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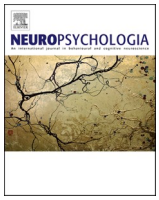

Twenty years of investigation with the case of prosopagnosia PS to understand human face identity recognition.Part II: Neural basis

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Patient PS sustained her dramatic brain injury thirty years ago, in 1992, the same year as the first report of a neuroimaging study of human face recognition.The present paper complements the review on the functional nature of PS's prosopagnosia (part I), illustrating how her case study directly, i.e., through neuroimaging investigations of her brain structure and activity, but also indirectly, through neural studies performed on other clinical cases and neurotypical individuals, inspired and constrained neural models of human face recognition.In the dominant right hemisphere for face recognition in humans, PS's main lesion concerns (inputs to) the inferior occipital gyrus (IOG), in a region where face-selective activity is typically found in normal individuals ('Occipital Face Area', OFA).Her case study initially supported the criticality of this region for face identity recognition (FIR) and provided the impetus for transcranial magnetic stimulation (TMS), intracerebral electrical stimulation, and cortical surgery studies that have generally supported this view.Despite PS's right IOG lesion, typical face-selectivity is found anteriorly in the middle portion of the fusiform gyrus, a hominoid structure.This face-selective right 'Fusiform Face Area' (FFA) has been widely considered as the most important region for human face recognition.This finding led to the original proposal of direct anatomico-functional connections from early visual cortices to the FFA, bypassing the IOG/OFA , a hypothesis supported by further neuroimaging studies of PS, other neurological cases and neuro-typical individuals with original visual stimulation paradigms, data recordings and analyses.The proposal of a lack of sensitivity to face identity in PS's right FFA due to defective reentrant inputs from the IOG/FFA has also been supported by other cases, functional connectivity and cortical surgery studies.Overall, neural studies of, and based on, the case of prosopagnosia PS strongly question the hierarchical organization of the human neural face recognition system, supporting a more flexible and dynamic view of this key social brain function in our species.

1. Introduction

The present review is devoted to neural, i.e., essentially neuroimaging, studies of the case of prosopagnosia PS, the first of which having been reported 20 years ago (Rossion et al., 2003).The review is theoretically driven, and also includes neural recording studies performed with other patients related to PS's case as well as with neurotypical individuals.It is the second part of an extensive review of this case of prosopagnosia studied for more than 20 years with numerous behavioral and neural measures.While the present review paper can be read on its own and there is little overlap between the two reviews, it is useful to reintroduce the case of PS by briefly summarizing the points made in the first paper devoted to functional aspects of PS's prosopagnosia and human face recognition (Rossion, 2022a).

Due to severe closed-head injury at the age of 42 and multiple brain lesions (Fig.1), Pierrette Sapey (PS), who is female and right handed, lost the ability to recognize people's identity by their faces, i.e., face identity recognition (FIR).PS is a real case of prosopagnosia according to

Abbreviations: FIR, Face Identity Recognition; FFA, Fusiform Face Area; OFA, Occipital Face Area; IOG, Inferior Occipital Gyrus; STS, Superior Temporal Sulcus; LatMidFG, Lateral MidFusiform gyrus; EVC, Early visual cortex; fMRI, Functional Magnetic Resonance Imaging; EEG, Electroencephalography; DCM, Dynamic Causal modeling; TMS, Transcranial Magnetic Stimulation; VOTC, Ventral Occipito-Temproal Cortex; VATL, Ventral Anterior Temporal Lobe.

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Bodamer (1947)'s classical definition of a *category-selective* disorder for faces: her object recognition from vision is intact, including the recognition of individual exemplars of nonface object categories.PS also fulfills other criteria of prosopagnosia as recently redefined (Rossion, 2018), i.e., a patient without neurological history or any evidence at FIR difficulties prior to the injury, who abruptly sustains a massive/complete loss of FIR at adulthood, both for face identities learned before the accident and encountered after the accident (i.e., retrograde and anterograde memory deficit).

To recognize someone's identity, PS uses other cues than his/her face such as the person's body shape, gait, voice, gender etc.and, most importantly, relies heavily on the context in which she is likely to meet this person.However, PS also tries to use the face: she tends to focus on individual parts of a face, including internal parts, and she can describe these parts very well (e.g., the color of the eyes, the thickness of the lips, etc.).However, contrary to typical observers, she is unable to perceive these face parts as a single unit, a so-called holistic/configural representation, at a level of resolution that is sufficient to recognize the identity.On account of her loss of holistic/configural perception of facial identity, PS shows no inversion effect, i.e., no advantage at recognizing the identity of a face at upright as compared to inverted orientation.

At a coarse level, PS is able to recognize a visual stimulus as a face holistically (e.g., a Mooney face or an Arcimboldo portrait).She can also recognize each individual part at a fine-grained level of resolution.Yet, she can no longer combine the two, i.e., derive a relatively fine-grained holistic representation (FGH).This expert process is required to individuate faces only, not other visual object categories, and is therefore proposed to be at the heart of the specificity of FIR in human adults.The inability to derive FGH representations particularly reduces the relative diagnosticity of the eye region of the face, a crowded region made of multiple elements, to identify people.Similarly, it causes relatively more difficulties at detecting differences in terms of relative distances between parts than a local part, especially in conditions of uncertainty, i.e., when the nature of the diagnostic cue to identify faces varies randomly across trials in an experiment.

PS's case of prosopagnosia is interpreted in a reversed way compared to classical models of human visual recognition: it is the degradation of (access to) (cortical) memories of faces that causes – rather than follows – her perceptual impairment.That is, her *recognition* deficit *causes* a *perceptual* deficit, perception being defined in this revised theoretical framework merely as the subjective experience occurring when low-level non-categorical sensory inputs match these cortical memories.[2] This in-depth investigation of PS's case not only leads to a deeper understanding of the very nature of FIR and its human specificity, but also contributes to improvement in developing diagnostic tests of the function with behavioral, eye movements, and electrophysiological recordings (Rossion, 2022a).

The present review (part II) on the neural basis of PS's prosopagnosia and human face recognition is based on a number of publications of her

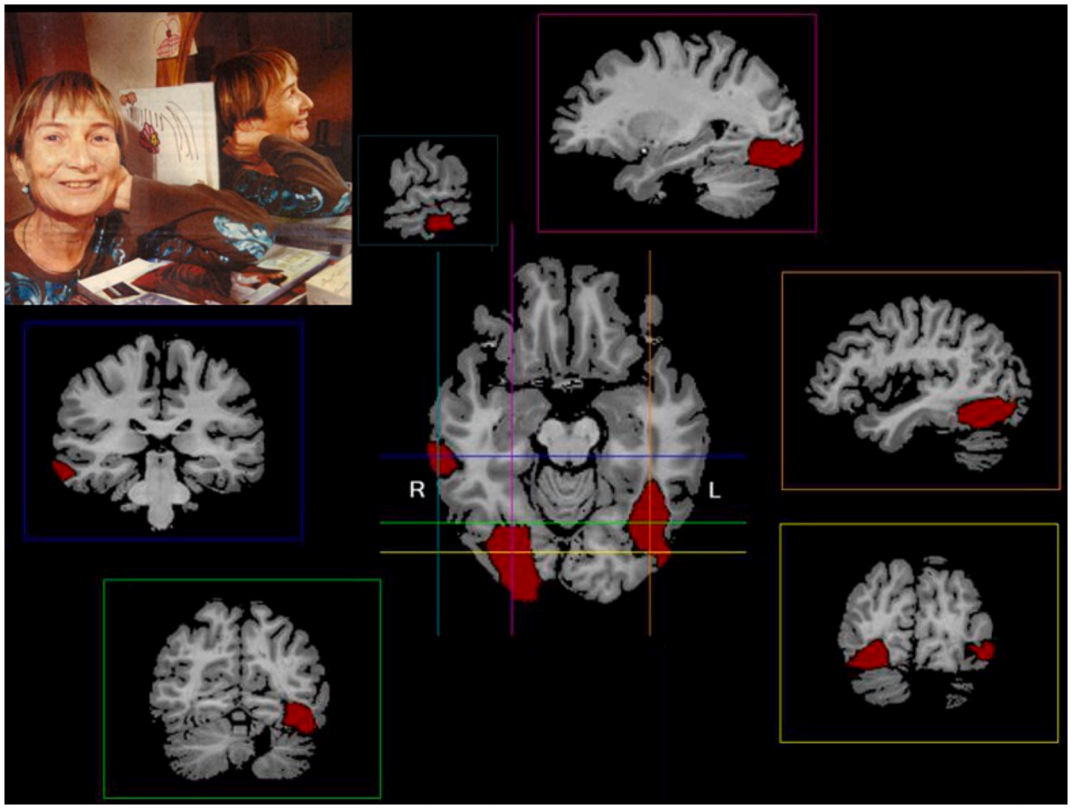


Fig.1. A. Pierrette Sapey, known as the prosopagnosic patient PS in the scientific literature, here photographed at home around 2005.**B.** As illustrated here (from Sorger et al., 2007), PS underwent severe brain damage 1) in the right inferior occipital gyrus and 2) the left middle fusiform gyrus, as well as 3) in the left cerebellum.4) An additional small 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.

[2] In Psychology, the term "recognition" often implies a judgment of previous occurrence (specifically "*the ability to identify information as having been encountered before*", APA Dictionary of Psychology; see also Mandler, 1980). However, the term is used here in keeping with the first review in a general biological sense to refer to *the production of a selective (i.e., discriminant) response to a given sensory input, a response that can be reproduced (i.e., generalized) across variable viewing conditions (i.e., generalized)*.As defined, face *recognition* is essentially the same function as face *categorization* (Rossion and Retter, 2020).

case (Table 1), and divided in 9 sections.

Following this brief introduction (section 1), the context is set by presenting the network of face-selective regions in the human brain as defined in neuroimaging studies (section 2).Next (section 3), PS's brain damage is described in detail, discussing which lesions most likely contributed to her prosopagnosia.It is made clear that these critical lesions concern brain regions that do not exist in a common animal model of human face recognition, the macaque monkey (section 4), a species that is poor at face identity recognition (Rossion and Taubert, 2019) and does not present with prosopagnosia (Heywood and Cowey, 1992).The next two sections set the context of a hierarchical model of face recognition (section 5), and describe in detail the direct and indirect contributions of PS's case to a *non*-hierarchical model and its functional implications (section 6).Section 7 attempts to explain why despite the evidence provided directly and indirectly from PS's case, the strict hierarchical organization of human face recognition persists and still dominates the field.Counterarguments and contradictions to this view are directly addressed.Section 8 summarizes the findings of a lack of sensitivity to differences between facial identities at the neural level in PS's face-selective regions, supporting the relevance of the repetition suppression/fMR-adaptation technique to characterize the neural basis of FIR and the (in)direct role of the right inferior occipital gyrus in this function.At the end of this section, transcranial magnetic stimulation (TMS) studies and case studies of transient prosopagnosia following electrical intracerebral stimulation inspired by the case of PS are described and discussed, providing further evidence for the role of the right IOG/OFA in FIR.An extended summary, conclusions and perspectives are provided in the last section (section 9).

Table 1
List of publications with data on the prosopagnosic patient PS to date (2022), including 32 full papers and three short reports (see bibliography for full references).In bold, papers containing neural data, as summarized and discussed in the present review (part II).

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.(2009a).*Soc.Cogn.Affect.Neurosci.*, 4, 268, 277.
12.Farivar et al.(2009).*Journal of Neuroscience*, 29, 5336–5342.
13. Righart, R.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 (2010a, b).*Cortex,* 46, 965–981.
17.Busigny et al.(2010a, b).*Neuropsychologia,* 48, 2051–2067.
18.Busigny, T.& Rossion (2010a, b).*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.(2011b).*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 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.Ramon, M.et al.(2016).*Visual Cognition*, 24, 1334-1341.
31.Fiset, D.et al.(2017).*Soc Cogn Affect Neurosci.*12, 1334–1341.
32.Burra, N.et al.(2017).*Brain and Cognition*, 113, 115-132.
33.Ramon et al., 2018.*Cognitive Neuropsychology*, 35, 304–313.
34. Gao, X.et al.(2019).*Cortex,* 119, 528–542.
35.Fysh, M.C., & Ramon, M.(2022).*Neuropsychologia,*165, 108119.

2. The context: an extensive cortical face network

What have we learned about the neural basis of human face recognition from studies of PS's prosopagnosia? How did her case study directly inspire and constrain neurofunctional models of human face recognition? And how did her case study also *indirectly*, i.e., through neural studies performed on normal participants and other clinical cases, contribute to improving our knowledge at this level? These questions have been already partly addressed in a previous review concerning the combined contribution of prosopagnosia and neuroimaging to the neural basis of human face recognition (Rossion, 2014). Since then, there have been only a handful of reports on additional neuroimaging studies of PS, even though she has also been tested in recent years for about 30 h of fMRI experiments spanning over 2 weeks at Stanford University by Kalanit Grill-Spector, Kevin Weiner and their colleagues, generating plenty of original data that will enrich the picture presented in the present review in the future.However, many neural studies performed on normal participants and other clinical cases inspired by, and related to, the case of PS have been reported in the last few years, enriching the contribution of her case study to our understanding of the neural basis of human face recognition.Moreover, I think that it is important to integrate investigations and observations of PS's brain in the context of our *current* knowledge regarding the neural basis of human face recognition, which I will try to do in the present review paper.

PS's dramatic accident occurred in 1992, the same year in which, coincidentally, the first report of a neuroimaging study of face recognition – at the time with positron emission tomography (PET) - appeared in the literature (Sergent et al., 1992).Over the following 30 years, until now, hundreds of neuroimaging studies in neurotypical individuals, mainly with fMRI, have been reported, highlighting the neural basis of human face recognition.Collectively, these studies have disclosed clusters of voxels of a few cubic millimeters with larger neural activation to pictures of faces than nonface visual stimuli in the human brain (e.g., Puce et al., 1995; Kanwisher et al., 1997; McCarthy et al., 1997; Halgren et al., 1999; Gauthier et al., 2000; Weiner and Grill-Spector, 2010; Rossion et al., 2012; Zhen et al., 2015; Gao et al., 2018; Schwarz et al., 2019; Gao et al., 2022).Despite a substantial amount of variability in the paradigms and stimuli used across fMRI studies (Duncan et al., 2009; Berman et al., 2010), these "face-selective" clusters have been reported in consistent gross anatomical structures across studies, mainly in both the Ventral Occipito-Temporal Cortex (VOTC) and the Superior Temporal Sulcus (STS) (Fig.2).

The different fMRI-defined face-selective clusters of the human occipito-temporal cortex have been labelled according to the anatomical region where they are usually disclosed.For instance, the most well-known is the "Fusiform Face Area" ("FFA", labelled by Kanwisher et al., 1997), a face-selective cluster (or series of clusters, Fig.2; see also Weiner and Grill-Spector, 2010; Rossion et al., 2012; Gao et al., 2022) identified in the middle section of the anterior-posterior axis of the lateral fusiform gyrus (LatMidFG).In the same vein, the "Occipital Face Area" ("OFA", labelled by Gauthier et al., 2000), is typically identified in the lateral section of the inferior occipital gyrus (IOG).Following this logic, up to 6 face-selective clusters, namely 4 in the VOTC [OFA, pFFA (posterior FFA, also called pFus-faces), mFFA (middle FFA, also called mFus-faces), ATL-FA (Anterior Temporal Lobe Face Area)] and 2 in the STS [pSTS-FA, aSTS-FA; posterior and anterior STS Face Area, respectively], have been defined in the most recent neurofunctional model of human face recognition (Duchaine and Yovel, 2015; for earlier models see Haxby et al., 2000; Calder and Young, 2005; Ishai, 2008; Rossion, 2008; Haxby and Gobbini, 2011).These face-selective clusters of voxels are thought to contain populations of (millions of) neurons (Logothetis, 2008) which, by definition, must play a key role in the recognition of a visual stimulus as a face.

Beyond this generic face recognition function, many fMRI studies have tested the sensitivity of these face-selective clusters – in particular

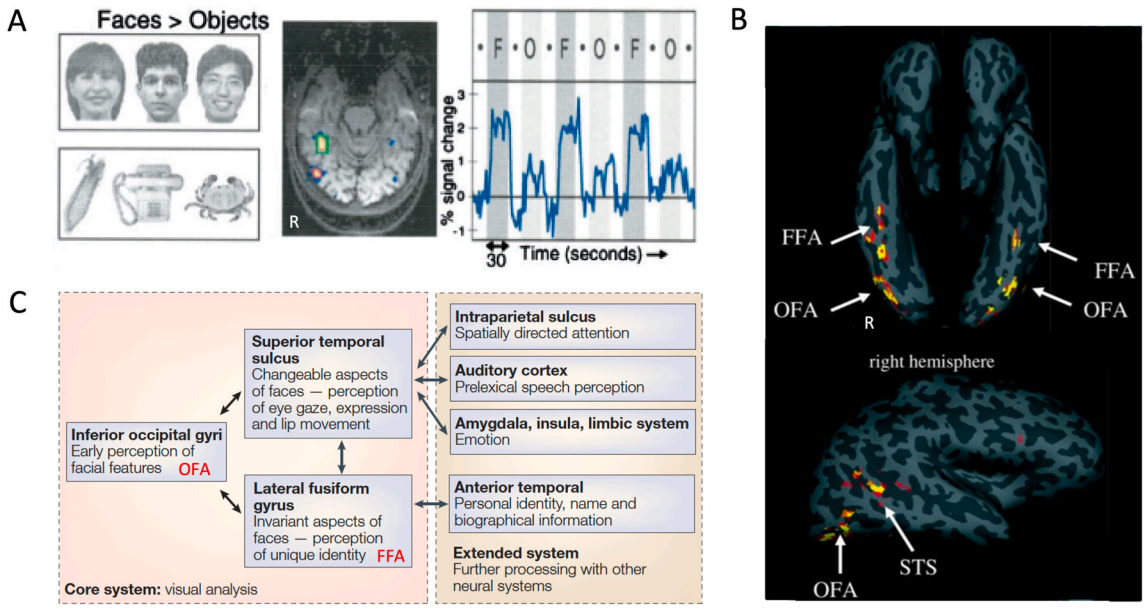


Fig.2. **A**.Following the seminal study of Kanwisher et al.(1997), face-selective regions are typically defined using a 'face localizer approach" in which neuroimaging activity that is significantly larger to pictures of faces (F) than nonface objects (usually presented in blocks) is isolated.Kanwisher et al.(1997) defined the largest significant cluster in the lateral portion of the middle fusiform gyrus (LatMidFG), with a right hemispheric advantage, as the fusiform face area (FFA).Face-selective activity is also found more posteriorly in the inferior occipital gyrus ('Occipital face area', OFA) as shown in A and also in **B** on an inflated surface of an individual brain (adapted from Kanwisher and Yovel, 2006) as well as in the posterior section of the superior temporal sulcus (STS).As illustrated in panel **B**, these regions are often constituted of several face-selective clusters and could well be referred to as e.g., "FFA-complex" or "MidFus-faces-complex" (see Gao et al., 2022).**C.**Haxby et al.(2000)'s neurofunctional model of human face recognition includes these three regions in a core system for visual analysis of faces, with the OFA as the hypothetical gateway of the face recognition system.The core system is thought to be connected with anterior regions of the parietal and temporal lobes to perform general functions triggered by face stimuli.

the FFA - to physical stimulus manipulations (e.g., position, size, head orientation and various image statistics; see e.g., Tong et al., 2000; Levy et al., 2001; Yue et al., 2011; Rice et al., 2014; Finzi et al., 2021), to attention (e.g., O'Craven et al., 1999; Peelen et al., 2009b) and conscious perception (e.g., Tong et al., 1998; Andrews et al., 2002; Fang and He, 2005), and investigated their putative role in finer-grained facial recognition functions (e.g., face familiarity and identity, facial expression, eye gaze direction, etc.; for reviews see Haxby and Gobbini, 2011; Rossion, 2014; Duchaine and Yovel, 2015; Grill-Spector et al., 2017).Another important line of research focuses on the origin and developmental trajectory of these fMRI face-selective clusters (Golarai et al., 2007, Golarai et al., 2017; Scherf et al., 2011; Nordt et al., 2021).

In these studies, the face-selective cortical clusters are usually considered as discrete components, conceptualized as information processing stages, of a well-defined neuro-functional network in the human brain, with a definite pattern of anatomo-functional connectivity (Fairhall and Ishai, 2007; Gschwind et al., 2012; Pyles et al., 2013; Weiner et al., 2017; Elbich et al., 2019; Wang et al., 2020; Kesssler et al., 2021).Comparative studies have also attempted to relate these face-selective neural clusters one-by-one across different species of the primate order (macaques and humans: Tsao et al., 2008; Rajimehr et al., 2009; Yovel and Freiwald, 2013; marmosets to macaques and humans: Hung et al., 2015; see Weiner and Grill-Spector, 2015).

Overall, the ultimate objectives of this research program on face-selective regions are to (1) define each component of the human cortical face network, (2) determine its anatomical features and intrinsic/extrinsic anatomico-functional connections and (3) understand the nature of its local representations and processes (Grill-Spector et al., 2017; see also Freiwald, 2020 and Hesse and Tsao, 2020 in non-human primates).For instance, in humans, fMRI studies have associated face-selective regions of the human STS with dynamic aspects of face recognition (e.g., facial expression, eye gaze and head orientation) while those in the VOTC are linked to more stable aspects of face recognition (e.g., identity, gender, etc.) (Allison et al., 2000; Haxby et al., 2000; O'Toole et al., 2002; Duchaine and Yovel, 2015; Bernstein and Yovel, 2015; Pitcher and Ungerleider, 2021).In both the STS and VOTC pathways, the prevalent view is that of a progressive evolution in the degree of view-invariance and complexity of facial representation from posterior to anterior face-selective regions.Most importantly, the human face recognition system is thought to be largely hierarchical, i.e., with a relatively anterior area being a higher-order stage of processing/-representation built upon (combinatorial activity, e.g., pooling in) a lower-order stage in a more posterior area (e.g., Duchaine and Yovel, 2015; Meyers et al., 2015; Weiner et al., 2017; Tsantani et al., 2021; see also DiCarlo et al., 2007).

Does the case of prosopagnosia PS directly and indirectly inform this research program, and if so, how?

3. A unique pattern of brain damage

In the James Bond movie *Spectre*, Bond's nemesis is torturing our hero using a head clamp fused with a robotic drill.Intending to erase Bond's memory of faces by making him prosopagnosic, the villain says he is directing his drill to the fusiform gyrus.However, the drill should have been aimed just in front of 007's ear, and not below the mastoid process under and behind the ear (Cusimano, 2015).Moreover, the drill targeted the *left* hemisphere, which is known to play a secondary role in FIR compared to the right hemisphere (Sergent, 1988; Rossion, 2014; Rossion and Lochy, 2022).While this failure in neuroanatomy may have saved Bond's FIR ability, PS was not so lucky following her dramatic brain injury, causing lesions that unfortunately overlap substantially with the neural circuits that are critical for FIR (Fig.3).

Yet, PS's pattern of brain lesions, as shown on Fig.1 and described in detail in the neurofunctional mapping of her brain (Sorger et al., 2007), is atypical, in fact truly unique, even considering the variability in the localization of brain damage causing severe long-lasting FIR impairment (e.g., Sergent and Signoret, 1992; Bouvier and Engel, 2006; Barton, 2008; Cohen et al., 2019, Fig.3).

