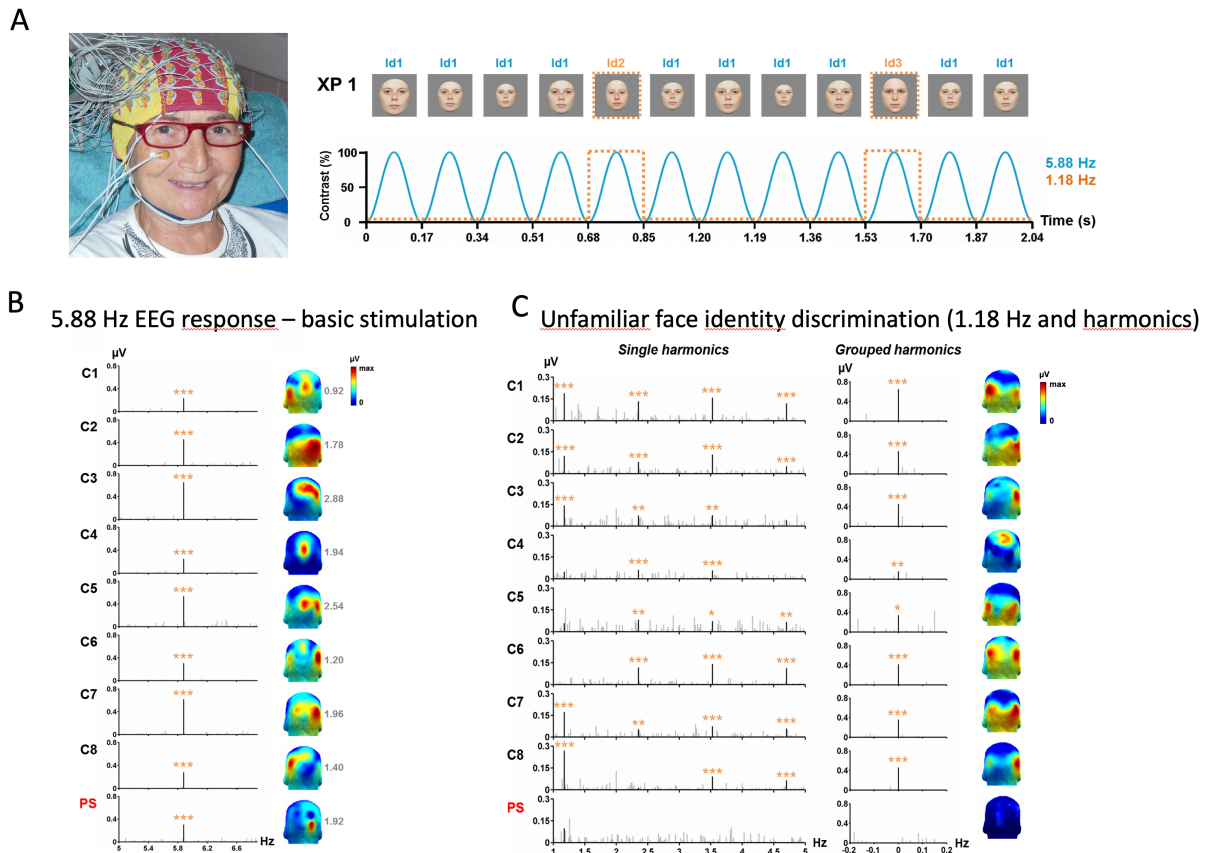


Figure 25. *A. PS as she was tested in FPVS-EEG in September 2013 in Louvain-la-Neuve (Belgium) with a 128 channels EEG cap. She was presented with the face individuation oddball paradigm illustrated on the right, in which different face identities interrupt a rapid 5.88 Hz train of the same face identity (across substantial changes of stimulus size) every 5 stimuli. B. As normal controls, PS showed a significant response at 5.88 Hz to the visual stimulation. C. However, contrary to every age-matched control, she failed to show any unfamiliar face individuation response at 1.18 Hz. Importantly, the lack of any significant EEG response at 1.18 Hz and harmonics for PS is not due to her brain's inability to respond at that frequency: if faces are presented at 1.18 Hz among nonface objects, she shows a clear generic face recognition response, as normal controls, and in line with her ability to recognize faces as faces (Liu-Shuang et al., 2016).*

PS and 8 age-matched controls were tested in 4 FPVS sequences of this paradigm (about 4 minutes of testing, corresponding to 288 individual face discriminations). All participants including PS showed clear responses at 5.88 Hz to the general visual stimulation (**Figure 25B**). However, while all neurotypical individuals also showed clear and significant peaks at the individual face discrimination frequency (1.18 Hz) and harmonics, there was no such EEG

response for PS anywhere on the scalp (**Figure 25C**), reflecting her impairment at FIR (Liu-Shuang et al., 2016).