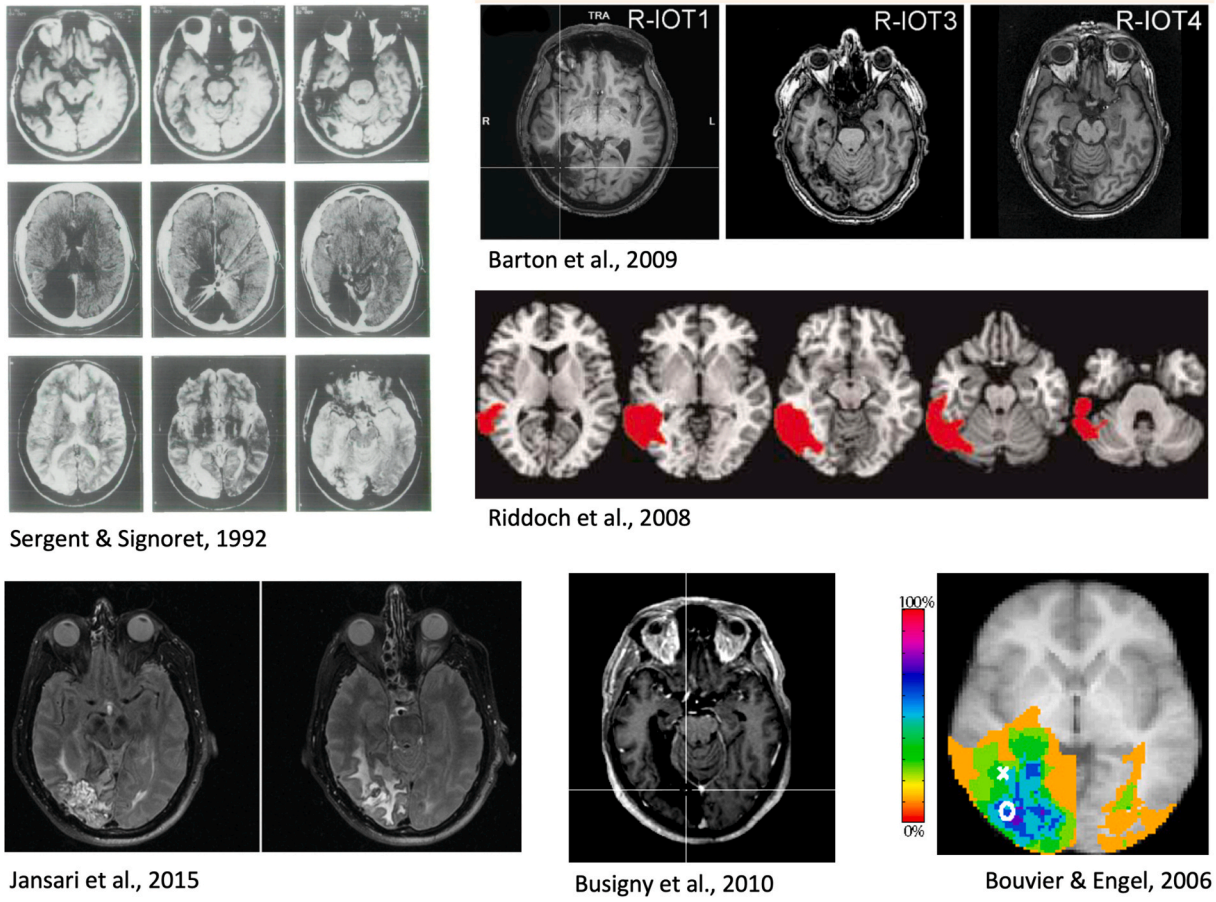


Fig.3. Lesion localization in a number of reported cases of prosopagnosia (with the right hemisphere on the left, i.e., radiological display convention), with permission.While most reported cases of prosopagnosia suffer from bilateral brain damage, patients with right unilateral lesions have also been reported (e.g., Sergent and Signoret, 1992; Busigny et al., 2010; Riddoch et al., 2008; Jansari et al., 2015) (with only few reports of left unilateral lesions in the LH, in left handed individuals; see Rossion and Lochy, 2022).When unilateral, the lesion usually encompasses the right inferior occipital gyrus and middle fusiform gyrus, as illustrated here in a number of reported cases from various sources.The schematic representation at the bottom right shows the percentage of overlap of lesions in a series of reported cases of prosopagnosia, with the mark 'O' for the location of the right OFA (as in Rossion et al., 2003), and 'x' for the location of the FFA (in Kanwisher et al., 1997).While PS's right IOG lesion overlaps with typical common lesions causing long-lasting FIR impairment, her global pattern of brain damage with 4 focal lesions as shown in Fig.1 (3 in red + the cerebellum) is clearly atypical.(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

In general, a unique pattern of brain damage is more likely to happen in neuropsychological patients who sustain a closed-head injury rather than a neurodegenerative disorder, or even a stroke of the (right) posterior artery, the most common aetiology for reported cases of prosopagnosia in the literature.(Busigny et al., 2013) In most of these patients, the FIR impairment follows right unilateral or bilateral brain damage, which usually concerns either a continuous, extensive region of the brain, or partly similar lesions across the two hemispheres, respectively (e.g., Meadows, 1974; Damasio et al., 1982; Sergent and Signoret, 1992; Bouvier and Engel, 2006; Barton, 2008; Barton et al., 2009; Riddoch et al., 2008; Cohen et al., 2019, Fig.3).In contrast, PS has four clear, spatially distinct, focal lesions that concern the left cerebellum, the right inferior occipital gyrus, the left posterior fusiform gyrus, and a smaller lesion in the right middle temporal gyrus (Fig.1).Thus, PS's brain lesions are bilateral, but largely asymmetric.

Even though the contribution of the cerebellum in cognitive functions beyond motor coordination is now widely accepted (Buckner, 2013; Schmahmann et al., 2019), there is no reason to think from any other sources of evidence that the FIR impairment of PS is related to damage at this level.[3]

For a long time, I was convinced that the right IOG lesion in PS's brain was key, perhaps even sufficient to account for her prosopagnosia (Rossion, 2014).My reasoning was based on many reasons.First, it is the largest lesion in PS's brain (Sorger et al., 2007).Second, there is long-standing and overwhelming evidence that the right hemisphere (RH) is dominant in human face recognition, especially human FIR (Hecaen and Angelergues, 1962; Sergent, 1988a; Grüsser and Landis, 1991; Rossion and Lochy, 2022).Moreover, in line with early proposals (Hecaen and Angelergues, 1962; Meadows, 1974), in right-handed people at least, a RH lesion can be sufficient to fully or partially impair FIR (Landis et al., 1986; De Renzi et al., 1991; Sergent and Signoret, 1992; Barton, 2008; Busigny et al., 2010b; see also Benton and

[3] PS does not experience motor coordination problems but she went through a motor rehabilitation program for several weeks after her accident in 1992, in which she had for instance to walk along a straight line.Interestingly, she claims that since her accident she tends to "deviate" from walking straight when she is tired for instance (and PS never drinks alcohol!).

Van Allen, 1972; Tranel et al., 2009).Third, PS's right IOG lesion encompasses a brain region that is often damaged in reported cases of prosopagnosia (Fig.3), and falls right at the location of the largest overlap of lesions in a series of reported cases of prosopagnosia (Bouvier and Engel, 2006, Fig.3).Fourth, PS's right IOG lesion corresponds well with face-selective activity in the IOG in typical individual brains (i.e., compare Figs.1 and 2 and section 5 below), and there is no evidence of face-selective activity in the remaining cortical tissue of the right IOG in PS's brain.Fifth, application of transcranial magnetic stimulation (TMS) over the right IOG in typical individuals (in studies that were directly inspired by PS's case, as described below) decreases FIR performance (Pitcher, 2021, for review).Sixth, the right IOG lesion is also responsible for a left paracentral scotoma, characteristic of a substantial proportion of reported cases of prosopagnosia (Hécaen & Angelergues, 1962; Bouvier and Engel, 2006).Finally, focal intracerebral electrical stimulation of the right IOG only can be sufficient to cause transient prosopagnosia (Jonas et al., 2012).

However, despite these apparently compelling reasons, I must admit that I am no longer convinced that the right IOG lesion is sufficient to account for PS's prosopagnosia.Instead, I now consider that the extensive damage of the left middle FG lesion must also have contributed significantly.My change of view is not based on the apparent prevalence of bilateral lesions in reported cases of prosopagnosia (Meadows, 1974; Damasio et al., 1982) or the claim that the FIR impairment is more severe in cases with bilateral as compared to unilateral lesions (Barton, 2008).Indeed, as mentioned above, there are many reported cases of prosopagnosia with right unilateral brain damage (Grüsser and Landis, 1991; Bouvier and Engel, 2006; Cohen et al., 2019).Moreover, Barton (2008)'s claim, despite being in line with the general pattern of more severe deficits for bilateral than unilateral hemispheric damage across many different sensory, motor, and memory domains (Schapiro et al., 2013), was not based on significant evidence; and an obvious confound in this reasoning is the volume of brain damage, which is usually larger in patients with bilateral than unilateral lesions.[4] Instead, I have been recently impressed with the fact that the left VOTC lesion of PS concerns almost only the *lateral* rather than the medial portion of the fusiform gyrus, where face-selectivity is typically found (i.e., cytoarchitectonic areas FG2 and FG4; Weiner and Grill-Spector, 2010; Weiner et al., 2017).Moreover, when using a recently developed valid and highly sensitive face localizer this left VOTC lesion overlaps more with the highest face-selective activity found in this hemisphere in neurotypical individuals than the right hemisphere IOG lesion (Gao et al., 2019) .

In addition, in recent years, my colleagues and I have identified two cases in which extensive cortical resection (in a clinical context) of the right IOG alone did not lead to prosopagnosia.The first patient, SP, had FIR difficulties pre-surgery, albeit not as severe as in prosopagnosia. Thus, it could be argued that her cortical face network was not working efficiently prior to right IOG resection (Weiner et al., 2016).However, most recently, KV, the same patient who showed transient prosopagnosia during focal intracerebral electrical stimulation of the right IOG but otherwise excelled at FIR (Jonas et al., 2012, 2014), showed only mild impairment at FIR following cortical resection of the right IOG, with no long-term complain of difficulties in real life circumstances (Yan et al., in preparation).These latter observations – which will be discussed in depth below – do not only question the claim that direct electrical stimulation constitutes the gold standard to detect the functionality of local brain regions (see Borchers et al., 2012; Jonas and Rossion, 2021), but suggest that PS might not have become prosopagnosic if her cortical lesion had been restricted to the right IOG.

Finally, a putative contribution of the third, much smaller, cortical lesion in the right temporal lobe of PS's brain cannot be fully excluded, even though it is unlikely.While Pitcher et al.(2011) were correct to mention that it is important to interpret PS's FIR impairment in with respect to all her lesions and not solely with regard to the damage to her right IOG, these authors' reference to cortical damage restricted to the right anterior temporal lobe as causing "*severe face perception impairments (Evans et al., 1995;Barton, 2008)*" in the context of PS's third cortical lesion was misleading.Indeed, impairments at FIR have been found following damage to the *ventral* anterior temporal lobe (VATL), a region where face-selectivity has also been identified in some fMRI studies (Rajimehr et al., 2009; Nasr and Tootell, 2012; Avidan et al., 2014; J.A Collins et al., 2016) but which is entirely structurally intact in PS's brain.Instead, PS's third cortical lesion concerns the (right) *middle temporal* gyrus (Fig.1; see Sorger et al., 2007).While the anterior section of the right middle temporal gyrus has been recently correlated with difficulties in face familiarity judgements across a variety of neurodegenerative disorders (Borghesani et al., 2019), this region does not usually light up in neuroimaging studies of face recognition.For this reason, it is not included in neuro-functional models of this function. Moreover, face-selective potentials recorded in this region (e.g., N200; Allison et al., 1994, 1999) could well be generated in deeper structures such as the occipito-temporal sulcus (OTS), diffusing laterally towards the lateral temporal cortex (see the schematic Fig.8 in Bentin et al., 1996).

Finally, I have described PS's lesions in terms of cortical (or cerebellum) structures, but they must also involve the white matter deep in these gyri, comprising incoming and outgoing fibers to this cortex (including fibers descending from the posterior part of corpus callosum) and the inferior longitudinal fasciculus (ILF; Catani et al., 2003).Since the lower part of the optic radiation fuses and is intermingled with the ILF, which is the main pathway from the extrastriate cortex into the temporal lobe (Zemmoura et al., 2021), a lesion of the lower part of the right optic radiation in the occipitotemporal region (accounting for PS's left upper quadrantanopia as described in Sorger et al., 2007; see review part I) will thus almost certainly involve the ILF and is also likely in addition to interrupt callosal connections between the ventral occipitotemporal cortex of the two hemispheres (Meadows, 1974; Fox et al., 2008; Grossi et al., 2014).Damage to these white matter tracts certainly plays a key role in PS's prosopagnosia (i.e., preventing sensory inputs to match cortical memories of faces in the IOG and fusiform gyrus, as described in the review part I) (see Herbet et al., 2018 for the critical role of the ILF in visual cognition).

4. Human specificity of the ventral cortical face network

It is important to stress that PS's critical brain damage for FIR impairment concerns hominoid-specific VOTC structures.In particular, these structures do not exist in the macaque monkey (Fig.4), an animal species often considered as offering the best available animal model of the human brain in the neuroscientific community (Passingham, 2009). Despite serving as a model of the neural basis of human face recognition for decades (Gross et al., 1972; Perrett et al., 1982; Freiwald, 2020; Hesse and Tsao, 2020), it is worth reminding that a macaque monkey brain is not only much smaller than a human brain (by a factor of 13–15 in size and in number of neurons; Herculano-Houzel, 2016), but that there are considerable differences between the two species in gyrification (Zilles et al., 2013), including in the temporal lobe (Bryant and Preuss, 2018, Fig.4).

In humans, the VOTC is divided by two major sulci: the collateral sulcus (CS) more medially, and the occipito-temporal sulcus (OTS) more laterally, these two sulci defining the borders of the fusiform gyrus,

[4] Even though the RH is clearly dominant for human face recognition in most individuals, there is no consistent evidence that the LH performs qualitatively different, i.e., complementary processing operations (Rossion and Lochy, 2022), which would provide a basis for the claim that bilateral lesions provide more severe deficits even if damaged cortical volume is matched.The two hemispheres may contribute additively to human face recognition, so that a bilateral lesion of the cortical face network could have, on average, the same consequences as a right unilateral damage if the amount of cortical volume is comparable.

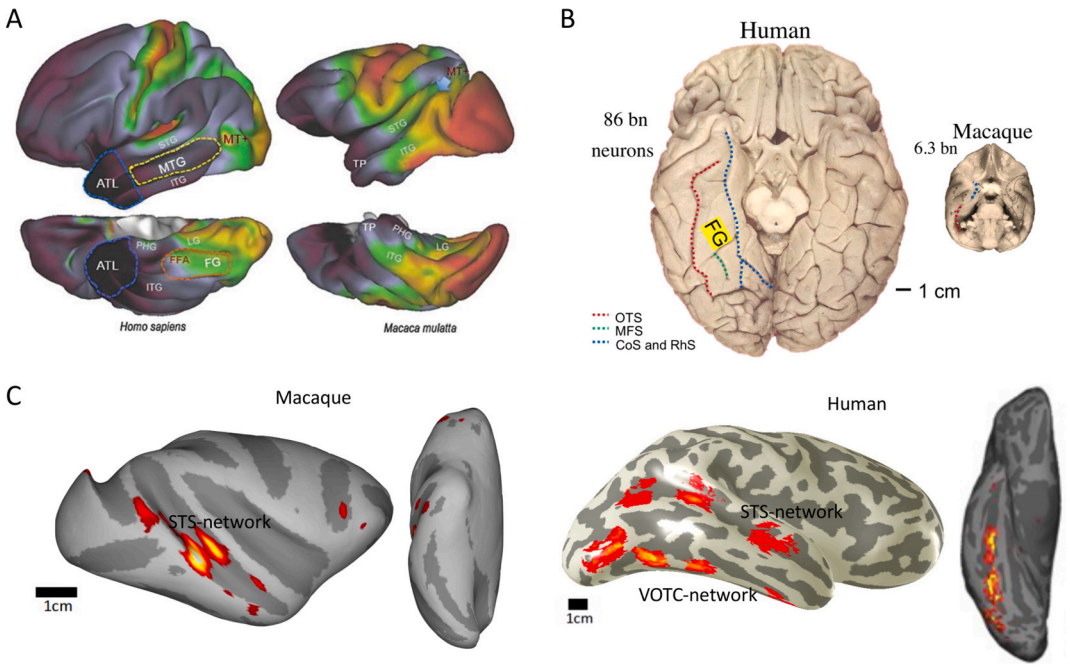


Fig.4. The 'core' ventral cortical face network is uniquely human.A.Comparison of a lateral and ventral views of a human and a macaque brain (adapted from Bryant and Preuss, 2018, with permission).Brains are not to scale.Colors indicates the density level of myelin from red for high to blue for low.Compared to humans, the ventral-occipito-temporal cortex of macaque monkeys is relatively much smaller and does not have a fusiform gyrus (FG; ATL: anterior temporal lobe, FFA: fusiform face area, ITG: inferior temporal gyrus, LG: lingual gyrus, MT+: visual motion area MT complex, MTG: middle temporal gyrus, PHG: parahippocampal gyrus, STG: superior temporal gyrus, TP: temporal pole).**B**.Ventral views at relative sizes showing the absence in macaque monkeys of key VOTC cortical structures for face recognition in humans, in particular the fusiform gyrus (FG) defined by the occipito-temporal sulcus (OTS) and the collateral sulcus (CoS) (RhS: rhinal sulcus; MFS, midfusiform sulcus) (see Weiner and Zilles, 2016; also Miller et al., 2020).The average number of neurons in the two species (in billion, bn; from Herculano-Houzel, 2016) is indicated on top.**C**.Inflated lateral and ventral surfaces of a macaque and a human brain showing face-selective regions.While these regions are found essentially in the STS of the macaque brain, they are found both the STS and VOTC in humans.Potential homology of these face-selective regions across species is largely unknown, but Heywood and Cowey (1992) showed that recognition of gaze direction rather than of face identity was disrupted following bilateral ablation of the monkey STS.This supports the view that these STS face-selective regions in the monkey brain are involved, as in humans, in recognizing dynamic aspects of faces, such as eye gaze direction, head orientation and facial expression (Perrett et al., 1985; Allison et al., 2000; O'Toole et al., 2002; Bernstein and Yovel, 2015; Taubert et al., 2020) rather than in FIR.(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

arguably the most important cortical structure for human face (identity) recognition.In contrast, macaque monkeys possess only one main ventral sulcus, labelled as the OTS, therefore lacking a fusiform gyrus (among other substantial neuroanatomical differences with the human VOTC) (Bryant and Preuss, 2018; Weiner and Gomez, 2021) (Fig.4A and B).Given their lack of the hominoid fusiform structure, it is not surprising that macaque monkeys do not possess a ventral cortical face network.Rather, their face-selective regions are found more dorsally, mainly in the STS, where face-selective-neurons have been recorded in this species since the earliest studies of Charlie Gross and colleagues (1972; see also e.g., Perrett et al., 1982; Rolls, 1992; Leopold et al., 2006; Tsao et al., 2006; Taubert et al., 2015).

The lack of a ventral cortical face network in macaques (and other monkeys[5]) is compatible with their poor ability to recognize conspecifics' identities based on faces only, and with the absence of markers of human FIR expertise in monkeys (e.g., lack of the face inversion effect, familiarity effect in matching tasks; see Rossion and Taubert, 2019; see also the review of PS, part I).In line with these observations, bilateral ablation of the entire STS in macaque monkeys has no or little effect on their learned ability to recognize the identity of conspecifics' faces (Heywood and Cowey, 1992).That is, there is no prosopagnosia model in monkeys and non-human primates (or other non-human animal species so far; see part I of this review).

Note that despite these clear anatomico-functional differences, it has been claimed that the monkey brain holds the same number of face-selective regions as the human brain (Tsao et al., 2008; Yovel and Freiwald, 2013; Weiner and Grill-Spector, 2015) and that the monkey cortical face network in the STS could be divided into two parts: (1) a dorsal part, homologous to the face-selective STS network in humans, and (2) a ventral part, which would correspond to the human face-selective VOTC network (Tsao et al., 2008; Yovel and Freiwald, 2013; Weiner and Grill-Spector, 2015; Freiwald et al., 2016; Conway, 2018, Fig.4C).According to this view, the putative ventral part of the monkey STS system would have been "pushed" onto the ventral cortical surface over the course of human evolution by the expansion of regions engaged in language and social cognition, in particular the temporal parietal junction (see also Lafer-Sousa et al., 2016).In my view, this hypothesis of a one-to-one homology of regions across the two species and of a ventral displacement of lower STS clusters through human evolution is not only far-fetched, but is also contradicted both by considerable anatomico-functional and behavioral evidence (Rossion and Taubert, 2019; Rossion, 2022b), falling flat in comparison to the wealth of converging evidence supporting the view that the face-selective VOTC network is indeed specific to the human (or hominoid) lineage.

The human specificity of the critical ventral cortical face network, and of prosopagnosia, considerably strengthens the interest of investigating the neural basis of face (identity) recognition in human patients such as PS who cannot - selectively- recognize facial identities.

[5] Since the rhesus monkey is by far the most widely used species in neurophysiological studies, rhesus monkeys and other macaques are often referred to as simply 'monkeys' in the common parlance of neuroscientists (Preuss, 2000).

5. A spared right MidFus/FFA

Back in 2000, when I met PS for the first time, I was shown only a crude MRI scan of her brain but I remember being puzzled that the cortical lesions apparently spared the middle section of the right fusiform gyrus.Today, this does not appear so surprising, as there are many reported cases of prosopagnosia whose lesion do not intersect with this region (Cohen et al., 2019).However, back in 2000, there was considerable emphasis on the right FFA, defined by Kanwisher et al.(1997) as the brain's center, a "module" in a Fodorian sense, for human face recognition (see also Kanwisher, 2017).Although the view of a cortical face network rather than a single localized module has been emphasized at the outset in neuroimaging studies (Sergent et al., 1992) and always remained influential (Tovee, 1998; Haxby et al., 2000; Ishai, 2008; see Weiner and Grill-Spector, 2013 for a historical perspective), the general consensus in the field at the beginning of the new millennium was that the right FFA was the most important region for human face recognition, in particular because it showed the largest and most consistent face-selective fMRI activity.This view is still very much dominant today in the field of human face recognition and beyond.

This is why when we finally managed to test PS in a fMRI face localizer experiment in Geneva, early 2001, my colleague Roberto Caldara and I were initially stunned to find face-selective activity in her anatomically intact right middle fusiform gyrus, i.e., a right FFA (Fig.5A).Yet, there was no doubt about it: we had used a classical face localizer experiment, repeated twice, and PS's level of face-selective activity was not at all below normal range in this region (Fig.5B). Importantly, the localization of the face-selective cluster in the middle fusiform gyrus was spatially undistinguishable from other – neurotypical age and sex-matched – participants (Fig.5C).

6. The non-hierarchical neurofunctional organization of human face recognition

I remember Roberto Caldara being greatly puzzled by the finding of a right FFA activation in PS's brain: he had seen it first hand and brought me the news in April 2002 at the Annual Meeting of the Cognitive Neuroscience Society in San Francisco.He did not like it very much: what if people question that PS is a real case of prosopagnosia then? How is it possible that PS cannot recognize facial identities and yet had an apparently perfectly normal right FFA? How were we going to explain this apparent paradox? I was not too bothered with respect to PS's prosopagnosia because we already had solid behavioral data to support it.Moreover, I had been involved in neuroimaging studies on human face recognition for many years with PET (Dubois et al., 1999; Rossion et al., 2000, 2001) so that the implications of this finding struck me almost immediately: a critical component of Haxby et al.,'s 2000 neurofunctional model of face recognition, namely the proposed *hierarchy* between the IOG/OFA and the Middle Fusiform/FFA (Fig.1) was probably incorrect and should be revised.Indeed, since the IOG/OFA had been defined as the gateway of the face recognition system, a simple prediction of this hierarchical model is that a complete destruction of the

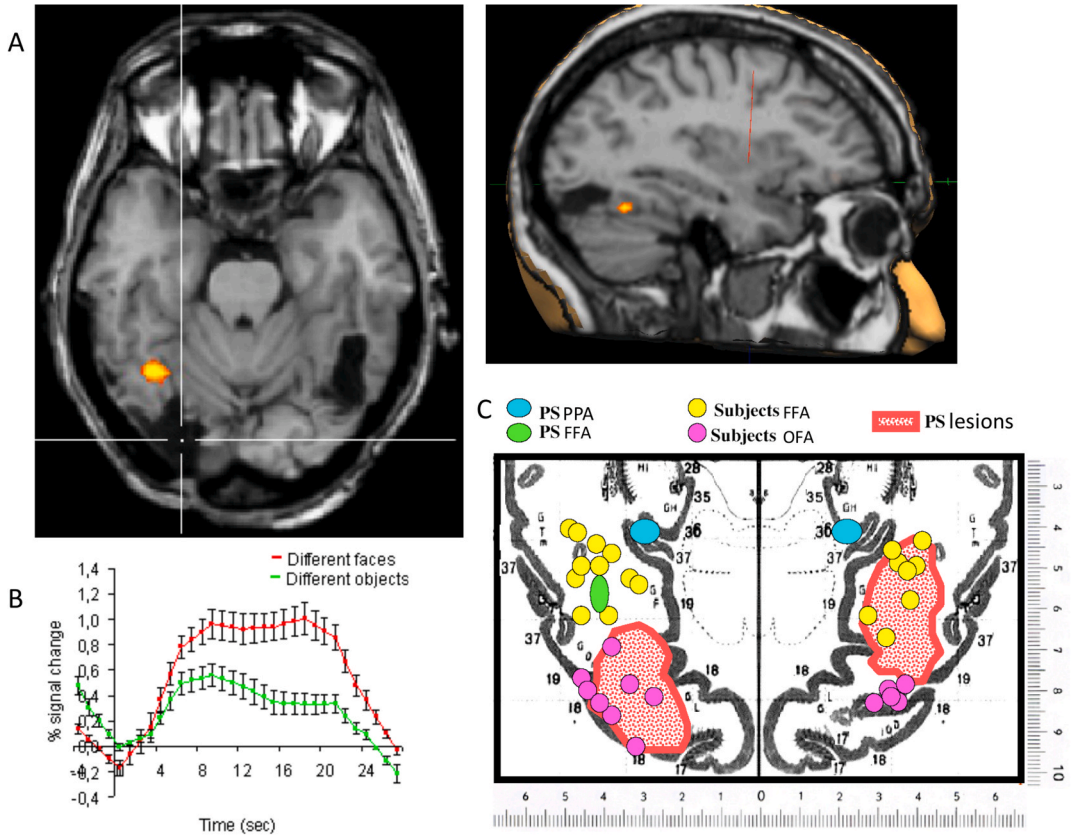


Fig.5. A.The case of PS provided the first evidence that face-selective activity can be elicited in fMRI in the right lateral middle fusiform gyrus (i.e., right FFA) despite brain damage to the right IOG and absent OFA in this hemisphere (Rossion et al., 2003).The transverse and coronal slices illustrate how this finding questions the hierarchical organization proposed in Haxby et al.(2000)'s neurofunctional model as illustrated in Fig.2: in her case, the absent right IOG/OFA cannot be the obligatory gateway of the face recognition system.This finding has been replicated in 10 published fMRI studies **B**.Blood oxygen level-dependent (BOLD) % signal change relative to a fixation cross baseline in the right FFA of PS for pictures of objects and faces (18 s block; from Schiltz et al., 2006).**C**.Schematic drawing on a transverse view of the Talairach atlas of PS's lesions, the localization of her right FFA among normal controls' face-selective responses in the IOG (OFA) and middle fusiform gyrus (FFA) (PPA, parahippocampal place area).Note that PS's lesions encompass most of the face-selective clusters found in neurotypical individual brains in the right IOG (i.e., right OFA) and left middle fusiform gyrus (i.e., left FFA).

IOG/OFA should prevent any face-selective activity in the downstream FFA (as well as the pSTS and any downstream area in the model). However, PS's neuroimaging findings clearly showed a right FFA despite ipsilateral IOG damage (Fig.5).Moreover, there was no evidence of face-selectivity posterior to the FFA, even at a lower statistical threshold (Rossion et al., 2003).Therefore, these findings really appeared to question a key aspect of Haxby et al.(2000)'s neurofunctional model of human face recognition (Fig.2).This is wherein lies the power of a single case study: you cannot really build a theory based on a single-case data without collecting a substantial amount of additional various supporting evidence in a coherent framework; yet, providing that a single observation is reliable, it can question a theory immediately.This line of reasoning has been applied at the cognitive level (Shallice, 1979; Caramazza and McCloskey, 1988), and it could also be applied here at the neural level.

The finding of a FFA in PS's brain thus suggested for the first time that the human cortical face network was not strictly hierarchical, i.e., that processes/representations in the IOG/OFA did not have to take place at all to elicit face-selective processes in the anteriorly located FFA. In truth, I had never been convinced by the view of a hierarchical human face recognition system.In particular, the limitations of a strict hierarchical system were obvious: block the (inputs to the) hypothetical gateway (e.g., low-level visual cortex to the IOG-faces/OFA, or the region itself) and the whole system would be deficient.Hence, a strict hierarchical system is not very resilient.Instead, multiple entry ways to the cortical face system from low-level sensory inputs, together with reentrant connections between face-selective regions could be highly advantageous.Inspired by several proposals of non-hierarchical cortical visual processing available at the time (Finkel and Edelman, 1989; Mumford, 1992; Hupé et al., 1998; Bullier, 2001; see also Hochstein and Ahissar, 2002), this is how the neuroimaging findings of PS were interpreted (Rossion et al., 2003).

This first journal publication on PS appeared in *Brain* in 2003, at a time when the journal was still interested in publishing single cases, before explicitly changing its policy a few years later.Around that time and for the next years, I presented PS's neuroimaging data and the interpretation in terms of a non-hierarchical model at many conferences and international seminars, including at a symposium on face processing at an Experimental Psychology Meeting (EPS) in London in January 2004[6] organized by Rik Henson, with Jim Haxby as guest speaker.To be honest, I am not sure that Haxby himself really cared that much about this issue of hierarchy in his proposed model, and his interest at the time seemed to have had already shifted to the issue of decoding visual category signals with multivariate pattern analysis in fMRI (Haxby et al., 2001).However, as I often found out in peer-reviews and comments at conference presentations, it can be extremely challenging to convince a neuroscientific community with single case data, however solid the data can be, and many questions were often asked: *what if PS had an unusual brain organization? After all this is only a single case.Since the results were obtained about 10 years after her accident, what if the finding of the right FFA without OFA was due to plasticity/reorganization? Maybe the system is truly hierarchical and PS is getting face-selective activity in the right middle fusiform gyrus from the IOG/OFA in left hemisphere? Could this face-selective activity come from face imagery rather than perception?* Etc.

Despite these (legitimate and sometimes not so legitimate) questions, it did not escape my attention that the next version of Haxby's neurofunctional model of human face recognition put together all the putative face-selective regions (OFA, FFA, STS) in a single "box", without any hierarchical relationship (Gobbini and Haxby, 2007).Yet, shortly after that, Ishai (2008) published a review paper on the human cortical face network, which was defined as being functionally organized in a strictly hierarchical, feed-forward architecture.The author's rationale was backed up by her then recent work on dynamic causal modeling (DCM) of fMRI activity in the normal brain, apparently supporting a strict unidirectional influence of the IOG/OFA on face-selective activity in both the fusiform gyrus and STS (Fairhall and Ishai, 2007; but see Kesssler et al., 2021 and discussion below).Notably, our data on PS (already replicated and strengthened at the time by other sources of evidence as described below) was not cited, even though I knew that the author was well aware of it.Since I was invited to write a brief commentary on Ishai's paper, I took this opportunity to remind the author and the scientific community that PS's findings were incompatible with this view, also proposing my own revised schematic model of the 'core' (ventral) neural system for human face recognition (Fig.6; Rossion, 2008).

My idea there was not to propose a fully elaborated model of the neural basis of human face recognition, but to draw attention to an alternative view of the standard hierarchical model, according to which there would be both bypassing and reentrant direct connections between face-selective brain regions, playing key roles in this function.Specifically, according to this schematic model, visual sensory stimuli could trigger face-selective activity in the middle fusiform gyrus (i.e., FFA) *independently* and even perhaps *before* face-selective activity arises in the posteriorly located IOG (i.e., OFA).In line with a coarse-to-fine view of human face recognition (Sergent, 1986) (see Part I of the PS review), I went further and suggested that such direct pathways could serve to initially recognize a stimulus as a face, at a very coarse level ('1.Holistic face detection' in Fig.6).

Then, following reentrant (i.e., dynamic recursive signaling rather than feedback; Edelman, 1978; Edelman and Gally, 2013) interactions with the IOG to extract finer-grained details, a full face-selective holistic representation of an individual might emerge (2.'Individual face percept' in Fig.6), allowing individuation of (familiar or unfamiliar) faces.I conjectured that the whole process could be achieved within 200 ms post-stimulus onset, a sufficient duration to individuate (upright) faces (Jacques et al., 2007; Rossion and Jacques, 2011).Importantly, I never proposed, as in Haxby et al.(2000)'s model or other neurofunctional models (e.g., Pitcher et al., 2011; Duchaine and Yovel, 2015; see also Pitcher, 2021) that the IOG/OFA would hold category-selective representations of facial parts (i.e., a neuron coding only for a mouth, or a nose, or an eye, etc.) independently of a full face.Rather, I hypothesized that neurons located in the IOG might have smaller receptive fields than in the middle fusiform gyrus (a hypothesis recently validated as detailed below; Finzi et al., 2021), allowing a more fine-grained analysis of parts to fill in the holistic representation.

In the following years, I noted that the view of a non-hierarchical human face recognition system started to grow in influence (Atkinson and Adolphs, 2011), and hypothetical direct pathways from the early visual cortex to the middle fusiform gyrus/FFA were incorporated in subsequent neurofunctional models of human face recognition (Pitcher et al., 2011, 2014; Duchaine and Yovel, 2015) (Fig.7).

How did we reach that stage? First, the finding of PS's right FFA in the absence of an ipsilateral IOG/OFA were replicated numerous times with different stimuli, paradigms, scanners, and by different research groups (e.g., Schiltz et al., 2006; Dricot et al., 2008; Peelen et al., 2009a; Righart et al., 2010 ; Simon et al., 2011; Rossion et al., 2011).While the initial findings were made with a 1.5 T scanner (Rossion et al., 2003) subsequent studies were performed at 3 T, but the localization of the right FFA is remarkably stable across studies, and there has been no evidence of changes during about 20 years of scanning (see Gao et al., 2019).Also, these fMRI studies have not found consistent face-selective activity in the right IOG around PS's lesion, a finding which could have been taken in favor of a preserved hierarchical organization after all.Moreover, despite very high sensitivity and many face localizers performed in patient PS, no consistent left IOG (i.e., OFA) response has been found (a small spot of activity in Sorger et al., 2007 and in Steeves et al., 2009 but with inconsistent localization across the two studies and also in comparison with typical localizations; no response in Gao et al., 2019, with a highly sensitive face localizer paradigm removing low-level

[6] https://eps.ac.uk/wp-content/uploads/2017/12/ProgJan2004.pdf.

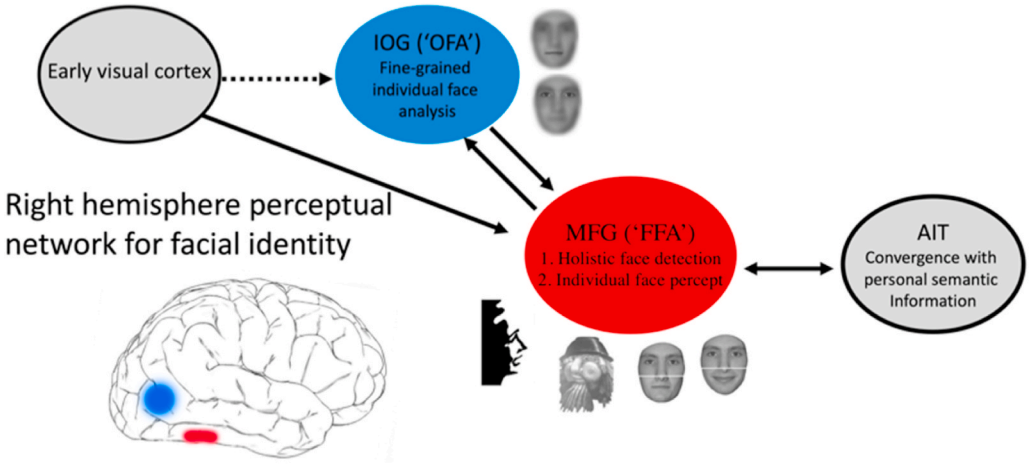


Fig.6. A revised schematic representation of putative connections and functions of face-selective VOTC regions inspired by PS's case of prosopagnosia (Rossion, 2008a).Compared to earlier proposals, the key novel feature is a direct connection from early visual cortex to the middle fusiform gyrus (MFG), bypassing the IOG.This direct connection could account for the initial holistic recognition of a stimulus as a face, i.e., at a coarse level of resolution. Additionally, putative reentrant connections between the MFG and the posteriorly located IOG are suggested in order to refine visual face-selective representations necessary for face identity recognition.Note that, as initially proposed, the IOG/OFA would not hold face-selective representations of parts but potentially neuronal populations with smaller receptive fields to enhance an analysis of fine-grained local details (AIT: anterior infero-temporal cortex).

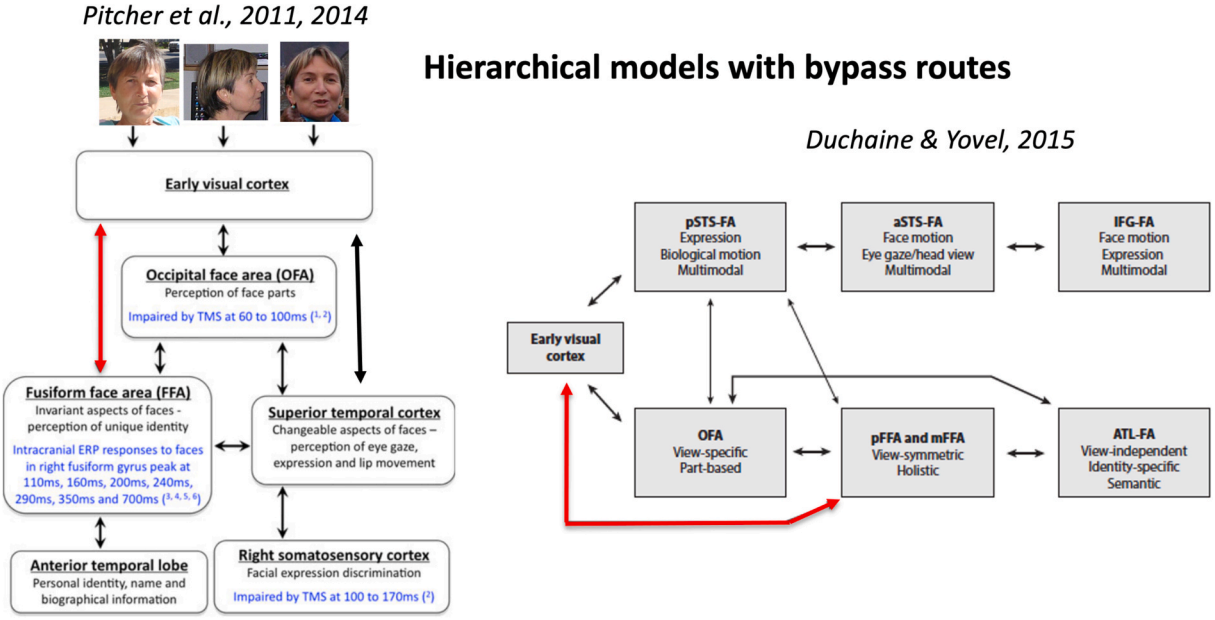


Fig.7. Neurofunctional models of Pitcher et al.(2011; left) and Duchaine and Yovel (2015) adapted from Haxby et al.(2000) and Gobbini and Haxby (2007)'s models, with permission.In these most recent models, direct connections from the early visual cortex to the middle fusiform gyrus (FFA), highlighted in red here, are incorporated, following PS's neuroimaging studies and converging evidence as reviewed here.Note also the hypothetical direct pathway from early visual cortex to the STS in the model on the left, as also initially suggested by PS's neuroimaging studies (i.e., STS face-selective activation without OFA; Sorger et al., 2007; see also Steeves et al., 2006).In Duchaine and Yovel (2015)'s model, connections from the early visual cortex to the pSTS are no longer mediated by the IOG/OFA.(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

visual confounds).Most importantly, a wide range of converging evidence has now been collected in other brain-damaged patients and neurotypical individuals to support a non-hierarchical, or even a *reversed* hierarchical organization (i.e., OFA after and potentially dependent on FFA inputs), of neural human face recognition.These sources of evidence are summarized below.

6.1. DF

The first support for PS's findings of a FFA without OFA came unexpectedly for me in a neuroimaging study led by Jennifer Steeves at York University with the brain-damaged patient DF, one of the most well-known neuropsychological case in the scientific literature.Since the early 1990s, DF has been investigated in detail for her astonishing ability to perform appropriate action towards visual objects that she can no longer explicitly recognize due to severe visual cortex damage sustained at the age of 34 from carbon monoxide poisoning (Milner et al., 1991; see Goodale and Milner, 2013; Whitwell et al., 2014 for reviews).This striking dissociation between vision for recognition and vision for action in DF provided a key piece of evidence for the formulation of Goodale and Milner's influential Two Visual Systems hypothesis, according to which the ventral (occipito-temporal) visual stream plays a critical role in constructing our visual percepts, whereas the dorsal (occipito-parietal) visual stream mediates the visual control of action, such as visually guided grasping (Goodale & Milner, 1992, 2013).

The first functional neuroimaging study of DF was reported at about

the same time as that of PS, showing extensive bilateral lesions in the lateral occipital cortex including the IOG region where the OFA is typically found (James et al., 2003).Despite this, DF was still able to tell apart pictures of faces from other visual objects and, when she was presented with these stimuli in separate stimulation blocks in fMRI, localized face-selective activity was recorded in the middle fusiform gyrus, i.e., a FFA without OFA, in both hemispheres (Steeves et al., 2006, Fig.8A).Most importantly, DF's *bilateral* lesions in the IOG ruled out a putative contralateral contribution of the left hemisphere to the right middle fusiform gyrus to elicit a right FFA (Fig.8A), providing further support for a *non-hierarchical* neurofunctional model of human face recognition.

Needless to say, I was very pleased to see this paper supporting our findings on PS published by an independent research group.Shortly after the paper appeared, Steeves and I met for the first time at a Society for Neuroscience meeting, and we decided to work together to compare DF and PS as tested in the same neuroimaging experiments.We met at Maastricht University, where PS was scanned most of the time, together with DF and her husband, who traveled there from Italy.We replicated the findings of DF's bilateral FFAs in the same localizer experiment as used with PS (Fig.8B) and performed additional experiments as described below (Steeves et al., 2009).

This experience also gave me the opportunity to see DF's behavior in experiments and in real life, realizing how, despite common findings in the face localizer neuroimaging experiment with PS, the two neuropsychological cases were markedly different, both from a functional and neural point of view.While DF has also been described as a case of prosopagnosia following a symptom-based definition (see PS review part I, and Rossion, 2018), her visual recognition impairment is not at all specific to faces: she cannot explicitly recognize visual shapes in general (Goodale and Milner, 2013; Whitwell et al., 2014).Hence, according to the classical definition of prosopagnosia (Bodamer, 1947) adopted in this review, DF should not be defined as a case of prosopagnosia (Rossion, 2018).To be fair, since DF does have severe low-level visual problems that contribute significantly to her visual object recognition impairment, I am not even convinced that her classification of a case of visual object agnosia, even of the 'apperceptive' type (Lissauer, 1890; Farah, 1990/2004), is accurate.However, this is a different issue, which does not change anything – on the contrary - for the interest of DF's case in neuropsychology and the validity of Goodale, Milner and their colleagues' influential Two Visual System view.

6.2. FFA without OFA in the normal brain

Extensive single case studies of brain-damaged patients such as DF and PS are there to both constrain and inspire the organization of human brain function.They constrain standard models or conceptions of certain functions, e.g., for DF with respect to the function of the ventral and dorsal stream as initially proposed by Ungerleider and Mishkin (1982) and the classical views of visual object recognition (Goodale & Milner, 1992, 2013).However, over the years, the two visual stream theory derived from observations in patient DF has also inspired, and been supported, by a broad range of additional evidence extending from monkey neurophysiology to neuroimaging studies of both patients and neurologically intact individuals (Goodale and Milner, 2013; Whitwell et al., 2014).

In the same vein, in the case of PS, our idea was now to show that in certain stimulation conditions, significant face-selectivity can be elicited in neurotypical observers' lateral middle fusiform gyrus (i.e., FFA) without any concomitant face-selective activity in the IOG (i.e., OFA). Therefore, in line with the proposal of an initial recognition of the stimulus as a face based on a holistic/configural representation in the FFA (Rossion, 2008, Fig.6 above), we sought to test how face-selective activity compares in the two pre-defined regions for stimuli that are recognized as faces based solely on their global configuration (i.e., stimuli with parts that are not recognized as facelike when presented in isolation; see Rossion, 2014 and part I of the present review).To do so, we presented pictures of the famous Arcimboldo paintings (Hulten, 1987) and so-called 'Mooney' face stimuli (Mooney, 1956), which are typically recognized as faces at upright but not at inverted orientation, both to PS and to a group of neurotypical individuals (Rossion et al., 2011).

In an explicit generic face recognition task, as described in part 1 of PS's review, the patient behaved exactly like normal observers, i.e., recognizing the upright stimuli but not the inverted stimuli as faces, therefore directly contradicting the widely held assumption that *'prosopagnosics can see the vegetables, but not the face in Giuseppe Arcimboldo's The Vegetable Gardener (Natura)'* (Harris and Aguirre, 2007) (see part I of the present review).In line with these behavioral observations, contrasting upright to inverted pictures of Arcimboldo paintings and Mooney faces elicited robust right FFA activity in PS's brain (Rossion et al., 2011).However, the focus of the neuroimaging study was not on PS here.Instead, we sought to test the hypothesis that such stimuli, which cannot be recognized as faces based on local parts, elicited FFA activity without OFA in neurotypical observers.This was demonstrated in two experiments, using an event-related stimulus presentation mode (Rossion et al., 2011, Fig.9).