Given that PS is able to discriminate pictures of unfamiliar faces well above chance level, as shown in numerous behavioral experiments throughout this review, one may wonder why she shows no electrophysiological face individuation response. In other words, one could have expected a weaker, yet significant, response in PS compared to normal controls. One simple explanation lies in the fast rate at which face stimuli are presented in the sequences, with each face identity appearing for less than 166 ms, allowing only one fixation per face. In these conditions, especially when the fixation point is located in between facial parts, i.e., at the optimal location for FIR (Orban de Xivry et al., 2008), PS's visual recognition system is simply unable to detect changes of identity. This is yet another illustration that the speed of the FIR process is a major aspect to consider in an evaluation procedure. More generally, here again, PS's case of prosopagnosia is used to validate a diagnostic tool, showing that this FPVS-EEG approach can be ideal to objectively identify impairments at FIR, in particular in single-case studies, and characterize these impairments (e.g., see Towler et al., 2020 for a recent application in cases of prosopagnosia). In the future, more recent developments of FPVS-EEG with natural images of familiar faces to measure FIR (Zimmermann et al., 2019; Yan et al., 2020) could also be used as diagnostic tools for FIR impairments²².

XIV. Summary and Conclusions

More than twenty years of behavioral laboratory experiments and observations of PS in real-life circumstances, as well as eye movement recordings and electrophysiology, have provided invaluable information to understand how she, and in contrast how we, recognize people's identity by their faces – arguably the ultimate recognition function for the human brain.

In a nutshell, these studies show that neurotypical human adults have a unique function to perceive a face stimulus holistically (i.e., as a single unit, with no part decomposition) at a relatively fine-grained level of resolution (FGH). Following brain damage at adulthood, this function broke down specifically in PS, leaving her visual object (identity) recognition intact. A

²² An EEG study performed on PS reported a significant difference in electrophysiological signals evoked by pictures of familiar vs. unfamiliar faces (which could not be distinguished behaviorally by PS), interpreted as evidence of unconscious recognition of familiar faces (Simon et al., 2011). However, there were no normal participants tested in the study, and the “effect” – a late (520-570ms) difference in amplitude over left prefrontal channels - did not correspond to any known electrophysiological marker of face familiarity, suggesting that it was no more than a fluke.

consequence of the loss of a FGH representation is that PS must use an inefficient, slow, part-based analytic strategy to recognize someone's facial identity (unless a coarse representation of the global head shape is sufficient, e.g., to recognize, often successfully, French actor Gerard Depardieu). Since the identity of other visual object categories can readily be recognized based on coarse holistic representations and/or detailed part-based analyses, this broken function in PS leads to a category-specific, i.e., restricted to the category of faces, recognition impairment. Thus, there is no conflict between a *domain-specific* account of prosopagnosia and an account in terms of an impaired *process*: it is an impaired *domain-specific process*. In the same vein, there is no conflict between a visual expertise account of prosopagnosia/human face recognition and domain-specificity: PS lost a *domain-specific expertise* at face identity recognition (FIR), an expertise characterized in neurotypical human adults by this single glance, automatic, holistic recognition of someone's face individuality.

Importantly, this level of expertise at FIR, and this function, may be specific to the human species. Indeed, while many nonhuman animal species have a configuration of sensory receptors positioned together in front of the brain to interact efficiently with the environment (Bruce & Young, 1998; Rossion & Retter, 2020), there is little evidence that this face is used naturally to recognize the identity of conspecifics, let alone at a comparable level of expertise as in humans. When it is the case, as in *Polistes Fuscatus* queen wasps for instance (Sheehan & Tibbetts, 2011), the number of exemplars to recognize is very limited (e.g., 6-10), and recognition appears to be based largely on external features without evidence of domain-specificity in neural substrates (Rossion, in press). While such studies are nevertheless remarkable and interesting from a comparative point of view, the studies of the case of prosopagnosia PS show that the ability of nonhuman species to learn to discriminate pictures of *human* faces are of little interest for understanding the nature of our expertise at this function. For instance, relatively recent studies in archerfish learning to discriminate pictures of human faces have prompted conclusions that “*archerfish have impressive pattern discrimination abilities*”, “*that view invariance in human FIR does not require a (cortical) specialized system*”, “*providing insight into the mechanisms employed in more complex organisms such as humans*” (Newport et al., 2016; Newport et al., 2018). In the same vein, sheep being able to learn to recognize the faces of four human (celebrity) faces, led to the conclusions that “*this species have advanced face-recognition abilities, comparable with those of humans and non-human primates*” (Knolle et al., 2017; see the criticisms of Towler et al., 2019). However, unsurprisingly, if the case of prosopagnosia PS reviewed here is tested in such tasks, she too performs very well, and in fact better than archerfish or sheep even to recognize face identity across head orientation or image changes (Rossion et al.,

in preparation). This suggests that there is little if any knowledge about neurotypical human face (identity) recognition that could be derived from such artificial FIR studies in nonhuman species.