Note that the finding of significant FFA activity related to conscious perception of a Mooney face stimulus was not new (Kanwisher et al., 1998).However, the contrast between the two regions in our study (Fig.9) was original, providing additional evidence against the standard view that the OFA is the mandatory gateway of the human cortical face network (Haxby et al., 2000; Calder and Young, 2005).That is, in certain stimulation conditions, a sensory stimulus can be recognized as a face in a relatively anterior, higher-order, region of the human brain[7] without any recognition occurring in the posteriorly located face-selective region of the cortical face network.

6.3. FFA despite cortical ipsilateral IOG resection

One outstanding question that was raised above regarding PS's FFA activation in the absence of posterior face-selective activity in the IOG concerns the potential long-term plasticity/reorganization that may have occurred in her brain between her accident in 1992 and the first fMRI experiments performed about 10 years later: what if PS (and DF) had re-learned to recognize visual stimuli as faces, leading to a new, atypical, selection of sensory inputs from early visual cortex to the LatMidFG triggering face-selective activity in the latter region? As far as we know, PS never complained of not being able to recognize a stimulus as a face and, in normal observers, FFA activity completely correlates with conscious recognition (Tong et al., 1998; Andrews et al., 2002; Fang and He, 2005).However, we cannot rule out that if we had scanned PS shortly after her brain damage occurred, face-selectivity in her LatMidFG, i.e., a FFA, might not have been found.

A unique opportunity to address this issue occurred to us around 2015 when a female patient with epilepsy refractory to medication, SP, required removal of the right inferior occipital cortex, including the right IOG, with the hope of eliminating her epileptic seizures (this patient's case was briefly mentioned in section 3 above).Since epileptic seizures usually concern medial and anterior temporal structures, this type of cortical surgery is extremely rare.Here, with the helpful collaboration of the patient, we were lucky enough to be able to acquire two fMRI face localizers in her brain both before and after a preplanned surgery and multiple measurements in typical controls.This enabled both within-subject/across-session comparisons (SP before resection *vs.* SP after resection) and between-subject/across-session comparisons (SP

[7] Note that this fMRI experiment performed in patient DF would not have given the same results since DF has severe visual segmentation deficits and, contrary to PS, she cannot see faces in Arcimboldo or Mooney stimuli (Steeves et al., 2006).

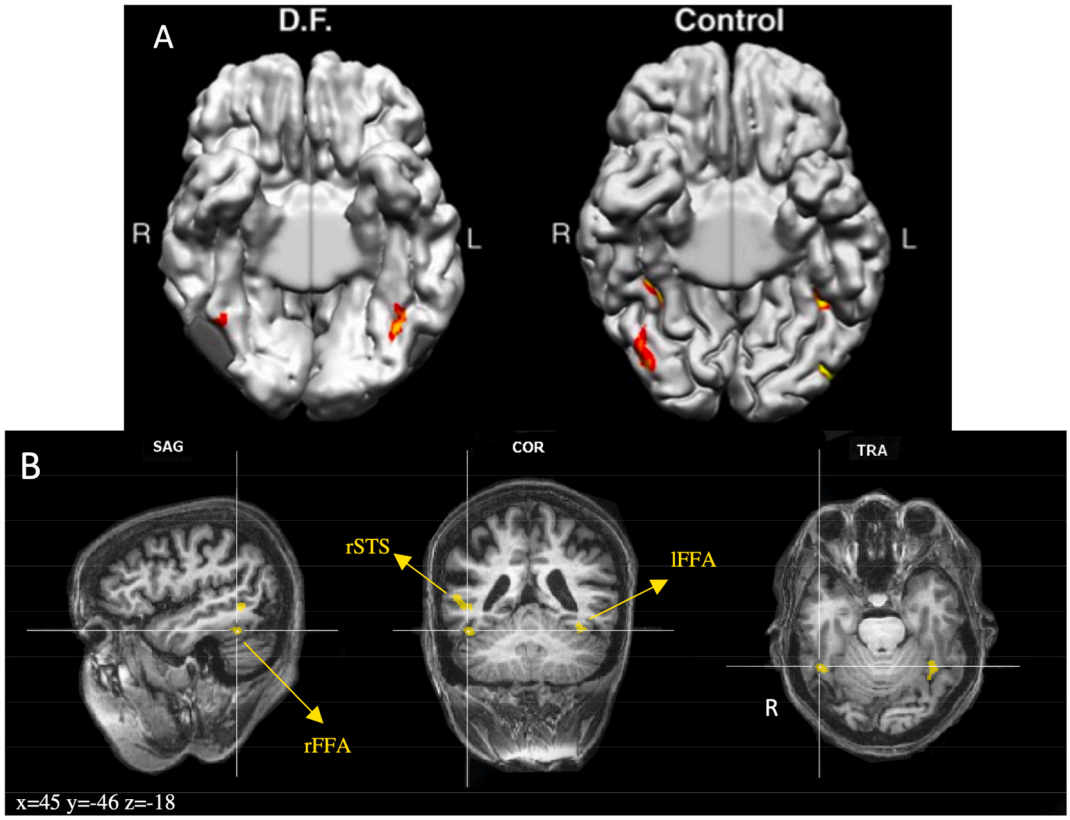


Fig.8. Despite extensive bilateral posterior brain damage in the IOG and no evidence of OFA, patient DF (Milner et al., 1991; Goodale and Milner, 2013) showed face-selective activity in the bilateral middle fusiform gyrus (FFA), replicating and extending findings made on patient PS.**A.** Original study from Steeves et al.(2006), with a lesion reconstruction over the inferior occipital gyrus (with permission; see also James et al., 2003 and Whitwell et al., 2014 for a description of DF's posterior lesions and cortical thinning); **B**.Replication in a direct comparative study with PS, showing the bilateral FFA activation, as well as face-selective activity in the right STS (Steeves et al., 2009).

vs. controls).The fMRI recording was performed at the University hospital in Nancy, where the surgery took place, but the research was led by Kevin Weiner, then at Stanford University with Kalanit Grill-Spector.

SP was scanned one month and 4 days prior surgery, as well as one month and 8 months after her (successful) surgery.Strikingly, while the cortical surgery removed face-selective activity in or around the IOG, we found that the spatial topology and selectivity of "downstream" ipsilateral face-selective regions were stable even at 1 month and also at 8 month(s) after surgery (Fig.10; Weiner et al., 2016).Additionally, the distributed pattern of face-selectivity across voxels in SP before versus after resection was as stable in SP as across recording sessions in normal controls.These results clearly indicate that face-selectivity in the Lat-MidFG does not critically depend, and may not even be modulated at all at least in these conditions, on face-selectivity in the posteriorly located ipsilateral IOG.Again, they support the view of a non-hierarchical cortical organization of human face recognition.[8]

[8] A limitation of SP's case was her below normal range performance at FIR already prior to surgery, although she was well above the level of a case of prosopagnosia.Moreover, her performance did not decrease following surgery and, on the contrary, she was in fact able to perform at the same level but faster at several FIR tasks (Weiner et al., 2016).In truth, these neuropsychological observations are difficult to interpret since the patient, being free of medication and cortical seizures, was much more alert and confident during behavioral testing after as compared to before surgery, a major confound in the interpretation of neuropsychological outcomes of cortical surgery for epilepsy refractory to medication.However, critically, this issue does not undermine the fMRI findings, which are not based on identification of faces.Moreover, compared to normal controls, SP showed no evidence of difficulties at recognizing stimuli as faces either before or after surgery (Weiner et al., 2016).

6.4. *Direct connections from early visual cortex to the FFA*

A key hypothesis derived from the neuroimaging investigation of PS is the presence of *direct* intra-hemispheric anatomico-functional connections from the early visual cortex (EVC) to the FFA, i.e., bypassing the IOG/OFA (Rossion et al., 2003; Rossion, 2008, Figs.6 and 7).This prediction can be tested at the anatomical/structural level using Diffusion Weighted Imaging (DTI), and at the functional level with various measures of correlated activity between brain regions either at rest (resting-state connectivity) or during active stimulus/task processing. Admittedly, none of these approaches is without serious limitations, and they all depend heavily on the definition (localization, extent) of the regions of interest, which is challenging and not free of subjective decisions (e.g., Fig.10).Hence, these approaches can only provide indirect evidence for or against anatomico-functional connections between brain areas.However, considered together across, or even within (Wang et al., 2020) studies, they can help evaluating the validity of the key hypothesis mentioned above.

6.4.1. *Anatomical connectivity*

Up to now, due to the right hemispheric posterior damage extending to low-level visual regions and posterior white matter fibers (Sorger et al., 2007), DTI sequences in our case of prosopagnosia PS have unfortunately not been successful at identifying white matter tracts connecting retinotopic areas to her FFA in the right hemisphere.In contrast, in the cortical surgery case of SP, discussed in the previous section, DTI identified white matter tracts connecting retinotopic areas to more anterior face-selective regions (pFus-faces and mFus-faces, also referred here as the FFA complex) anterior to the lesion (Weiner et al., 2016), which were preserved after surgery and presumably contribute to the

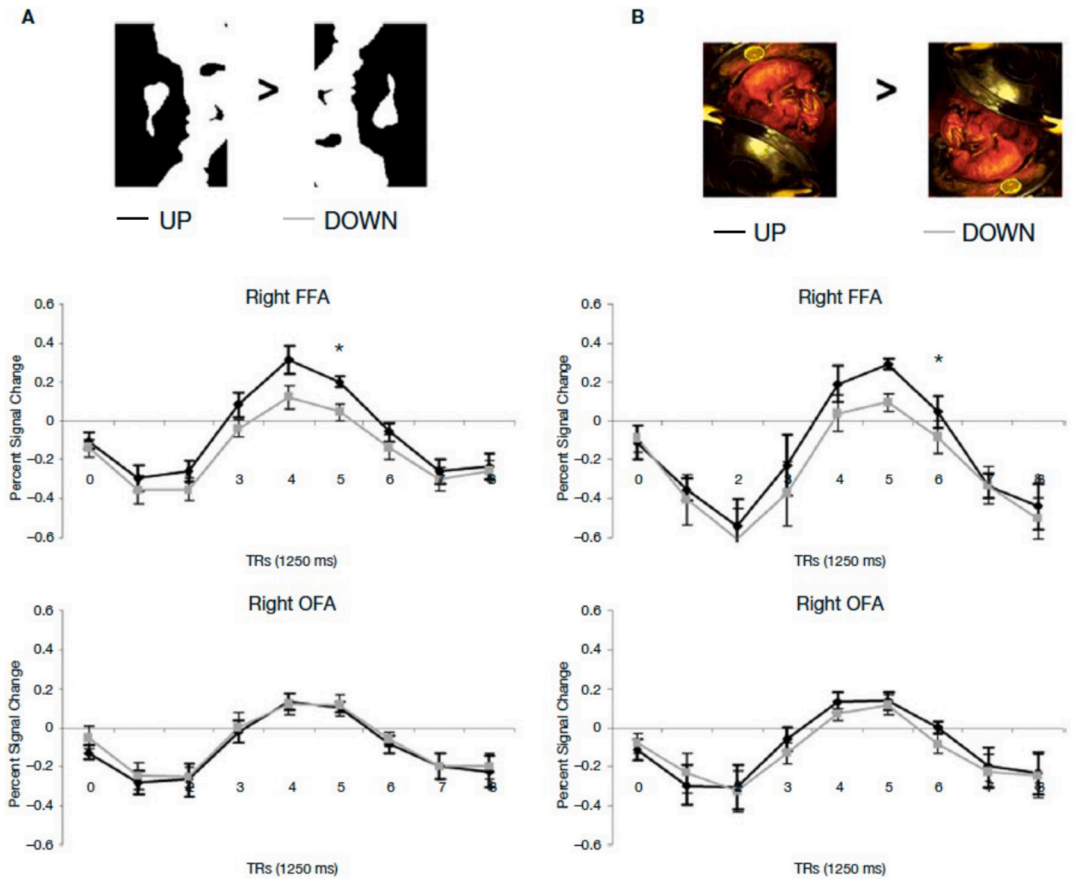


Fig.9. Percent signal change in an event-related experiment showing significantly larger response in the FFA of normal participants to the stimuli recognized as faces (Mooney faces on the left, A, or Arcimboldo paintings on the right, B) as compared to their physically identical versions presented upside-down, which are not recognized as faces.In both cases, there is no significant difference between the two stimulation conditions in the OFA.The two functional regions were pre-defined with a typical face localizer fMRI experiment (see Rossion et al., 2011).

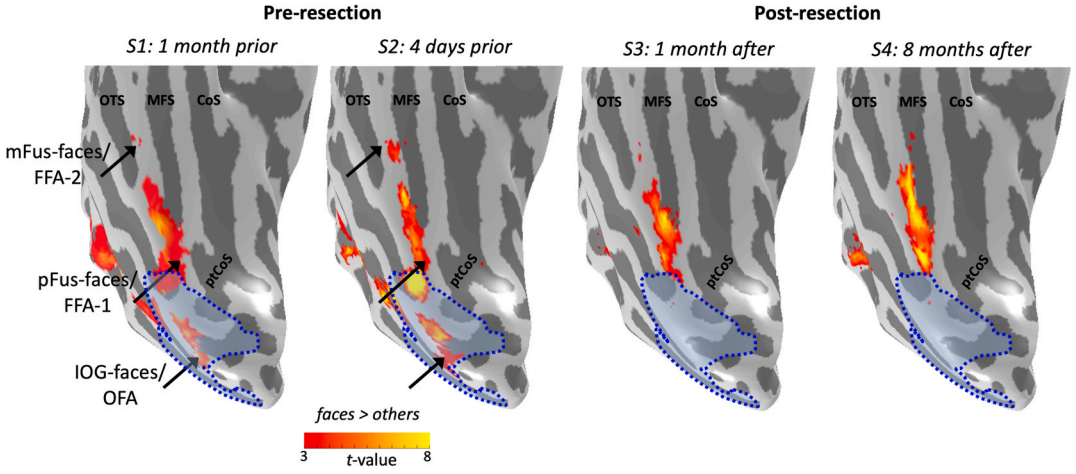


Fig.10. A case of stability of the cortical face network after resection.The cortical face network before and after resection on the inflated cortical reconstruction of the right hemisphere of patient SP (Weiner et al., 2016).Despite resection of IOG-faces/OFA and the posterior portion of pFus-faces/FFA-1, anterior face-selective activation is preserved 1 month and 8 months after surgery.Blue shading represents resected cortex.(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

stable features of SP's cortical face network across sessions (Fig.10). Importantly, in that study, such direct connections were also found in control participants (Weiner et al., 2016).

Besides this positive evidence, to my knowledge, only a handful of studies explored putative white matter tract connectivity of the cortical face network with DTI in neurotypical individuals: one study evaluated connections only within the face network (Pyles et al., 2013), and the three other studies that tested direct connections between EVC and the FFA all found supporting evidence for such direct connections (Gschwind et al., 2012; Wang et al., 2020; Finzi et al., 2021,

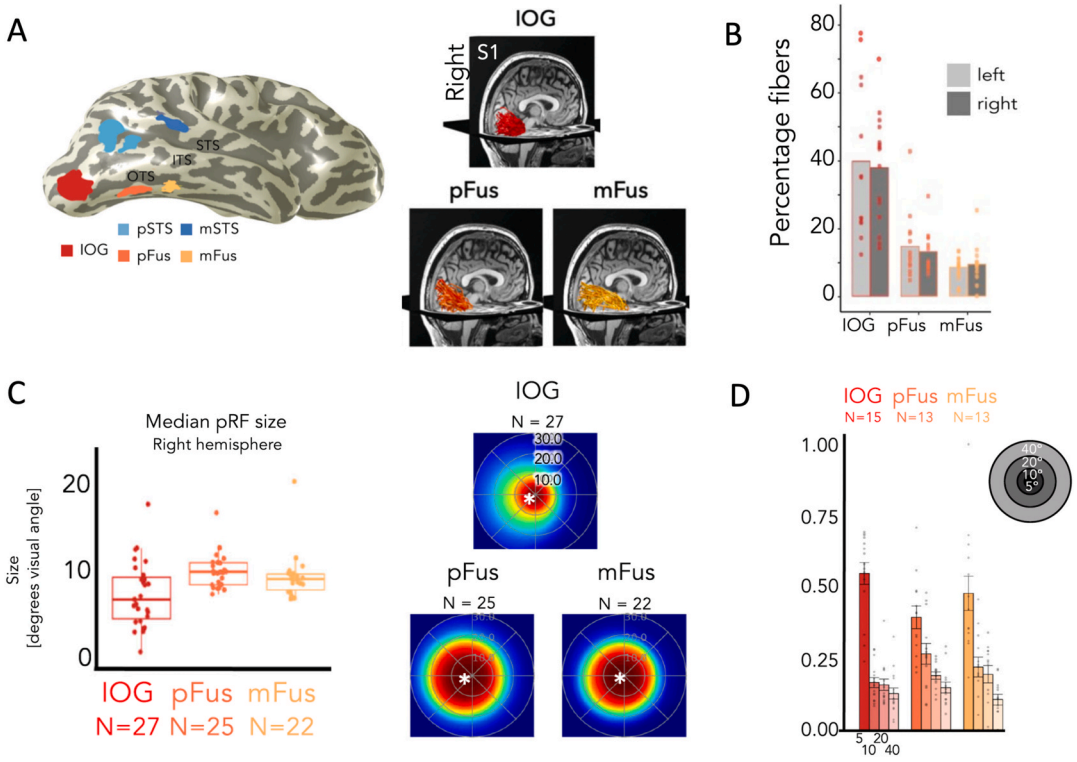


Fig.11. Adapted from the recent study of Finzi et al.(2021) with permission.**A.**White matter tracts directly connecting EVC and face-selective VOTC regions (IOG/OFA; pFus and mFus as part of the FFA complex) in an example participant (right hemisphere).**B.**Mean percentage of white matter tracts of each functional ROI connected to the EVC (i.e., close to 40% of fibers from the IOG connect to the EVC).Percentages are calculated for each participant (dots) and then averaged across participants.While a higher percentage of fibers from the IOG connect directly to the EVC, more anterior brain regions that are more diversely connected also have a substantial proportion of their fibers connecting directly to the EVC.**C.**Left: Median population receptive field (pRF) size in ventral face-selective regions.Box: median, 25%, and 75% percentiles; lines: ±1.5 times interquartile range.Right: Average visual field coverage of each ROI of the right hemisphere across participants (number above each plot).Asterisk: average location of the center of mass of all pRF centers in each ROI.Note the slight contralateral bias, with the smaller average receptive field of the IOG/OFA compared to regions of the FFA complex.**D.**Average proportion of tract endpoints from each ROI that terminate in each of four EVC eccentricity bands (right hemisphere; 0°–5°; 5°–10°; 10°–20°; 20°–40°).Note the relatively larger proportion of fibers from the IOG ending in the 0°–5° eccentricity as compared to regions of the FFA complex (pFus and mFus).

Fig.11A&B).

In all these studies, connections are less dense – or reduced in connection strength/connectivity probability - between EVC and the FFA than between EVC and the spatially closer OFA (Gschwind et al., 2012; Wang et al., 2020).This appears to be the case also in the most recent study of Finzi et al.(2021), in which the FFA complex is divided in two clusters (pFus and mFus, after Weiner and Grill-Spector, 2010; or pFus-faces and mFus-faces; after Weiner and Grill-Spector, 2012, Fig.10) and the EVC holds direct connections with each of these clusters (in all participants in which these regions are successfully localized (Fig.6 in Finzi et al., 2021; see Fig.11&B here).Thus, despite the longer spatial distance between EVC and FFA than EVC and OFA, and the dominance of short-range fibers in the cortical face network overall (Wang et al., 2020), DTI studies considered together overwhelmingly support the early hypothesis of direct connections from EVC to the FFA complex (Rossion et al., 2003; Rossion, 2008, Figs.6 and 7), against a strict hierarchical view of the cortical face network.

Note, however, that such anatomical connections provide no evidence that they drive nervous inputs leading to face-selectivity.For instance, one cannot exclude that direct connection from the EVC to the fusiform gyrus do not lead to face-selective activity (i.e., FFA) before receiving inputs from the OFA.Conversely, it could be that direct inputs of the EVC to IOG does not lead to face-selective activity (i.e., OFA), and that it is only *after* reentrant interactions with the FFA that face-selectivity arises in the IOG.This issue will be further discussed below.

6.4.2. *Functional connectivity*

Functional connectivity between brain regions of the human cortical face network has been assessed in multiple fMRI studies, with various methods (Furl et al., 2015; Kesssler et al., 2021 for reviews).While these investigations are undoubtedly valuable, the results of these studies should be taken with even greater caution than DTI studies because of the sluggishness of the BOLD response compared to the speed at which faces are recognized in the human brain (Rossion, 2014).Also, the methods are constantly refined (see Kesssler et al., 2021) and many subjective parameters can influence the results, in particular the ROI definition and different paradigms used during fMRI data recording.

While some studies have showed significant correlations of activity across time between the core brain regions of the cortical face network during resting state (Zhu et al., 2011) or stimulus/task processing (Davies-Thompson and Andrews, 2012), these findings do not imply direct connectivity (let alone inferences about directionality of signal exchanges) because these correlations could be entirely driven by other regions.This is why most studies have used DCM, which allows testing of specific hypotheses regarding effective connectivity and uses Bayesian model selection to determine which model of connectivity best explains the data (Friston et al., 2003).

To recall, the two hypotheses of the non-hierarchical cortical face recognition model originally derived from PS's studies are the presence of (1) direct functional connections from EVC to the FFA, bypassing the OFA and (2) reentrant inputs from the FFA to the OFA.

Let me start with the second hypothesis.In the first study exploring functional connectivity of the cortical face network, as mentioned

above, Fairhall and Ishai (2007), who did not test the first hypothesis, provided evidence that the best model within the core network was strictly feedforward and hierarchical (i.e., OFA→FFA, without a role of reverse FFA→ OFA projections).This view remains highly influential. However, a recent study that aimed at strictly replicating (and extending) this original study found instead that the best model had reentrant connections between FFA and OFA, contradicting the conclusions of the original study (Kesssler et al., 2021).Contrary to Fairhall and Ishai (2007), Kesssler et al.(2021)' study had four different data sets and isolated face-selective activity (rather than absolute responses to faces, or faces *vs.* scrambled faces), supporting a more complex model than the originally proposed model, with a high degree of interaction between regions.Other DCM studies have also generally supported reentrant FFA→OFA projections, e.g., during face identity adaptation (Ewbank et al., 2013) or face-selectivity (Wang et al., 2020; for an exception see Lohse et al., 2016).Thus, overall, it is fair to say that the original report of a strict hierarchical organization of the 'core' regions of the cortical face network by Fairhall and Ishai (2007) has not been supported.

The first hypothesis of direct inputs from EVC to FFA, which is most important for our purpose, has unfortunately not been not tested in most DCM studies, either because the EVC is not included in the models (e.g., Fairhall and Ishai, 2007; Kesssler et al., 2021) or the models include connections from the EVC to the OFA only (e.g., Frässle et al., 2016a, b). However, whenever direct EVC-FFA connections have been included in the models, their significant contribution has been unambiguously supported (Lohse et al., 2016; Wang et al., 2020, e.g., Fig.4 in the latter study).

6.4.3. Anatomico-functional connectivity

In the revised model with direct connections from the EVC to the FFA based on PS's findings I tentatively proposed a role for this pathway as providing an initial coarse holistic representation of a face (Rossion et al., 2003; Rossion, 2008, Fig.6).Then, reentrant interactions with the IOG would lead to face-selectivity in this latter region (although there would also be direct EVC inputs to IOG/OFA).Based on the closer localization of the IOG to low-level retinotopic areas, I hypothesized that populations of neurons in the OFA would have smaller receptive field than in the FFA, allowing a finer-grained analysis to fulfill an individual face percept.The aforementioned recent study of Finzi et al.(2021) supports this hypothesis.

In that study, the authors used fMRI retinotopic mapping to show that face-selective regions of the STS have a wide coverage of the visual field with a strong contralateral bias.In contrast, face-selective regions of the human VOTC, i.e., the regions that do not exist in the monkey brain (Fig.4; Rossion and Taubert, 2019), are centered on the fovea (as shown previously for the FFA; Levy et al., 2002) with little lateralization bias (Fig.11C).Most importantly for our purpose, there are differences between the OFA and the FFA.In general, the OFA (IOG-faces after Weiner and Grill-Spector, 2012) is associated with a smaller median receptive field (Fig.3 of Finzi et al., 2021) with a significantly larger bias towards the central point of vision than the FFA complex (Fig.4 of Finzi et al., 2021).To explain these differences, Finzi et al.(2021) tracked white matter fibers from these regions to the EVC with DTI.While the majority of tracts connecting EVC to ventral face-selective ROIs originated within the central 10°, there was a relatively larger proportion of tracts falling within 5° of visual angle for the OFA than for the FFA (in both hemispheres) (Fig.7 of Finzi et al., 2021, Fig.11C&D here).That is, direct fibers between the fusiform face-selective regions and the EVC are more widely distributed across the visual field for the FFA complex (pFus and mFus) than for the OFA (Fig.11 C&D).

Besides supporting the view that OFA neurons have smaller receptive field than FFA neurons, perhaps for a finer-grained analysis of face stimuli, what would be the functional implications of these findings for our question of interest? One possibility is that a stimulus appearing in the periphery of the visual field, or at a large size, is recognized as a face better/faster in pFus/mFus-faces (FFA) than in the IOG-faces (OFA). Thus, it would make sense that holistic recognition of a Mooney face, i.e., based on the simultaneous integration of (weak) sensory cues across the whole stimulus, is preferentially supported by the FFA complex as compared to the OFA (Rossion et al., 2011).

6.5. Intermediate summary

Our scientific journey started with an incidental observation on PS, a single case of prosopagnosia who showed normal range face-selective activity in the lateral section of the right middle fusiform gyrus, corresponding to a typical right FFA (Rossion et al., 2003, Fig.5).This finding occurred at a time when the (right) FFA was often considered as the main, sometimes even unique (Kanwisher et al., 1997; McCarthy et al., 1997; Kleinschmidt and Cohen, 2006), center for face (identity) recognition in the human brain (even if its specificity for face signals was fiercely debated; e.g., Kanwisher, 2000; Tarr and Gauthier, 2000).The preserved right FFA in a rare case of prosopagnosia thus served to highlight the critical role of other specialized cortical regions in face recognition, in particular the right IOG/OFA – hence, the title of this first paper on PS: "*A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing*" (Rossion et al., 2003).It directly inspired subsequent research evaluating the criticalness of the right OFA in face (identity) recognition mainly with transcranial magnetic stimulation (TMS; Pitcher et al., 2007; for review Pitcher, 2021) and also intracerebral electrical stimulation (Jonas et al., 2012; for review: Jonas and Rossion, 2021), as will be described below.

Most importantly, as reviewed above, the finding of a right FFA in PS's brain, replicated numerous times in different conditions, led to a revised neurofunctional model of human face recognition according to which the IOG/OFA is not a mandatory stage of selective face processing before reaching the LatMidFG/FFA.Instead, contradicting a strict hierarchical model (even including hypothetical feedback connections between regions; e.g., Haxby et al., 2000), these findings suggested direct inputs from low-level non-face-selective EVC to the LatMidFG/FFA, bypassing the IOG/OFA (Rossion et al., 2003; Rossion, 2008, Fig.6).

Complementing this initial observation in PS's brain, there is now substantial evidence from studies in neurotypical individuals and brain-damaged patients that face-selectivity in the human brain is indeed not organized in a strict hierarchical manner.Specifically, face-selective neural signals can be absent in the bilateral IOG due to brain damage or the lack of local diagnostic face cues, while face-selective activity is present in the LatMidFG.In addition, the proposal of direct inputs from EVC to the LatMidFG/FFA, bypassing the IOG/OFA, is now supported by solid DTI evidence (Weiner et al., 2016; Finzi et al., 2021, Fig.11).

Moreover, as also shown early on in both DF and PS, face-selective activity in the pSTS can also emerge in the absence of IOG/OFA (Steeves et al., 2006; Sorger et al., 2007), a finding replicated in other brain-damaged patients (Dalrymple et al., 2011; Sliwinska et al., 2020). Since the IOG/OFA is located in the VOTC, this finding offered initial support to the currently acknowledged neurofunctional dissociation between a ventral (i.e., VOTC) and a 'dorsal' (i.e., STS) pathway for human face recognition (Duchaine and Yovel, 2015, Fig.7; see also Pitcher and Ungerleider, 2021).

Finally, as noted above, these findings do not allow to draw definite conclusions regarding the origin of face-selectivity in the IOG (i.e., OFA), and the nature of the direct interaction between the OFA and FFA. At first glance, the view that direct inputs of the EVC to IOG would not lead to face-selective activity (i.e., OFA) *before* reentrant interactions with the FFA seems a bit far-fetched.However, a neuroimaging investigation of a single case of visual agnosia (NS, Delvenne et al., 2004) who had damage in the bilateral parahippocampal gyri and the right fusiform gyrus, with largely preserved brain tissue in the IOG (Rossion, 2009) provided some evidence for it.Despite excellent fMRI signal-to-noise ratio, there was no evidence whatsoever of face-selective activation around the lesion in the fusiform gyrus (i.e., no FFA), nor in the inferior occipital gyrus (i.e., no OFA).In fact, there was only a hint of

face-selective activation in the patient's pSTS (Fig.7 in Rossion, 2009). Hence, without the right fusiform gyrus, face-selectivity may not be initiated at all in the IOG.Since this was a no-result based only on a single fMRI session (due to limited availability of the patient), such observations should be taken with great care.Yet, while a number of brain-damaged patients with FIR impairment have been tested with face localizers in fMRI (e.g., Marotta et al., 2001; Dalrymple et al., 2011; Sliwinska et al., 2020), I am not aware of a case showing a clear right OFA with a damaged ipsilateral fusiform gyrus and no FFA.Thus, face-selectivity in the IOG (i.e., OFA) may well depend on the integrity of the ipsilateral Midfusiform gyrus.Importantly, *following* emergence of face-selectivity in the OFA, there would still be reentrant outputs to the FFA to synchronize neural activity between these face-selective regions. Indeed, TMS applied over the right OFA decreases neural activity in the fusiform gyrus, although these effects generally lack category-selectivity (Pitcher et al., 2014; Solomon-Harris et al., 2016; Groen et al., 2021).

7. A resilient hierarchical view

Despite the evidence reviewed above, the notion of a strict hierarchical face recognition system in the human brain remains largely dominant in the scientific community, which struggles to incorporate both the notions of (1) direct connections from EVC to an anterior face-selective region (FFA) bypassing the most posterior face-selective region (OFA) and of (2) reentrant rather than simple OFA→FFA feedforward connections.For instance, a recent review on the functional neuroanatomy of face perception still conceptualizes the ventral human face recognition system as a strict feedforward hierarchy, even if the authors acknowledge that this organization could be "*refined in future research when understanding the full connectivity pattern including feedback connections and bypass routes*" (Grill-Spector et al., 2018, Fig.12A).In the same vein, despite questioning the hierarchy of the dorsal pathway for face recognition in their fMRI study of a brain-damaged patient, Sliwinska et al.(2020)'s model does not incorporate direct connections from EVC to the FFA, the OFA being still considered as the sole gateway of the ventral face recognition system (Fig.1 in that study; see also Pitcher, 2021).Another instance is provided by the most recent extensive modeling (DCM) study of functional (effective) connectivity of the cortical face network, in which direct connections from EVC to the FFA are not even included (Kesssler et al., 2021).

At first glance, this lack of consideration for non-hierarchical features in the human face recognition system is difficult to understand. After all, as noted above, a strictly hierarchical system is not resilient: break down the putative first stage (i.e., OFA), and the entire face recognition system collapses.So why did Haxby et al.(2000) proposed a hierarchical organization of the neural basis of human face recognition in the first place, and why does this view remain so influential? The short answer is that the view of hierarchical cortical processing is dominant not just in face recognition research but in visual (object) recognition in general (e.g., Marr, 1982; Riesenhuber and Poggio, 1999; Serre et al., 2007; Ullman, 2007; Freiwald and Tsao, 2010; Connor, 2010; DiCarlo et al., 2012; Serre, 2016; Conway, 2018; Grill-Spector et al., 2018; see also Vezoli et al., 2021) (Fig.12).That is, despite the long-standing evidence of largely bidirectional connections between cortical areas of the monkey visual system (Felleman and Van Essen, 1991) and even bypass routes (Kravitz et al., 2013; Conway, 2018), the functional role of such connections is largely unknown, neglected, or considered as being negligible.[9]

While the relatively recent growing popularity of predictive coding theories of perception (Rao and Ballard, 1999; Friston, 2005) could change that perspective by attributing key roles to reentrant/feedback connections (e.g., to correct for 'error' signals), the hierarchical view has instead even been strengthened by advances in computational models such as deep neural networks (DNNs).Indeed, these artificial networks which, in the field of visual object and face recognition in particular, are often thought to have brought artificial systems' performance to a level comparable to human performance (e.g., Phillips et al., 2018), have a clear hierarchical organization, with convergent, feedforward connections passing information from lower to higher layers, and divergent feedback connections shaping plasticity in the connections from lower layers (LeCun et al., 2015).

In the present section VII, I would like to discuss the key features of this hierarchical view as applied to human face recognition in order to confront them with the evidence reviewed above on PS, as well as other brain-damaged patients and neurotypical individuals questioning this hierarchical view.Let me start by quoting the first paragraph of the paper of Serre et al.(2007, p.6424), in which the authors advocate a strict hierarchical feedforward view of visual object recognition:" *(Visual) object recognition in the cortex is mediated by the ventral visual pathway running from the primary visual cortex (V1) through extrastriate visual areas II (V2) and IV (V4), to the inferotemporal cortex (IT), and then to the prefrontal cortex (PFC), which is involved in linking perception to memory and action.Over the last decade, a number of physiological studies in nonhuman primates have established several basic facts about the cortical mechanisms of recognition.The accumulated evidence points to several key features of the ventral pathway.From V1 to IT, there is an increase in invariance to position and scale and in parallel, an increase in the size of the receptive fields as well as in the complexity of the optimal stimuli for the neurons*".

All of the key features of this strict hierarchical view, which is presented almost as an established fact by the authors (see also e.g., the first paragraph of Connor, 2010), are present in this quote: an organized order of brain areas involvement, a progressive increase of receptive field and invariance, an increase in complexity of optimal stimuli, and even a strict division between perception and memory, with the output of perception being associated to memory representations at the latest stage.How are these features usually applied to human face recognition, and what is the evidence that, despite what we have reviewed so far in PS and other studies, the face recognition system would be organized in such a strict hierarchical manner?

7.1. Receptive fields in posterior and anterior face-selective regions

The notion of a hierarchical organization of the visual system can be traced back to Hubel and Wiesel (1962).Beyond showing increases in complexity of responses and receptive fields of neurons to simple visual stimuli from the retina through the lateral geniculate nucleus of the thalamus and then the primary visual cortex (V1), these outstanding scientists described simple and complex cells in V1 and proposed a hierarchical organization according to which the output of two (or more) spatially offset simple cells might provide the input to a complex cell (Hubel and Wiesel, 1962).Yet, they did not perform much recordings in higher-order areas of the visual cortex, even acknowledging later in their career their lack of success in understanding neurons' response properties in these regions (Hubel and Wiesel, 2005).

When Charles Gross and his colleagues started recording neurons in the monkey infero-temporal cortex, much more anteriorly than V1, they found cells responding also only to visual stimuli but with much larger receptive fields (Gross et al., 1969; see Gross, 1999 for a historical perspective).These neurons also showed more complex response properties than in EVC, and some of these neurons fired selectively to faces (i.e., face-selective cells; Gross et al., 1972; also Weiner and Grill-Spector, 2013 for a historical perspective).

These findings form the basis of the view that there is a hierarchical organization of function in the visual system.However, to my knowledge, an increase in receptive field *within* the cortical face network of macaque monkeys – which has now been intensely explored (Freiwald,

[9] A notable exception are studies on figure-ground segregation, in which the role of reentry/feedback has often been considered as critical (e.g., Sporns et al., 1991; Roelfsema et al., 2002; Klink et al., 2017).

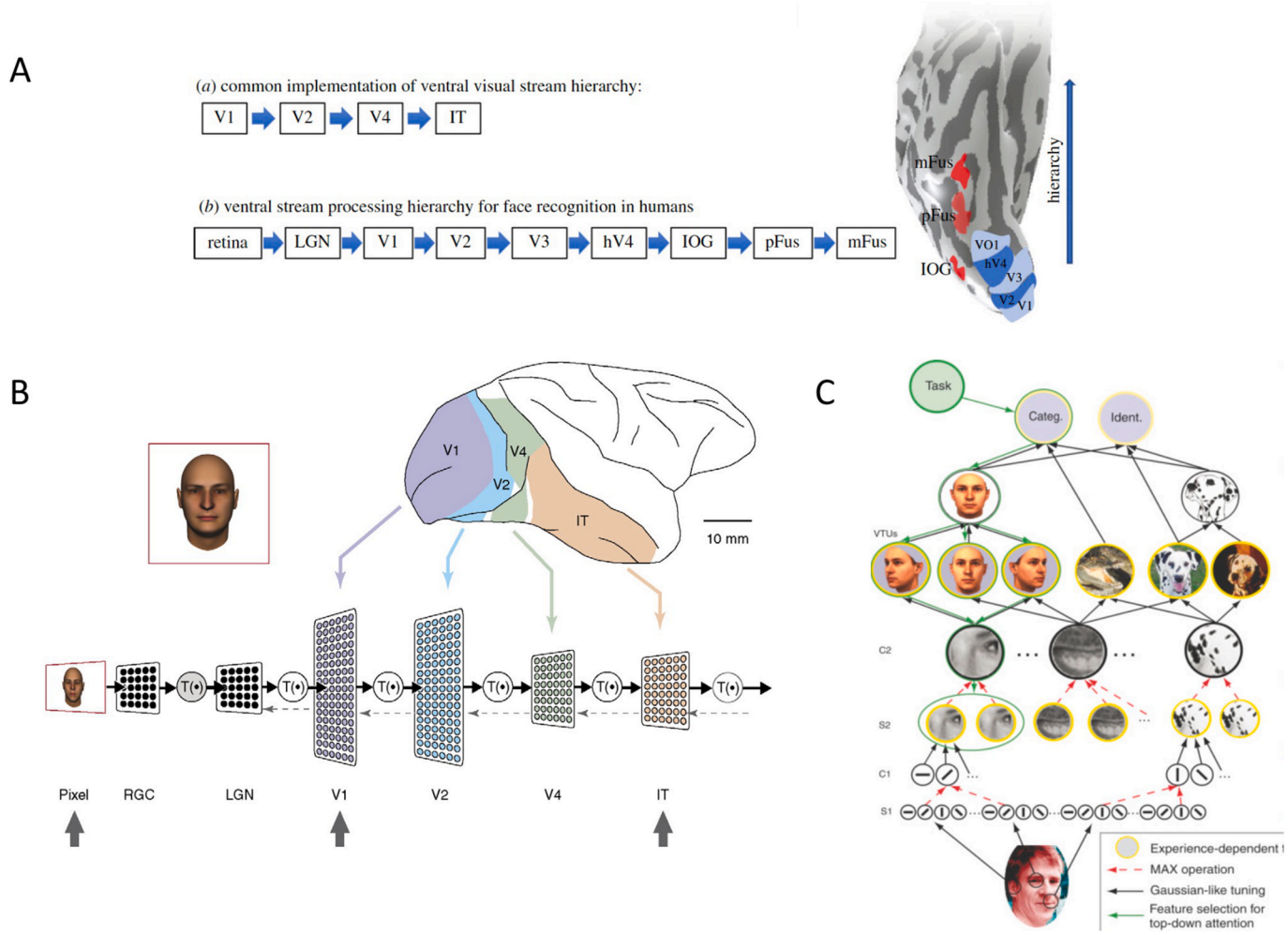


Fig.12. Various illustrations of the dominant hierarchical view of human face recognition at the neural level.**A.**A recent conceptualization of the ventral stream processing hierarchy for human face recognition, adapted from Grill-Spector et al.(2018) with permission.**B.**This view is inspired from the putative hierarchical organization of the "ventral" visual stream in the macaque brain and computational analyses in feedforward architectures, with little if any role of feedback connections (here for face identity recognition from DiCarlo and Cox., 2007; with permission).**C.**The HMax hierarchical model (Riesenhuber and Poggio, 1999) as applied to both visual object and face recognition (in separate streams), with a progressive construction of face representations from isolated parts to whole view-dependent and then view-invariant representations.According to this model, view-invariant visual representations of faces are built incrementally from the decoding of objective information from the stimulus in a part-to-whole manner.Categorization/identification is thought to occur only at subsequent stages based on representations stored in memory (from Walther and Koch, 2007, with permission).

2020; Hesse and Tsao, 2020) - has not been demonstrated.In any case, let me state again that macaques do not have a fusiform gyrus and a human-like VOTC network (Fig.4; Rossion and Taubert, 2019), preventing to make direct inferences from this species to the human face recognition system.

Admittedly, Finzi et al.(2021) showed that the (population) receptive field of the OFA is smaller than in the FFA complex (Fig.11C), which could be taken in favor of a hierarchical organization between these functional regions.However, within the two face-selective clusters of the FFA complex (pFus-faces and mFus-faces), there is no evidence of increase in receptive field in the postero-anterior direction (and if there is any trend, it is in the opposite direction of a hierarchy; Fig.11C).In any case, an increase in receptive field does not imply a hierarchical pooling mechanism by which the output of several neurons in the OFA would combine to provide the input to a neuron in the FFA.Quite the contrary, Finzi et al.(2021)' results point to direct connections from EVC to the FFA, in line with the fact that relatively large stimuli, or stimuli in the periphery, can be recognized as faces at a single glance (Crouzet et al., 2010; Hershler et al., 2010).

7.2. *Is the OFA active earlier than FFA?*

The view of a hierarchical organization of function in the visual system also rests on relative response *latencies* of neurons, which generally increases from early visual areas (e.g., V1) to higher-order areas (but see Bullier, 2001).Thus, according to a strict hierarchical view, face-selective activity should be completed, or at least well under way (as in a cascade system), before face-selective activity starts in the next stage.That is, according to this view, clear differences in onset latency of face-selectivity between these regions are expected: OFA first, then FFA.Is there any evidence supporting this hierarchical view?

7.2.1. *Timing of TMS effect*

Pitcher et al.(2011) claim, indeed, that selectivity to faces occurs much earlier in the IOG than in the fusiform gyrus (i.e., OFA before FFA), in line with the strict hierarchical view (Fig.7).One obvious limitation of this view is the unwarranted assumption that direct outputs from EVC to the FFA, which are included in their model, would be transmitted more slowly than those from EVC to OFA.Most importantly, Pitcher et al.(2011)'s claim is based on a fundamental misinterpretation of TMS effects on brain areas (see also Pitcher, 2021).Indeed, in their

seminal study, Pitcher et al.(2007) found an interference of FIR during TMS over the right IOG when two consecutive magnetic pulses were sent at 60–100 ms after stimulus onset but not at later latencies (from 100 to 140 ms) (Pitcher et al., 2007).However, these authors' interpretation of these findings that face-selective processes take place extremely early, i.e., between 60 and 100 ms in the OFA, is incorrect, for several reasons.

First, as demonstrated in other TMS studies combined with fMRI, this early effect could well be due to indirect interference of neural activity in more anteriorly located ventral areas including the FFA (Pitcher et al., 2014; Solomon-Harris et al., 2016; Groen et al., 2021).Second, the interference effect concerns FIR, but not face-selectivity (as would be shown by impairment at a task requiring recognition of a stimulus as a face for instance, i.e., generic face recognition).As far as I know, no impairment in the ability to recognize a stimulus as a face has been demonstrated following TMS over the right OFA (Solomon-Harris et al., 2013).Finally, more fundamentally, with a dual pulse TMS paradigm as used by Pitcher et al.(2007), the maximal effect of stimulation should *not* fall *in between* the two pulses (i.e., not between 60 ms and 100 ms). Instead, the effect of these two pulses should add up, so that the interference on face-selective activity in the stimulated brain region should be maximal right *after* the second pulse, i.e., from 100 ms (see the discussion section in Jacques et al., 2019).

Note that this latter interpretation of the original study (Pitcher et al., 2007) is in line with the finding of a subsequent study of Pitcher et al.(2012) in which the TMS pulses over the OFA were separated only by 10 ms, revealing the earliest category-specific effects at 100–110 ms. Yet in another study, significant impairments of FIR with TMS over the OFA were found with dual pulse stimulation at 130–170 ms (the earliest window tested) (Cohen Kadosch et al., 2011).Considering both the results of these latter studies as well as the fact that the optimal time at which TMS should be applied relative to a brain area's activity (i.e., just before or during this process) is unknown, Pitcher and colleagues' continuous claim from their original TMS study that the (right) OFA generates the earliest face-selective neural activity before 100 ms, well ahead of the fusiform gyrus, is unfounded.

7.2.2. EEG/MEG evidence

Another argument used in support of a putative earlier involvement of the OFA in face recognition comes from combined fMRI and scalp EEG face-selective responses, supposedly showing correlations across individual brains between the OFA and a P1 ERP component recorded on the scalp at around 80–120 ms, while the FFA would rather be correlated with the later N170 component (Sadeh et al., 2010; see also Yovel, 2016).That is, there would be about 70 ms difference between onset and peak activity in these two neighboring face-selective regions in the cortex.This time difference is simply not realistic and, indeed, the findings of Sadeh et al.(2010) are based on low correlation values, a small sample (with an outlier point) and a dubious computation of EEG face-selectivity (see discussion in Jacques et al., 2019).Moreover, while face-selectivity of the P1 component is based on low-level visual cues (amplitude spectrum, Rossion and Caharel, 2011), this factor does not play a role in OFA activity (Rossion et al., 2012; Gao et al., 2018).

With respect to scalp EEG or MEG, source localization procedures applied to face-selective neural signals as recorded with either technique, or the two techniques combined (e.g., Deffke et al., 2007; Hauk et al., 2021), cannot provide reliable data to disentangle OFA from FFA activity.At this level, let me just mention the recent study of Fan et al.(2020), who combined MEG with fMRI during face stimulation to address this issue.Interestingly, while these authors interpreted the relative timing of activity putatively in the OFA and FFA in terms of a hierarchy, their conclusion was based on the latency of the *peak* of activity, while the onset of face-selectivity was not significantly different, and in fact with a trend for an earlier response in FFA than OFA.In any case, in that study, 95% of the face-selective activity in the two regions overlaps in time (in fact the whole time-window with face-selective activity in the FFA happens when the OFA is simultaneously showing face-selective activity).Moreover, Fan et al.(2020) also found a delayed and prolonged response to Mooney faces as compared to full face pictures in the OFA but not in the FFA of the right hemisphere (with no apparent difference in onset time, but a delayed peak latency in the OFA for Mooney faces; see Fig.3 in that study) again rather against a hierarchical neural organization of human face recognition.