In fact, there is no evidence that even other primates such as macaque monkeys, who rely heavily on facial cues of expressions, eye gaze and head orientation or dominance for social interactions (Barraclough & Perrett, 2011), show a human-like FIR function: their FIR ability is seriously limited and qualitatively different as compared to humans (Rossion & Taubert, 2019). Consequently, there is no macaque model, or animal model for this matter, of prosopagnosia (Heywood & Cowey, 1992), making studies of the function and neural basis of such rare cases in our species particularly invaluable. Given this, it must be clear that human expertise at FIR depends on genetic constraints: it will not develop with the genes of a macaque brain, even with a typical human experience with faces. However, the role of active experience with faces during development from birth to adulthood to tune this function is critical: with human genes but the typical experience of a macaque with faces, the human face recognition system will not be able to reach this level of FIR expertise. Moreover, when one is exposed only, or primarily, during development to a specific morphological regime of faces, expertise at FIR is reached only for these types of faces, leading to a striking phenomenon known as the other-race face effect (Meissner & Brigham, 2001; Rossion & Michel, 2011). Hence, studies of FIR impairments can provide the clearest clues about the nature of this function when this impairment occur (suddenly) in a mature system, i.e., at adulthood, as in the case of PS reviewed here.

Contrary to PS, in a neurotypical human adult system, FGH perception of someone's identity can be achieved with only a single glance at a face, usually on its center of mass (Orban de Xivry, 2008; Peterson & Eckstein, 2012), and takes a few hundreds of milliseconds at most (Hsiao & Cottrell, 2008; Zimmermann et al., 2019). It is a rapid, natural, and mandatory process for efficient FIR. Yet, the strength of a familiar face representation in memory depends on many other factors such as the face typicality/distinctiveness (Bruce et al., 1994), within-face variability (Andrews et al., 2015; Burton et al., 2016), and its rich network of semantic associations, including context and affect. This is where cultural and interindividual differences at FIR will be the most salient (Miellet et al., 2013; Wilmer, 2017).

The loss of FGH has a wide range of consequences for the diagnosticity of facial cues: it particularly impairs the contribution of those that are typically enriched by the holistic combination of several local parts, such as the eye region or the relative distance between the eyes and the nose. This is not due to the specific loss of a putative 'part-based representation of faces', the eyes only, or "configural cues": the impairment can also suddenly concern the mouth of a face if all other trials in an experiment drag PS's fixation (i.e., attention for her) elsewhere. Thus,

although there has been intense valuable research to define the nature of the most diagnostic cues for human FIR for decades (e.g., from Davies et al., 1977 to Abudarham et al., 2019), what matters most is to understand the nature of the underlying process.

I have proposed here that FGH perception loss in PS is caused by damage to (cortical) memories of faces, i.e., populations of neurons in the VOTC that have learned to respond selectively to faces and distinguish facial identities based on unimodal visual inputs only (i.e., a unimodal memory). That is, rather than a perceptual impairment causing an impossibility to register this percept in memory, prosopagnosia is a *memory loss disrupting the (holistic refinement of the) percept*. According to this view, the definition of visual agnosia as “*an intact percept stripped of its meaning*” (Teuber, 1968) is incorrect: either it is a memory-based visual agnosia, which can be specific to the category of faces (i.e., prosopagnosia), or a multimodal semantic disorder (Gainotti, 2013).

Although, for obvious reasons, PS does not complain of difficulties at recognizing unfamiliar faces in real life, she cannot tell whether a face is unfamiliar or not, and the presence of those truly unfamiliar face identities play a key role in her inability to recognize familiar ones (e.g., as when she once failed to recognize that an unfamiliar child did not belong to her classroom). Contrary to widespread views, I argue that the recognition of *both* familiar and unfamiliar faces is *always* concerned in prosopagnosia: they both tap into the same face-selective unimodal cortical memory system, although only familiar faces connect to a rich network of multimodal associations. Whether familiar faces also have richer, i.e., more diverse, visual representations than unfamiliar faces into this unimodal cortical memory system remains unknown, and will be discussed further in the second part of this review on the neural basis of PS’s prosopagnosia.

At the outset and throughout this review, while acknowledging that FIR disorders and difficulties are common in neurological and psychiatric populations, including neurodevelopmental disorders (Young, 2011; Avidan & Behrmann, 2021; Barton et al., 2021), I have emphasized the need of a highly restrictive definition of prosopagnosia, i.e., not as a symptom but a condition with both exclusive and inclusive criteria: category-specificity, massiveness of the deficit, sudden onset at adulthood, in a typically functional system, retrograde and anterograde impairment for face identities (see Rossion, 2018a). This conservative definition seems necessary, in my view at least, to understand the true nature of human FIR. While one may be tempted to think that a highly specific and rare neurological disorder cannot offer clues about brain function in general, I argue for the opposite: this highly specific disorder isolates, and

therefore offers a unique window to deeply understand, a key brain function, arguably the pinnacle of all recognition functions for the human brain.

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