7.2.3. Intracranial recordings

In principle, human intracranial recordings should provide the most compelling source of evidence regarding the respective timing (onset and duration) of face-selectivity in the IOG and LatMidFG.However, even if local field face-selective potentials such as the N170 (or the N200, Allison et al., 1994, 1999) can be recorded in both the FFA and OFA (Jonas et al., 2012; and Jacques et al., 2019, respectively), there is no certainty that they truly originate from these regions (rather than being spread from distant cortical regions).At this level, it is worth mentioning the study of Kadipasaoglu et al.(2017), who recorded face-selective high frequency intracranial (gamma) activity in both regions (as pre-defined by a fMRI localizer) in response to clear pictures of faces and control stimuli in a few patients implanted with EcOG.In principle, such high-frequency neural activity, being considerably lower in amplitude, is thought to reflect more local responses than low frequency activity (Crone et al., 1998; Miller et al., 2007).With cautious consideration given the substantial variability across the few individuals and electrodes tested and a limited control of stimuli, the results of that original study provide no evidence of an earlier onset (or offset) of face-selectivity in the OFA as compared to the FFA (Fig.13), suggesting instead independent signal propagations between EVC and both regions, as well as bidirectional, not feed-forward, interactions between these regions.In a study yet again directly inspired by PS's case, as mentioned by the authors, the findings were interpreted as being incompatible with hierarchical models, instead supporting a parallel, distributed network underpinning human face recognition.

7.2.4. Time-resolved fMRI: FFA before OFA?

With PS, we attempted to provide some information about this issue of time onset using both EEG and MEG, but only with moderate success: while we were able to disclose face-selective N170/M170 activity over the right hemisphere despite PS's right IOG lesion, her EEG/MEG activity during this standard visual stimulation mode was associated with a low signal-to-noise ratio and atypical scalp topographies (due to the presence of trepanation), preventing to draw strong conclusions on this issue (Prieto et al., 2011); see also Simon et al., 2011 on PS; see also Dalrymple et al., 2011 on other brain-damaged patients).

To inform about the relative (rather than absolute) timing of activity in the OFA and FFA, we thus turned to time-resolved fMRI in a series of studies, also directly inspired from the neuroimaging findings on PS.Our investigation was motivated by our fMRI studies with Mooney or Arcimboldo faces, in response to an alternative interpretation that had sometimes been raised about these findings: that they merely reflect a statistical threshold issue, since face-selective activity is usually more consistent and significant in the FFA than in the OFA.Thus, stimuli that are difficult to recognize as faces and elicit lower activity in general could lead to an artificial dissociation between FFA (activity) and OFA (no activity).

To counteract this alternative view, we had to show face-selective activity in *both* functionally pre-defined regions of interest, but with a head start in the FFA.With my former postdoctoral researcher, Fang Jiang, now at the University of Nevada - Reno, we therefore designed an fMRI experiment in which we progressively and dynamically revealed the appearance of face and nonface stimuli, so as to slow down visual recognition.This work was inspired by studies that slowed down visual stimulation in fMRI to reveal the relative time course of activation and sensitivity to stimulus manipulations between visual areas (e.g., James et al., 2000; Carlson et al., 2006; Eger et al., 2007).Critically, in our study, we used a stimulus manipulation that held low-level image

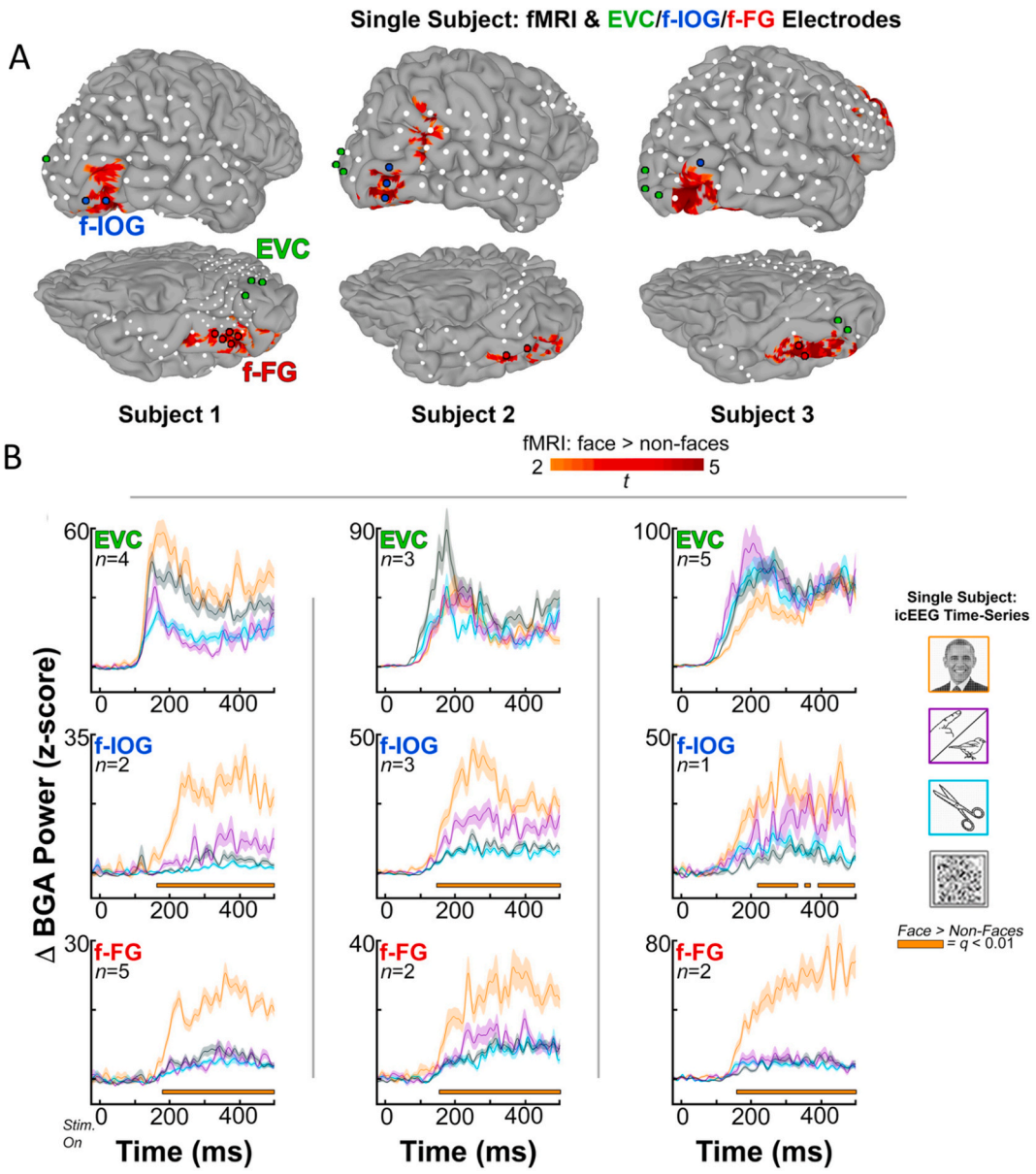


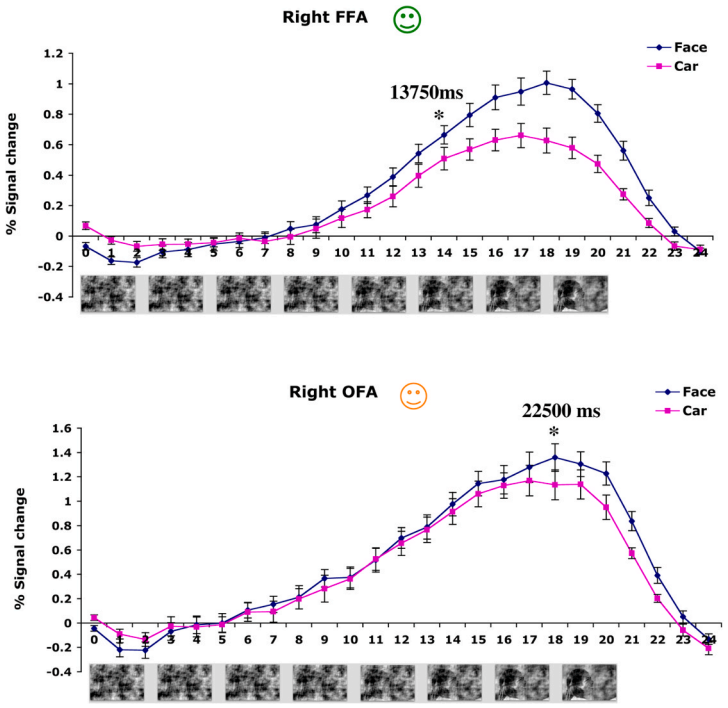
Fig.13. Adapted from Kadipasaoglu et al.(2017) with permission.A.Location of intracranial electrodes in the right hemisphere of three subjects, with electrodes in the fMRI-defined OFA (f-IOG, in blue), the FFA (f-FG, in red) and the early visual cortex (EVC, in green).B.Time-course from stimulus onset of high frequency neural activity to 4 types of stimuli, showing virtually no difference in stimulus onset of face-selective activity between the two regions (with an earlier response in the FFA than the OFA in the third subject on the right).(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

properties constant by progressively de-noising only the visual stimulus' phase spectrum (Sadr and Sinha, 2004) (Fig.13).[10] Since low-level visual stimulation was constant for a sustained period of time, we could temporally dissociate the onset of activity in low-level visual regions (e.g., V1) from higher-level regions, i.e., those involved in visual recognition (see also Ramon et al., 2015).

Strikingly, during this stimulation mode, larger response to scenes containing faces *vs.* cars was observed earlier in the FFA than in the OFA. In fact, among all face-selective regions identified by an independent localizer, the right FFA showed the earliest significant difference between activation for faces and cars (Jiang et al., 2011, Fig.14).Again, these observations contradict the standard view of the OFA as a gateway to the human cortical face network, even more so because of two complementary findings.First, under this stimulation manipulation, the *absolute* BOLD % signal change was larger in the OFA than the FFA (Fig.14), showing that the result could not be due to a lack of sensitivity of the OFA to the visual stimulation.Second, activation in the OFA rose *before* activation in the FFA, and yet, *face-selective* activity emerged earlier in the latter region (Fig.14).

These spectacular – at least in my view – findings were quite difficult to publish, in particular because reviewers, well aware of the limitations of fMRI in terms of temporal resolution, did not seem to appreciate the use of this technique to make inferences about the relative timing of activation in different brain areas (even though the method of temporal chronometry with fMRI had been well demonstrated in other domains; see Formisano and Goebel, 2003).Another criticism came from the use of natural visual scenes in which nonface body parts were sometimes apparent, potentially contributing to our findings because of apparent

[10] Movie available here: http://face-categorization-lab.webnode.com/products/face/.



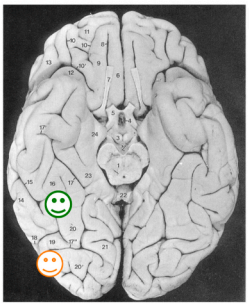


Fig.14. Slowing down the appearance of a face, while keeping constant low-level visual stimulation points to a temporal reverse hierarchy in the emergence of face-selectivity in the human brain (Jiang et al., 2011). Note that the absolute activation starts in the pre-localized OFA (below, volume 6, corresponding to 7500 ms for repetition times (TRs) of 1250 ms), ahead of the FFA (data point 9).However, this initial activation does not differ between faces and cars.The onset of the difference between faces and cars emerges earlier in the FFA (significant at 1350 ms) than in the OFA (significant at 22, 500 ms).Similar findings were made in four independent fMRI studies, including this one (see also Esterman and Yantis, 2010; Jiang et al., 2011; Jiang et al., 2015; Gentile et al., 2017).

FFA sensitivity to body parts (Peelen and Downing, 2005; although see Schwarzlose et al., 2005).Because of that, there was a long delay between our presentation of the paradigm and results at several international conferences and our final publication, so that we were even scooped by other researchers who used our design with an active detection task instead of an orthogonal task to show anticipatory increases in the face-selective regions when expecting faces instead of houses (Esterman and Yantis, 2010).Interestingly, that study essentially showed the same key finding as ours, i.e., an earlier face-selective activity from isolated pictures of faces in the pre-defined FFA than the OFA (Fig.3 in Esterman and Yantis, 2010), even though the authors did not discuss it.In a subsequent study, we then replicated and extended these and our findings by showing that irrespective of such category expectations, face-selective fMRI activity systematically emerged earlier in the FFA than the OFA (Jiang et al., 2015).

Finally, my former postdoc Francesco Gentile (now at Maastricht University) and I expanded these findings further by using face stimuli only, without other body parts, a short sampling rate (500 ms) of fMRI acquisition by focusing on a few slices centered on the pre-defined OFA and FFA to maximize the chance to disclose time differences, and a single subject statistical analysis.To further support the validity of the technique, we also compared the relative timing of fMRI activation for upright and inverted faces, knowing that inverted faces elicit delayed neural activity as recorded with EEG (Rossion et al., 1999; Itier and Taylor, 2004) or intracranial EEG in the VOTC (McCarthy et al., 1999). In our fMRI study, in both the OFA and FFA, a generic face recognition response emerged at a lower level of structural information for upright than inverted faces, in line with behavioral responses (see Fig.6 in Gentile et al., 2017).Most importantly, in that study, we showed again, in each of the 6 individual participants, a face-selective response emerging *earlier*, that is, at a lower level of structural (i.e., phase) information, in the FFA compared with the OFA (Gentile et al., 2017).

All in all, no less than four fMRI studies using this approach of slowly revealing faces and nonfaces in a stable low-level sensory stimulation context show FFA preceding OFA activation in neurotypical observers (Esterman and Yantis, 2010; Jiang et al., 2011, 2015; Gentile et al., 2017).These findings therefore offer overwhelming support for a non-hierarchical organization of the human cortical face network (or even for a reverse hierarchy, i.e., OFA after and dependent on FFA inputs).

Note that we do not conclude from these studies that when suddenly presenting a face at full view to the visual system, the onset of face-selective activity occurs earlier, in terms of absolute timing, in the FFA than the OFA.This could indeed well be the case, as supported by a BOLD latency mapping analysis to compare the time-course of activations across brain regions in a large sample of individuals (N = 36; Rossion et al., 2012).However, given the sluggishness of the BOLD response and the variability of this response's characteristics across regions depending on general factors (vein size etc.), such results should be taken with caution.

Instead, a careful interpretation of the results of the four fMRI studies using slowly revealed visual stimuli is that populations of neurons in the FFA require fewer sensory cues to elicit face-selective activity than populations of neurons in the OFA.Therefore, since the stimuli are presented according to an increasing order of sensory cues (Fig.13), the FFA, being more resistant to stimulus degradation, onsets before the OFA.There are in fact many real-life situations where such degraded conditions of visibility occur, e.g., during occlusion or when faces appear from a long distance.Our results suggest that in these conditions, sensory inputs sent directly from low-level (i.e., retinotopic) cortices to populations of neurons in the FFA lead to face-selectivity and the stimuli being recognized as faces, without any prior involvement of face-selective inputs from the OFA.

In summary, there is no valid evidence in the literature that face-selectivity emerges significantly earlier in the OFA than the FFA, with, if anything, the available data often pointing to the opposite.As initiated by Kadipasaoglou et al.(2017), resolving this issue for good will require extensive recordings of neurophysiological face-selective activity in these two regions (testing a wide variability of stimuli and excluding low-level visual confounds), ensuring that the recorded activity is generated locally.

7.3. *Parts before wholes?*

Another key aspect of the hierarchical view is that a face stimulus is thought to be represented in terms of a collection of its basic *parts*, or

features, in the first face-selective processing stage, the OFA, and then as a whole, a complete face, at the next stage, i.e., the FFA.In the Haxby et al.(2000) model, the putative function of the OFA is indeed the representation of "early facial features" (Fig.2).In subsequently adapted neurofunctional models, the OFA would be a stage at which the "perception of face parts" is instantiated (Pitcher et al., 2011; Pitcher et al., 2014, Fig.7A; see also Sliwinska et al., 2020), or at which faces would be represented in a view-dependent "part-based" manner (Duchaine and Yovel, 2015, Fig.7B).Then, at the next stage, i.e., the FFA, the representation of faces would be (view) invariant and "holistic" (Duchaine and Yovel, 2015, Fig.7B).

The basic idea here is that a face stimulus would be first represented in a category-selective stage/area, the OFA, as a collection of independent parts/features, which would then be combined (i.e., pooled) to form a whole face at a subsequent processing stage, the FFA.As already discussed extensively in part I of this review on PS, this view of an initial part-based decomposition followed by a combination of the parts into a global representation is pervasive in cognitive (neuro)science of human face recognition, and in visual object recognition in general (Fig.12). Where does this view come from? What are its roots? And what sort of evidence is there that the human neural face recognition system would work that way?

Once again, a primary source of inspiration for this idea comes from the original proposal of a hierarchical organization of the early visual system and pooling of activity between neurons at a certain level of the hierarchy to progressively increase the receptive field and the complexity of the neurons' responses along a hierarchy of processing stages (Hubel and Wiesel, 1962).As indicated above, this hierarchical view has been extended to the whole visual object recognition system. Another root is the influential conceptualization, from a computational perspective, of visual object recognition as being based on an initial decomposition of the stimulus in parts (i.e., the 'primitives' for Marr and Nishihara, 1978; the 'geons' for Biederman, 1987; the hierarchical 'fragments' for Ullman, 2007).Finally, these conceptual views have been implemented into actual computational models of visual object recognition that are defined as being biologically inspired (Riesenhuber and Poggio, 1999; Serre et al., 2007).The HMax model of Riesenhuber and Poggio (1999), extended to face recognition (Jiang et al., 2006), is a typical example of a strictly hierarchical feedforward model in which there is a progressive increase of receptive field, invariance and complexity of responses across a series of stages linked by simple pooling operations (Fig.12C).

The present review on patient PS is not the place here to discuss whether this view is correct or not with respect to visual object recognition in general.However, what I am interested in is the derived idea that the most posterior face-selective region of the human brain, the OFA, would hold category-selective representations of facial parts, which would then be combined to form a whole face only in an anteriorly located region, the FFA.Is this view supported by any sort of evidence that contradicts our findings on PS and related studies as reviewed above?

To make it clear, there is no *direct* evidence that a face-selective neuron in the OFA would fire only to one face part (e.g., one eye) and not to another part (e.g., the mouth).There are not many opportunities to record the activity of single neurons in the human brain (Fried et al., 2014), and it is in fact only recently that face-selective units have been recorded in human face-selective cortical areas (Axelrod et al., 2019; Decramer et al., 2021; Khuvis et al., 2021).Single neuron recordings in macaque monkeys have shown that a subset of face-selective units in the STS may fire for the eyes of a face only (Perrett et al., 1985; Issa and DiCarlo, 2012), but this is not because they would represent features/-parts to be combined at a later stage: instead, these units appear to be involved in recognizing *eye gaze direction* in faces, in combination with head orientation, an essential function for monkey's social interaction (Barraclough and Perrett, 2011).

Given this, what kind of *indirect* evidence has been advanced to support the view that the OFA would represent faces in a part-based manner? Of course, if one presents a relatively large face stimulus at fixation or an isolated facial part, given that neurons in this region respond preferentially to foveal input (Finzi et al., 2021), the response in the OFA might be tuned mainly by the feature/part that is close to the fixation point and not the other features/parts of the face (Henriksson et al., 2015).At the level of the FFA, the response would thus be driven by a larger space across the face.In fact, this is predicted in the schematic model illustrated in Fig.6 (Rossion, 2008) and, as mentioned above, it has nothing to do with part-based *vs.* holistic representation (i.e., if the fixation point moves to another location, the population response is driven by another part/feature).

A finding that is usually taken as providing key evidence for a part-based face-selective representation in the OFA is the impairment for (early) TMS to this region during the discrimination of faces differing by a single part but not when they differed by relative distances between these parts (e.g., interocular distance) (Pitcher et al., 2007).I have already discussed above the serious limitations of interpretations of the TMS effects made in that study.In any case, behavioral impairment at matching faces that differ according to a single part (providing that we know what the basic parts/primitives of faces are) does not mean at all that the disrupted brain region would selectively represent this face part. Indeed, in normal observers, a face part (e.g., the eyes, one eye, the left or right half, the top half of a face, etc.), is not recognized/perceived independently of other parts and of the whole face (except for PS of course).As discussed extensively in part I of the review on PS, this is the basics of holistic/configural representation of facial parts (see also Tanaka and Farah, 1993; Young et al., 1987; Rossion, 2013).An alternative, and much simpler, interpretation of Pitcher et al.(2007)'s TMS findings is again that the receptive field is smaller in the OFA (as hypothesized in Rossion et al., 2003; Rossion, 2008 and demonstrated in Finzi et al., 2021).Thus, distinguishing faces based on local parts might be more difficult than based on spatial relations which, by definition, require integration across a larger space of the face.

Other frequently cited sources of evidence for initial part-based category-selective representations of faces come from EEG/MEG studies.For instance, Liu et al.(2002) claimed that an early MEG component termed the M1, peaking at around 100 ms over occipito-temporal channels, was face-selective and driven by face parts irrespective of their arrangement in a face configuration.However, 'face-selective' effects at the level of this early component are rarely found and in fact associated with a particularly low SNR in that study. Most importantly, such early effects of face-selectivity to be driven entirely by low-level sensory cues (Halgren et al., 2000; Rossion and Caharel, 2011; see Rossion and Jacques, 2008), and there is no solid evidence for its generation in the IOG/OFA (as discussed above).Finally, the above-discussed fMRI/MEG study of Fan et al.(2020) also shows that for rearranged face parts (i.e., breaking the face configuration), activity is delayed in all of the face-selective regions.This is in line with findings from many EEG studies showing that a perceived face stimulus with its configuration disrupted by face inversion, misalignment, or rearrangement of face parts, is associated with a delayed face-selective response latency (e.g., Bentin et al., 1996; Rossion et al., 1999; Jacques and Rossion, 2009), again providing little support for an early perception of isolated facial parts in the human brain.

Finally, to evaluate this issue, we can also come back to PS, whose key impairment is a loss of a holistic representation of facial identity (Rossion, review part I).While PS is impaired at matching whole faces differing by a single part, especially when the nature of the part that differs between faces changes from trial to trial (as in Pitcher et al., 2007's experiment; see Ramon and Rossion, 2010), her recognition based on an isolated single part, especially the mouth, may be as good as normal observers (Van Belle et al., 2010a; Ramon et al., 2016).Moreover, she is better at matching isolated parts of faces for their identity than parts inserted in whole faces (Ramon et al., 2010).In short, her right OFA lesion with her preserved FFA does not seem to have left her with

an inability to recognize isolated parts of faces, as predicted in a hierarchical model of human face recognition.

All in all, I think that there is really no evidence supporting the common view that the human face recognition system works through an initial category-selective part-based decomposition, integrating these parts together at later stages.This would involve presumably some form of pooling mechanisms, e.g., the output of one neuron representing one eye of the face stimulus would be combined with the output of another neuron representing the other eye and an output representing the mouth, etc.to make a whole face.When it is considered seriously, this view makes little sense in fact, is contradicted by a number of empirical observations, and should be abandoned for good in order to make significant progress in the field of human face recognition.

7.4. Face detection before identity recognition?

Another pervasive idea in the field of human face recognition that is intrinsically linked to the hierarchical view is that there would be first a face "detection" stage, i.e., a stage at which the visual stimulus would be recognized as a face, and *then* a stage at which its identity would be recognized.This is a quite old idea, incorporated explicitly in the first cognitive model of human face recognition (Hay and Young, 1982) although not followed through in its more widely adopted successor (Bruce and Young, 1986).This view of an initial face detection stage was also implicitly incorporated in Haxby et al.(2000)'s neurofunctional model, where sensitivity to face identity was supposed to emerge after the OFA, at the level of the FFA (Fig.2), this hierarchical distinction having been preserved in subsequent neurofunctional architectures (Pitcher et al., 2011; Pitcher et al., 2014; Duchaine and Yovel, 2015, with sensitivity to identity emerging at the level of the most anterior FFA cluster; Fig.7).This is in fact also a widespread view in the scientific community (e.g., Degelder and Rouw, 2001; Tsao and Livingstone, 2008; Freiwald and Tsao, 2010; see also Connor, 2010), with a number of studies having even linked these putative well-distinct functional stages to clearly demarcated temporally successive EEG/MEG components (albeit different ones; e.g., Liu et al., 2002; Sadeh et al., 2010; Amihai et al., 2011; Schweinberger and Neumann, 2016).

There is also, unfortunately, a substantial amount of empirical inconsistency and conceptual confusion at this level: it is not because recognizing a visual stimulus as a face is easier and faster than in terms of its identity (for obvious reasons, as discussed in review part I; see also Quek et al., 2021) that there should be a processing *stage* devoted to generic face recognition followed by a processing *stage* for FIR.In fact, currently, there is no evidence of a human brain region being involved only in recognizing a visual stimulus as a face and not in other face recognition functions.As for the OFA, its absence in PS's brain does not prevent her to recognize a visual stimulus as a face very well indeed (Rossion et al., 2003, 2011; Schiltz et al., 2006), directly contradicting the view that it would represent a face detection stage.Most importantly, the next section will address directly the question of face identity recognition, and the key role of the OFA in this function.

8. (Lack of) sensitivity to face identity

Although we were initially surprised to disclose right FFA activation in PS's brain, there is no paradox at the functional level indeed because PS is able to recognize a visual stimulus as a face accurately, rapidly and automatically (Rossion et al., 2003, 2011; Schiltz et al., 2006).As extensively reviewed in the accompanying paper (part I), her problem is to recognize people's *identity* from their faces, i.e., FIR.This impaired function for PS has been demonstrated across a wide variety of stimuli, both for familiar or unfamiliar faces, and tasks (part I).

8.1. Release from fMRI-adaptation as a face identity biomarker

The contribution of face-selective populations of neurons in the LatMidFus gyrus, i.e., the FFA (complex), in human FIR remains somewhat controversial in the scientific literature.Unfortunately, this controversy is also mainly due to conceptual confusions, unwarranted claims based on null effects (e.g., Kriegeskorte et al., 2007), as well as methodological weaknesses in some studies, rather than to fundamental limitations in our methods of investigations and current knowledge.

Evidence for sensitivity to neural differences between facial identities comes essentially from *fMRI-adaptation*, or repetition suppression, in which the neural response to a stimulus is reduced with its repetition (Grill-Spector and Malach, 2001; Grill-Spector et al., 2006; Henson, 2016).If repetition suppression is released in a given brain region when two (or more) different stimuli are presented as compared to the repetition of the same stimulus, then one can reasonably assume that populations of neurons in this region can tell apart the (two) stimuli.Such release from adaptation to face identity (i.e., face A preceded by face B *vs.* face A preceded by face A) has been found in the FFA in numerous fMRI studies (e.g., Gauthier et al., 2000; Eger et al., 2007; Schiltz and Rossion, 2006; Gilaie-Dotan and Malach, 2007; Davies-Thompson et al., 2009; Ewbank et al., 2013; Avidan and Behrmann, 2009; Hermann et al., 2017; see Rossion, 2014; Henson, 2016; Jacques et al., 2020 for reviews).The FFA effect has been found both for familiar and unfamiliar faces, and is generally stronger in the right than the left hemisphere (Rossion, 2014; Jacques et al., 2020).The significant release from adaptation to face identity in the FFA has generally been interpreted as evidence that this region is involved in FIR.

Importantly, the cellular mechanisms of such neural adaptation effects (i.e., how neurons code for different faces) in fMRI are unknown, and interpretations at this level (e.g., in terms of different populations of neurons coding for different faces) could be seriously misleading (Sawamura et al., 2006; see Grill-Spector et al., 2006; Rossion, 2014). Yet, the basic finding from fMRI-adaptation and its conservative interpretation remains: in a given human brain region, here the FFA for our concern, there is sensitivity to differences between facial identities.The fact that presenting different facial identities in isolation does not lead to significant variability of signal across voxels to decode each identity in a multivariate voxel analysis in the FFA (Kriegeskorte et al., 2007; Anzellotti and Caramazza, 2014), or only weak and inconsistent effects across studies (Nestor et al., 2011a,b; Goesaert and Op de Beeck, 2013), does not question the validity of the fMRI-adaptation effects.Instead, it only shows the inadequacy of the multivariate approach (without adaptation) to reveal sensitivity to face identity (beyond low-level image differences) (Rossion, 2014; Dubois et al., 2015; Kanwisher, 2017).After all, a single voxel in the FFA at conventional fMRI resolution contains millions of neurons (Logothetis, 2008)[11].Thus, without a trick such as repetition suppression, there is no reason to expect an intrinsic absolute difference in signal at the level of a single voxel in response to two different facial identities.Using variability across many of such insensitive voxels (in a region of interest, a large portion of the brain, or a moving volume) should not change anything: when successful "decoding" of face identity occurs in a brain region with voxelwise multivariate analysis, this effect is likely to be due to obvious low-level sensory cues differing between the faces, and unlikely to show much generalization across meaningful changes of viewing conditions (see Rossion, 2014).

Of course, in fMRI-adaptation designs, repetition effects could also be entirely, or partly, due to low-level sensory cues, and one must be careful at this level: repetition suppression is a general property of brain

[11] The number of neurons in a voxel at standard spatial resolution (e.g., 3 × 3x3 mm) of the fusiform gyrus is difficult to estimate.While Logothetis (2008) estimates this number at about 7 million neurons, this estimation must be based on analysis of V1 density of neurons, which is much higher than in higher-order areas (see e.g., C.E.Collins et al., 2016 for relative estimation in a chimpanzee hemisphere).According to the number of cortical minicolumns in the human fusiform gyrus (Chance et al., 2013), this number should be closer to 2.5 million neurons (Rossion, 2022b).

(which is a change detector) so that in principle, even cells of the retina will be sensitive to the immediate repetition of the exact same face image compared to different images just because of local, pixelwise, differences in contrast.Fortunately, there are methodological ways to go around that such as varying size, position, luminance, or even head orientation of the repeated face identities (Schiltz and Rossion, 2006; Ewbank et al., 2013).One can also show that fMRI-adaptation goes well beyond mere sensory cues by showing that it is abolished or reduced by inversion (Yovel and Kanwisher, 2005; Mazard et al., 2006; Gilaie-Dotan et al., 2010), a simple manipulation that preserves all physical differences between the faces.

8.2. No release from fMRI-adaptation to face identity in a prosopagnosic FFA

With some of this knowledge in hand already in 2003, an outstanding issue for us, following the observation of PS's right FFA activation, was thus to assess whether this region was sensitive to differences between facial identities.To do that, we designed a fMRI-adaptation study with pictures of unfamiliar faces, comparing PS to normal controls.The leading researcher on this project was my colleague Christine Schiltz, now at the University of Luxembourg, and then working as a postdoc in my laboratory.In a first experiment, PS and control participants were presented with blocks of identical face stimuli, as compared to the successive presentation of different face stimuli.Whereas, in line with many studies as cited above, neural activation decreased for repeated facial identities compared to different identities in the right FFA of all neurotypical participants, PS showed only a small non-significant difference between blocks of different or identical face identities (Fig.15A).

That is, despite showing a larger response to faces than objects in the normal range, PS′ right FFA showed virtually no face identity adaptation effect in fMRI.To be more accurate, the level of signal in PS′ right FFA was as large as in normal participants when identical faces were presented repeatedly, but failed to show a release from adaptation when *different* faces were presented: her pre-localized right FFA seemed to treat different face identities as being identical.Hence, on second glance, PS's right FFA does *not* function normally: while recognizing a stimulus as a face (as opposed to other visual objects), the signal in this brain region does not provide sufficient information to discriminate different face identities, in line with her prosopagnosia (Schiltz et al., 2006).

In the original study, these observations were made with full front stimuli devoid of external features (color change detection task) both in a block design and in an event-related (ER) paradigm (experiments 1 & 2 respectively; Schiltz et al., 2006, Fig.15A and B).During the fMRI experiments, an orthogonal task (detecting the occurrence of rare face or car stimuli that appeared slightly reddish) that the patient was able to perform as well as control participants was used.That is, in line with the face localizer studies, we used a task that the patient was able to do (Price and Friston, 1999) as well as normal controls, in order to avoid that any altered response in PS's brain areas reflected a decrease of general attentional level and/or performance during scanning.Moreover, to avoid the type of low-level confound mentioned above, successive face stimuli varied either in spatial position (experiment 1, block design) or size (experiment 1, ER) (Schiltz et al., 2006).Overall, the lack of sensitivity to (unfamiliar) face identity repetition in PS's right FFA reported in two experiments in this study (with 3 sessions for experiment 1) has been replicated in three fMRI-adaptation studies using different stimuli, stimulation paradigms, and tasks (Dricot et al., 2008; Steeves et al., 2009; Gao et al., 2019) (and is also in line with EEG evidence as reported in Liu-Shuang et al., 2016; see the review of PS part I).

The original dissociation in the same brain region of PS between intact generic face recognition and impaired face identity recognition (FIR) held several original implications.First, it showed that the level of activation, or face-selectivity, in this region does not indicate normal face recognition: finer-grained recognition (e.g., face identity recognition), as revealed by fMR-adaptation, might be impaired.Second, these

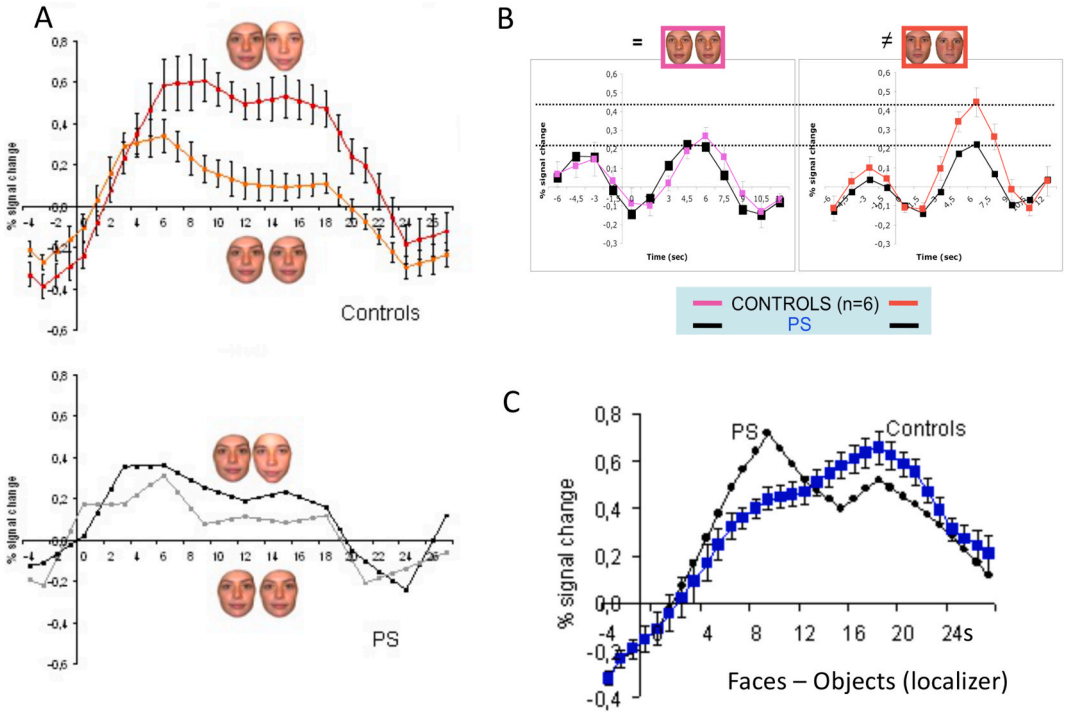


Fig.15. *Compared to neurotypical individuals, PS shows weak (**A**) or no (**B**) difference in fMRI signal in her right FFA to the repeated presentation of different face identities as compared to the presentation of the same identity (Schiltz et al., 2006): her right FFA does not differentiate face identities.The first experiment with a block design (**A**) was performed three times for PS (9 runs in total), who had the three lowest indexes of release from adaptation among all participants. **B**.In the event-related experiment, there was no difference at all for PS between the two conditions, contrary to clear effects in normal controls **C**.The % signal change (vs.fixation baseline) for blocks of different faces vs. different objects in the right FFA shows an initially above average category-selective response for PS which, unlike in normal controls, is not sustained, presumably due to the lack of release from adaptation.Overall, there is no significant difference between PS and controls in magnitude of face-selectivity (see Schiltz et al., 2006).*

findings were in line with PS's prosopagnosia, pointing towards a *critical* function of the right FFA region in FIR.This had not been demonstrated before the study on PS, and, to date, while such results have been replicated also in patient DF (Steeves et al., 2009), there is still no other sources of evidence beyond lesion analyses (Cohen et al., 2019) showing the *critical* role of the (right) FFA in FIR.For instance, studies of electrical intracranial stimulation are often cited as offering such evidence of a critical role of the (right) FFA in FIR (Parvizi et al., 2012; Rangarajan et al., 2014; Schalk et al., 2017).However, while focal intracranial stimulation of the FFA in these studies leads to subjective perceptual changes (e.g., distortion of the face percept in the above cited studies; or face palinopsia in Jonas et al., 2018), no evidence of behavioral FIR impairment has been provided.Interestingly, the case of Parvizi et al. (2012) was tested at a FIR task during intracranial electrical stimulation of his right FFA and showed no impairment (see Jonas and Rossion, 2021 for discussion of this issue; see also below).

Third, the lack of release from adaptation in PS's right FFA suggested that successful FIR in this region requires interactions with other regions.In particular, the right IOG-faces/OFA, which also shows such release from adaptation effects in the normal brain (see below) but is damaged in PS's brain, may be necessary.Thus, contrary to an early incorrect interpretation of our findings on PS (Kleinschmidt and Cohen, 2006), they do not support the view of the right FFA as a module for FIR but rather that this function is supported by a *distributed network* of brain regions, also highlighting the critical role of white matter connections between regions (Rossion, 2014).Finally, these findings of lack of fMRI-adaptation in the right FFA of a clear case of prosopagnosia show that such effects, at least when measured carefully (e.g., by varying the repeated images in low-level properties) are not unspecific (as claimed in Mur et al., 2010) and can provide conclusive evidence for a neuronal

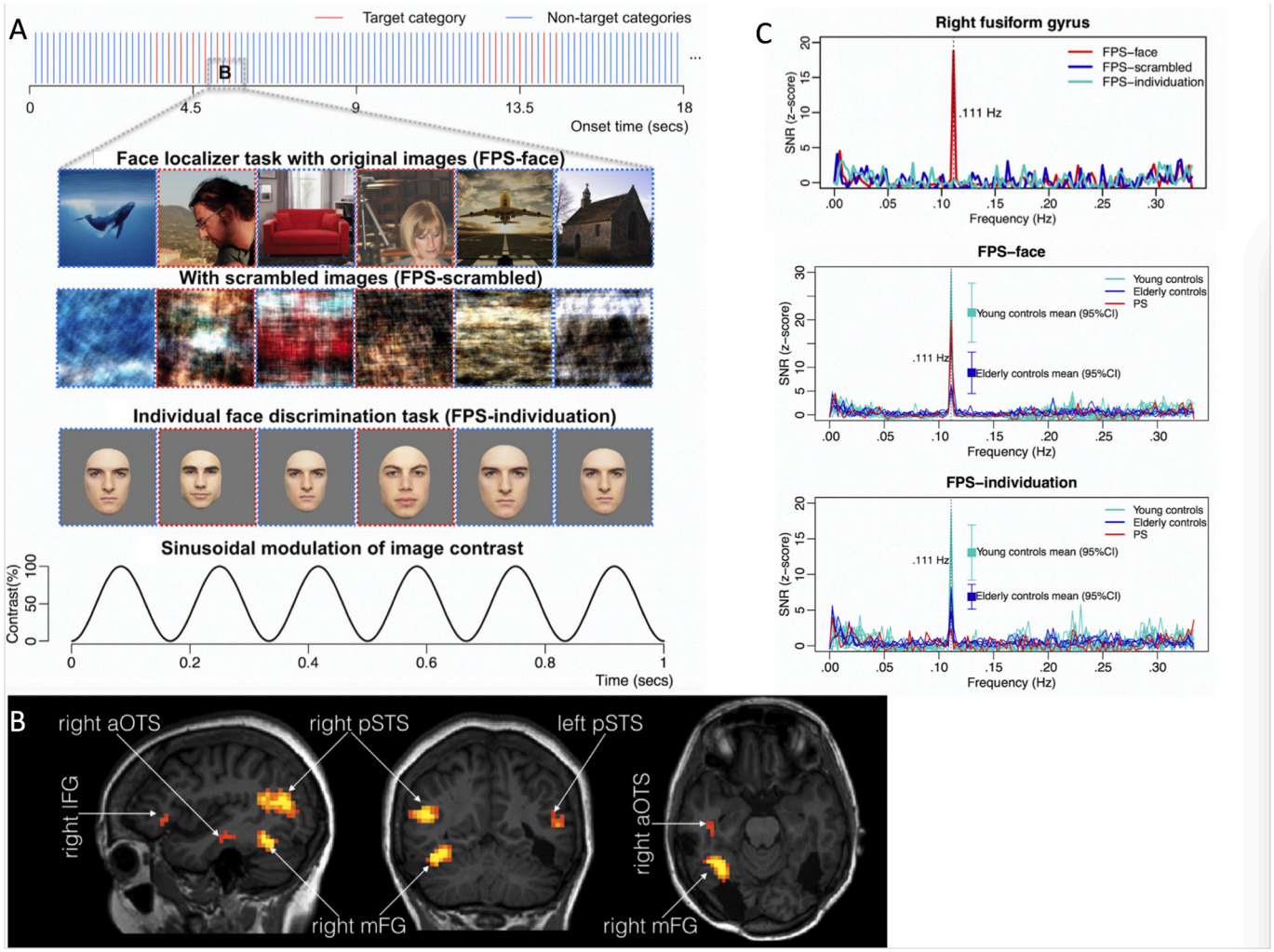


Fig.16. **A**.A highly sensitive and valid face localizer in fMRI inspired from EEG frequency-tagging studies (Gao et al., 2018).Images are presented at a fast periodic stimulation (FPS) rate (6 Hz).Every 9 s, a burst of 7 images from the target category (red bars) alternates with images from the non-target categories (blue bars) for 2.167 s.Below, a 1-sec interval in the face localizer task (FPS-face), where faces are the category of interest, among non-face objects.The scrambled versions of the images are shown below their corresponding original images (FPS-scrambled), above a 1-sec interval in the individual face discrimination task, where one individual identity (in blue frames) is presented throughout the stimulation at different sizes, and 24 other identities serve as the category of interest (in red frames) to form a direct contrast between individual faces (Gao et al., 2019).The sizes of the faces changed randomly up to 20% from trial to trial to minimize low-level repetition effects.The contrast of the images was modulated by a sinusoidal function.**B**.Face-selective regions identified in this localizer in PS's brain (Gao et al., 2019).Note the large response in the right middle fusiform gyrus (FFA) anterior to the IOG lesion as well as the right pSTS activation.Other typical face-selective regions are located anteriorly (e.g., anterior occipito-temporal sulcus, aOTS in the VATL) but despite the extremely high signal-to-noise ratio, there is no posterior activation to the FFA/pSTS in the right or left hemisphere.**C**.Above: Signal-to-noise ratio in PS's right FFA at the face stimulation frequency (0.111 Hz).Below, the SNR spectrum across the lateral portion of the right middle fusiform gyrus is shown for the FPS-face and FPS-individuation experiments.Despite showing above average face-selective activity in this region, PS showed no significant sensitivity to differences between faces.(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

representation of the changed stimulus property.

8.3. Face identity adaptation to different faces in localizer tasks

A small but interesting point for the attentive reader is the following: isn't there a contradiction between the normal right FFA activation in PS's brain in a face localizer paradigm and the lack of release from adaptation in this region? Indeed, a typical fMRI face localizer paradigm contains blocks of pictures of *different* face identities (compared to blocks of different nonface objects; e.g., Fig.1).Thus, if PS's right FFA fails to release from adaptation to different face identities, i.e., if all faces are processed as being the same, shouldn't this region show a lower signal than in normal controls *also* in a face localizer task? A limitation is that any effect at this level is likely to be masked by the high variability between individual brains in terms of the magnitude of face-selective activity in the FFA complex and other face-selective regions (e.g., Rossion et al., 2012; Zhen et al., 2015).Nevertheless, a careful look at the temporal evolution of fMRI activity in suggests indeed an adaptation effect for PS when she is shown different faces in a face localizer, this effect being masked by an above average early face-selective response (Schiltz et al., 2006, Fig.15C).

Note also that even with different facial identities, neural adaptation effects to the general category of faces may be present in such block designs, both for PS and neurotypical observers, leading to an underestimation of face-selectivity in standard face localizer paradigms.It is partly to counteract this kind of effect that Xiaoqing Gao, a former postdoctoral researcher in my lab, Francesco Gentile and I recently developed an original frequency-tagging fMRI face localizer in which highly variable face stimuli are used, and each face stimulus in a mini-block is sandwiched in between a nonface object image (Gao et al., 2018, Fig.16A).Compared to a standard block design localizer with the same stimuli, this frequency-tagging face localizer activates the same high-level regions without contributions of low-level visual cues, and is associated with a substantial increase in signal-to-noise ratio (Gao et al., 2018; see also Gao et al., 2022).As used recently with PS, this face localizer confirmed previous observations, with a particularly high signal-to-noise ratio in her FFA, and no contribution of low-level cues contained in the amplitude spectrum.Most importantly, contrary to normal controls, there was still no effect whatsoever of unfamiliar face identity discrimination for PS in this region (Gao et al., 2019, Fig.15C).

8.4. Generic sensitivity to exemplars in vLOC

There is yet another paradox, or apparent contradiction, between our fMRI findings and PS's behavior: as shown in detail in part I of PS's review, she always scores below normal controls but also usually well above chance level to individuate (i.e., match or discriminate for their identity) pictures of (unfamiliar) faces.How is it possible that her right FFA signal does not discriminate identities, even below normal range then? One possibility, already mentioned in the review part I, is that PS requires a long time to perform above chance level individuation of faces in behavioral tasks, but face stimuli are presented too briefly during the fMR-adaptation paradigms (e.g., 800–1000 ms in Schiltz et al., 2006; Dricot et al., 2008; 166 ms in Gao et al., 2019).Yet, even during an easy face identity discrimination task in the scanner with full (i.e., uncropped) pictures of faces, for which PS performs much better than at chance level, there was still no release from fMRI-adaptation in her right FFA (Dricot et al., 2008).While discrepant results between neural and behavioral measures are not uncommon in cognitive neuroscience, this raises the question of which brain region(s) subtend(s) her residual

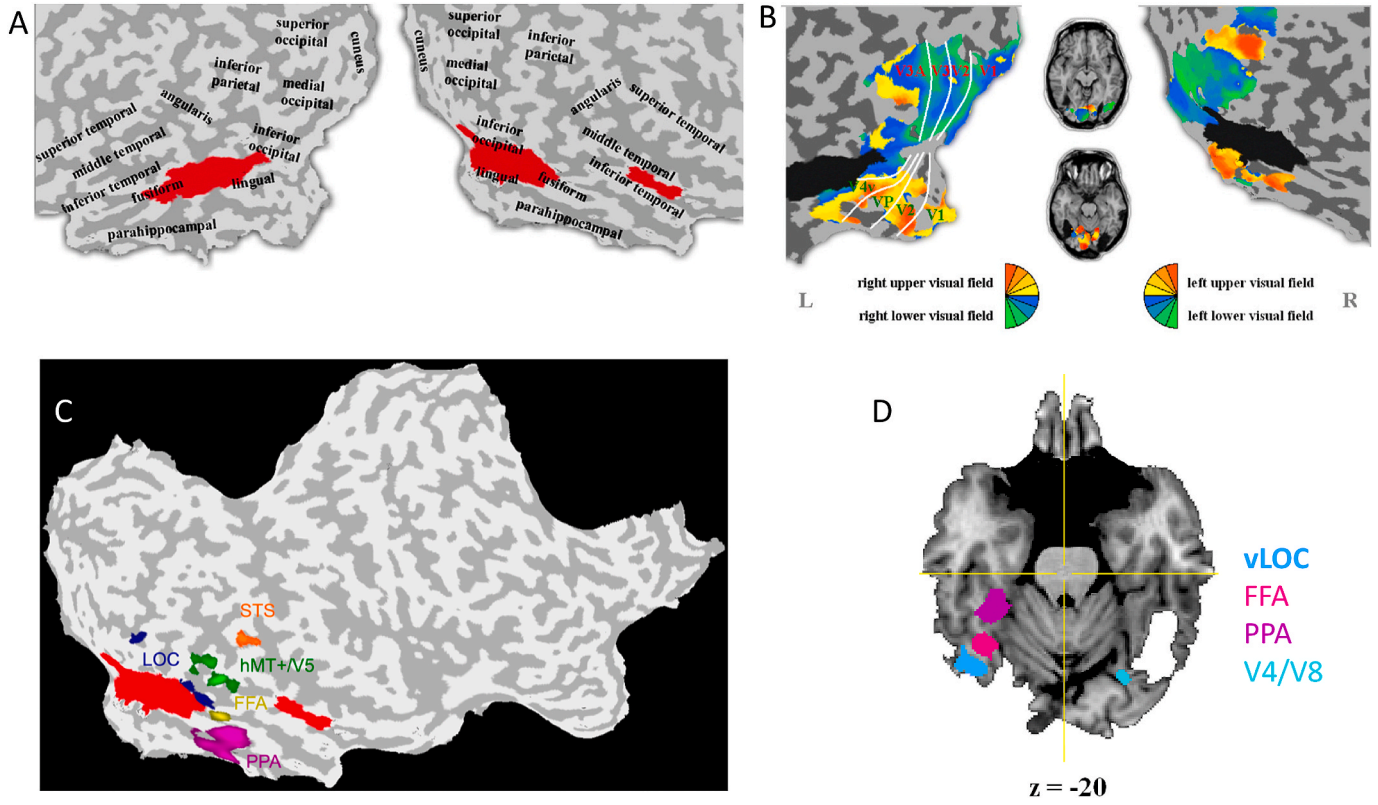


Fig.17. From Sorger et al.(2007).**A**.PS's cortical lesions displayed on flattened views of her posterior brain regions in MRI (compare to Fig.1).**B**.Visual field maps in PS's brain.While brain damage in the left hemisphere spared early visual areas, these maps could not be well-defined in the RH due to brain damage.**C**.A flattened map of PS's brain in MRI, with a number of functional regions around the cortical lesions (FFA, PPA, hMT+/V5, STS, LOC dorsal and ventral).Note the ventral portion of the vLOC abutting the extensive right IOG lesion.This is represented in **D**.in a transverse slice of PS's brain, showing the sparing of the right middle fusiform region, where the FFA is located, and the right vLOC.These functional regions were not found in the left hemisphere (Sorger et al., 2007).

performance at such FIR tasks.

This issue arose in 2007, right after we had just reported an extensive (f)MRI investigation of PS's brain, in which we defined in her cortical lesions relative to known gyri and sulci, retinotopic visual maps as well as a series of known visual regions (hMT+/V5 for motion, V4/V8 for color, etc.) with multiple functional localizers (Sorger et al., 2007) (Fig.17A).In that study, led by Bettina Sorger at Maastricht University, we also identified the so-called lateral occipital complex (LOC), a region divided into a dorsal (dLOC) and ventral (vLOC) portions showing a significantly larger response to object shapes than their destructured versions (Malach et al., 1995).

Somewhat unexpectedly, this observation turned out to be highly valuable, in particular because of the definition of the vLOC in the right hemisphere, just at the border of the IOG lesion (Fig.16).Indeed, the preservation of this region, known to be involved in visual object recognition in general (James et al., 2003), offered a reasonable explanation as to why PS's impairment was restricted to faces, i.e., why she was a case of prosopagnosia (see review part I).Most importantly, when we performed a whole brain analysis of our fMRI-adaptation study with full pictures of faces (Fig.17A; Dricot et al., 2008) and we found significant release from adaptation to different faces in PS's brain in a relatively small spot of activation near the lesion, we knew exactly which region was concerned: unlike her FFA, it is PS's vLOC, a non-face-selective region, which showed neural discrimination signals between different facial identities (Fig.17B).

While this finding was also unexpected, I remember the level of excitement in the laboratory when the spot of activation appeared in the whole brain analysis: there was almost a perfect overlap with the vLOC region (Fig.18B).In this region, PS's level of release from adaptation for face identities was not even significantly below normal range (Fig.18C). Moreover, both PS and neurotypical individuals showed release from adaptation to exemplars of a non-face object categories (butterflies) in both the vLOC and the FFA.In short, and this may seem difficult to believe at first glance, the only non-significant effect was for PS's right FFA with its preferred category of signals, faces (Fig.18C).In fact, contrary to normal observers, there is no face-selective region in PS's brain that seems to be sensitive to differences between face identities (Gao et al., 2019).It is as if her residual face-selective cortical system had become blind to differences between face identities.How could this be?

8.5. How does the right IOG/OFA contribute to FIR?

Both in the initial report of PS's case (Rossion et al., 2003) and in the first study showing a lack of release from adaptation to face identity in (PS's) prosopagnosia (Schiltz et al., 2006), we proposed a critical role of face-selective neural activity of the right IOG: even though face-selectivity in the IOG does not, evidently now, serve as an obligatory gateway to the cortical face system, it may be indeed critical for FIR in 'downstream' regions of the network.More specifically, the FFA (complex) – through its putative direct inputs from the EVC – could initially generate a coarse holistic representation of a face, subsequently refined through reentrant interactions with the OFA to individuate faces (as hypothesized in Rossion, 2008, Fig.6; see also Rossion et al., 2003).

In line with this view, it has long been known that the (right) OFA also shows strong and consistent release from fMRI-adaptation to face identity (e.g., Gauthier et al., 2000; Mazard et al., 2006; Gilaie-Dotan et al., 2010; Hermann et al., 2017).Most recently, we applied our EEG frequency-tagging design to measure individuation of unfamiliar faces based on the principle of release from adaptation (Liu-Shuang et al., 2016; Rossion and Retter, 2020) to direct intracerebral recordings in the VOTC of a large (N = 69) sample of individual brains (Fig.19A and B; Jacques et al., 2020).By subtracting activity in response to inverted from upright faces, we isolated neural individuation responses that cannot be accounted for by low-level sensory cues and showed a significant,

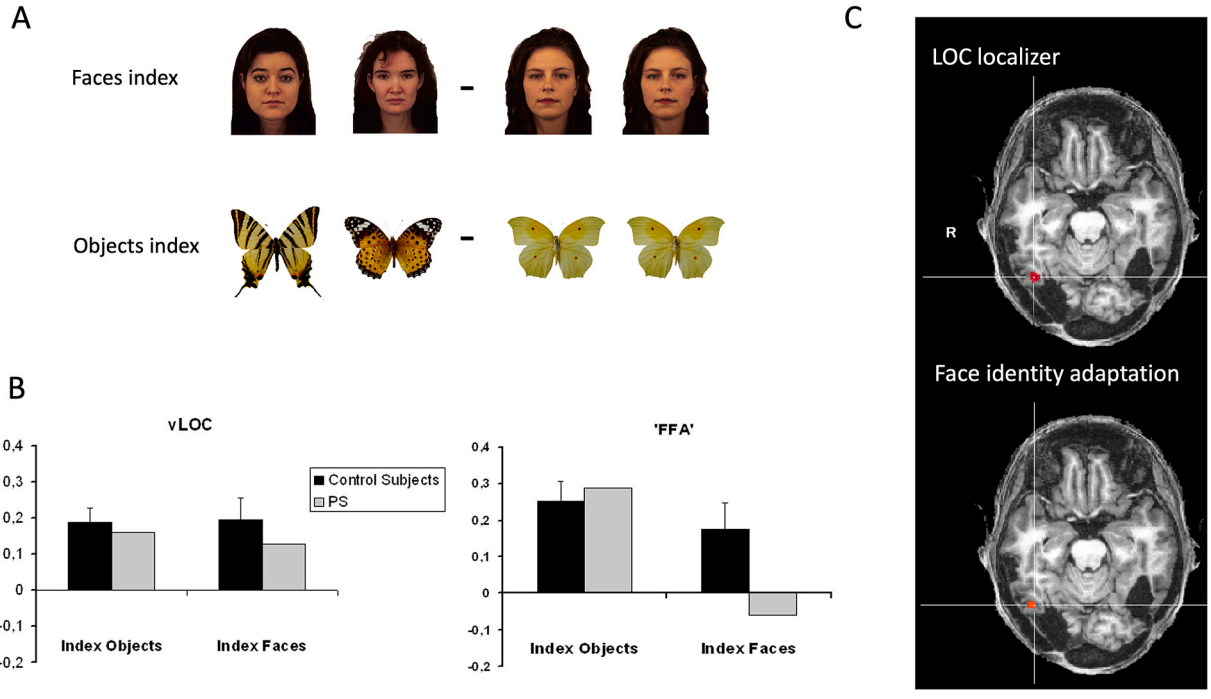


Fig.18. In Dricot et al.(2008; also Steeves et al., 2009), PS was tested in an event-related design in fMRI, with either different face identities or the same face identity repeated and an explicit face matching task.Stimuli were presented with external features to make the task easier for PS.The same task was performed with pictures of a nonface living object category, butterflies.The difference between the 2 face conditions or the 2 butterfly conditions provided an index of release form adaptation.**B.** Release from face identity adaptation was found in exactly the same spot as in an independent vLOC localizer (Sorger et al., 2007, Fig.17).**C.**While in this region, both PS and normal controls showed significant release from fMRI-adaptation, a different pattern was observed in the right FFA, where PS failed again to show a significant release from adaptation to faces.Note that release from adaptation is larger for nonface objects than faces in the FFA even in normal observers, but the physical difference between two butterflies was much larger than the difference between two faces.

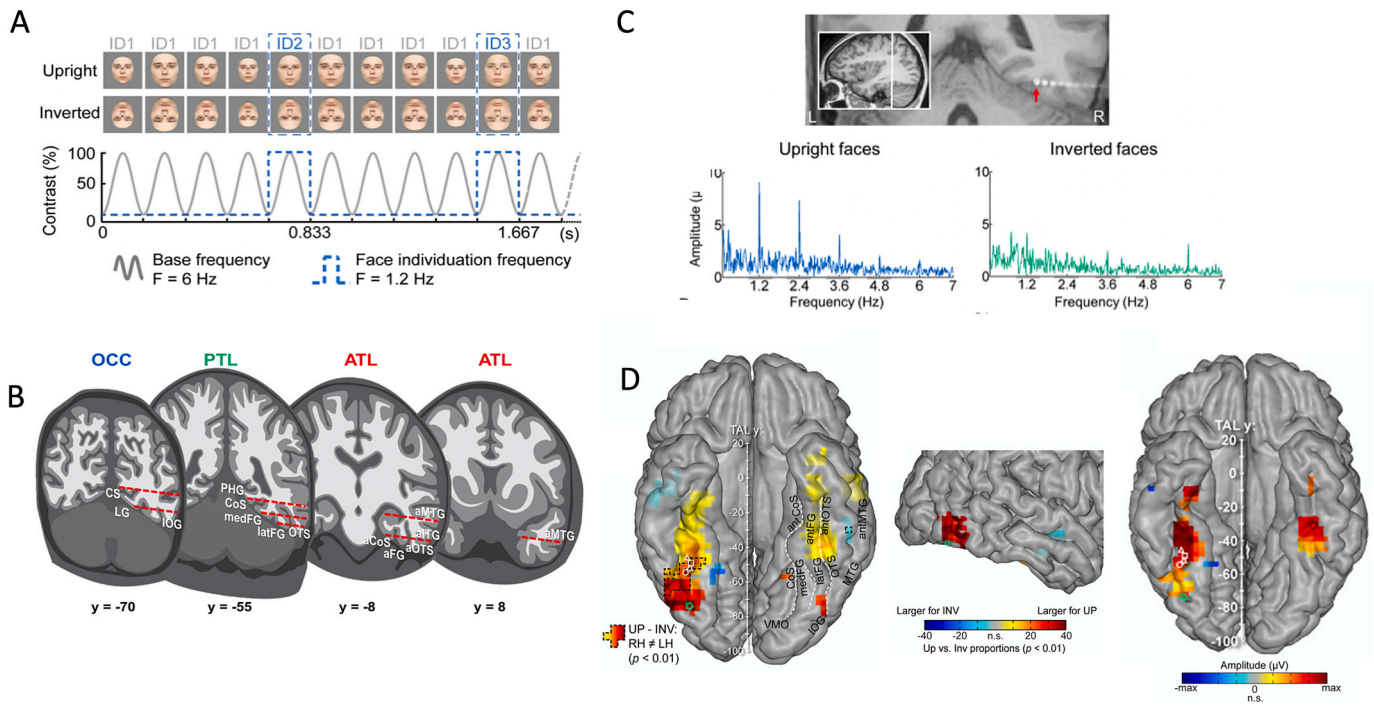


Fig.19. **A**.A frequency oddball paradigm with the same unfamiliar face identity repeated at different sizes at a rapid rate of 6 Hz, interrupted every 5 stimuli (1.2 Hz) by a different face identity (Liu-Shuang et al., 2016; Rossion and Retter, 2020).The same stimulation sequences can be presented at upright or inverted orientation, with a large decrease of 1.2 Hz (and harmonics: 2.4 Hz etc.) response for inverted faces in EEG.**B**.Patients with epilepsy refractory to medication implanted with several intracerebral electrodes in the VOTC.**C**.A typical electrode contact in the right LatMidFG recording a significant face individuation response for upright faces (i.e., at 1.2 Hz and harmonics in the intracerebral EEG spectrum in blue) with a weak or absent response to inverted faces (iEEG spectrum in green on the right).**D**. Group maps (N = 69) showing the proportion of significant electrode contacts when subtracting neural activity to inverted faces from upright faces.Note the peak in the right IOG as shown also on the lateral view in the middle of the panel.On the right, the relative SEEG amplitudes on these contacts, highlighting again the right hemispheric dominance and the particularly large amplitude in the right LatMidFG (see Jacques et al., 2020).(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

relatively narrow, strip of cortex in the right hemisphere, running from the lateral IOG all along the fusiform gyrus (Fig.19D).

Overall, these findings complement those obtained with indirect measures of brain activity (i.e., fMRI) with adaptation paradigms and supports the view that the IOG, mainly in the right hemisphere, contributes directly to FIR.In the left hemisphere, the contribution comes mainly from the middle and anterior portions of the fusiform gyrus, located in or around PS's left hemisphere lesion (Fig.1).Thus, if we put together the findings on patient PS and evidence that these regions are involved in human FIR from direct neural recordings (Jacques et al., 2020), we conclude that direct inputs from early visual cortex to PS's right middle fusiform gyrus are not sufficient to generate sensitive representations of identity: other regions such as the right IOG and/or the left middle lateral fusiform gyrus, which are partially destroyed or deprived or relevant sensory inputs due to brain damage in PS, appear to be necessary.

8.5.1. TMS over the right OFA disrupts face identity recognition

On way to assess the function of a brain region is to transiently disrupt its activity with TMS in neurologically normal experimental participants, as discussed above (section 7.3).TMS studies was not applied in human face recognition research for many years in part because of the widely held belief that the FFA was the sole key region for this function.Unfortunately, the middle fusiform gyrus is relatively far from the cortical surface and the stimulation coil would be too close to the ear so that direct disruption of FFA activity with this technique cannot be achieved.However, this is not the case for the OFA, whose critical role in FIR as illustrated by the case of PS provided the impetus for the first TMS studies of human face recognition (Pitcher, 2009, p.11).

In their first study, Pitcher et al.(2007) showed that TMS over the right IOG of neurotypical individuals disrupts the delayed matching of pictures of unfamiliar faces for their identities.More specifically, performance at a difficult task dropped by about 10% (roughly from 80% to 70%), with no effect for stimulation over the left IOG.This finding was interpreted as providing evidence in neurotypical individuals of a critical contribution of the right OFA in FIR, complementing evidence from PS's case (Rossion et al., 2003) and lesion overlap of reported cases of prosopagnosia (Bouvier and Engel, 2006).

Although the drop of performance at the FIR task was replicated in three experiments in this original TMS study (Pitcher et al., 2007), the findings and their interpretation were not convincing, not only because, as discussed above, the interpretation of the timing of the effect and of its selectivity to the matching of faces differing by facial parts was incorrect, but also because the OFA was not localized with fMRI in individual participants.Instead, the experimenters used the mean Talairach coordinate of the right OFA of individual participants as found in PS's first neuroimaging study (Rossion et al., 2003).Yet, due to substantial interindividual variability in OFA location, this average coordinate did not correspond to more than a couple of individual OFAs.

This limitation may explain why online disruption of FIR with TMS applied to the right OFA in subsequent studies has not always been successful (e.g., Pitcher et al., 2008 with the same standard OFA coordinate; Gilaie-Dotan et al., 2010b during matching of famous faces and a fMRI face localizer; see also Ambrus et al., 2017a,b and the discussion in this latter study).Yet, several studies have replicated and extended the findings of the original study of impaired FIR during TMS to the right OFA (Pitcher, 2009; Pitcher et al., 2012; Solomon-Harris et al., 2013; Bona et al., 2018; see Pitcher, 2021 for review).The study of Solomon-Harris et al.(2013) is noteworthy for our purpose since it is based on the functional dissociation observed on patients PS and DF, showing

that TMS to the right OFA affects FIR performance but leaves generic face recognition intact.

An obvious limitation of TMS applied over the OFA is that the effect cannot be unambiguously attributed to disruption of function at this local level.Indeed, given the above reviewed evidence showing that brain regions of the cortical face network are anatomically and functionally connected, disruption of neural activity in the OFA should affect the function of other regions of the network.This is indeed what is observed when combining TMS and fMRI (Ruff et al., 2009; Bergmann et al., 2021): TMS over the right OFA affects face-selectivity in the FFA (Pitcher et al., 2014).Most importantly, with the same paradigms designed for PS and DF studies (Steeves et al., 2009), it has been shown that TMS over the right OFA decreases release from adaptation to face (but not object) identity in the bilateral FFA (Solomon-Harris et al., 2016).Effect on other regions of the cortical face network could also explain a recent series of impressive findings from Gyula Kovacs and his colleagues, showing that TMS over the right OFA during familiarization with variable views of facial identities prevents matching these facial identities better across (novel) views as compared to unfamiliar faces (Ambrus et al., 2017b), reduces face-name priming effects (Ambrus et al., 2019) and (without hemispheric difference) the correct recall of face-related semantic information (Eick et al., 2020).

Overall, TMS over the right IOG/OFA, directly inspired by the observations on patient PS, have confirmed the critical role of this region in human FIR, even though such effects are not large (i.e., they do not cause transient prosopagnosia) and somewhat inconsistent across studies.It is also fair to say that these studies have not clarified the specific role of the (right) OFA in FIR.While the findings of the original study of Pitcher et al.(2007) were interpreted in favor of a relatively low-level and (very) early contribution (features, early effects) of this region, I have explained above why the timing of the effect is ambiguous and certainly not specific to faces before 100 ms post-stimulus onset (Cohen Kadosh et al., 2011; Pitcher et al., 2012), as originally claimed. Instead, the most recent studies suggest a contribution of the right OFA to (very) high-level processes linked to FIR (Ambrus et al., 2017a,b, 2019; Eick et al., 2020), processes that take place well after 100 ms following stimulus onset and can last until 250–400 ms (e.g., Pickering and Schweinberger, 2003; Wiese et al., 2019; Yan and Rossion, 2020).

In sum, either TMS to the (right) OFA disrupts local processes taking place in this region after 100 ms, or the main effect disruption takes place in anterior regions of the cortical face network after 100 ms. Moreover, as discussed above, the view of a part-based face-selective representation in the right OFA as advocated by Pitcher et al.(2007; Pitcher, 2021) is not supported.Again, the alternative view that populations of neurons in this region, associated with the most centered receptive visual field of all face-selective regions (Finzi et al., 2021, Fig.11), help refining an initially coarse holistic representation through reentrant interactions with face-selective regions of the fusiform gyrus (FFA or FFA complex; Rossion, 2008a; see also (Goffaux et al., 2011) for evidence of coarse-to-fine representation of faces in the cortical face network) is strengthened.

8.5.2. Intracerebral right OFA stimulation causes transient prosopagnosia

Early 2011, I was contacted by colleagues at the university hospital in Nancy, in France, who knew of my research on the neural basis of prosopagnosia with PS, and had just observed an epileptic patient with a spectacular transient interruption of FIR upon electrical stimulation through an electrode contact inside the right IOG.The patient, KV, was a young woman who had been implanted with intracerebral electrodes (StereoElectroEncephalography, SEEG) in December 2010 to define the source and extent of her epileptic seizures refractory to medication.The discovery of the phenomenon occurred incidentally, the patient suddenly reporting that the features of the face of one of the neurologists in the room were rearranged during intracerebral stimulation of this region.Following this observation, several trials with pictures of faces presented one-by-one to the patient objectively showed that, upon direct intracerebral stimulation, KV would suddenly, consistently and transiently lose the ability to recognize a presented famous face identity (Fig.20; see Jonas et al., 2012 and Jonas and Rossion, 2021 for links to videos).Strikingly, the critical stimulated contact was located in the right OFA, as defined in fMRI after the stimulation procedure (Fig.20), in the region corresponding well to PS's main cortical lesion (Fig.1).

KV's failure to recognize a famous face identity during right OFA stimulation happened on 6 out of 7 stimulation trials and lasted only a few seconds, i.e., only during the stimulation: she could recognize the famous face identity right after the end of the stimulation.The patient, who was not aware of the time and location of stimulation during any of the trials, was also able to describe very well why she failed to recognize the identity, reporting either a disturbance in perceiving the spatial relationship of facial elements (i.e., the mouth and eyes changed position; video 1 in Jonas et al., 2012) or an inability to perceive the face as a whole (video 2 in Jonas et al., 2012).There was no effect upon stimulation of other electrode contacts (including a contact located in the right FFA), and KV never reported failures to recognize or such perceptual effects for pictures of objects and scenes upon stimulation on the same electrode contact evoking the FIR impairment.

Admittedly, this was not the first report of impaired FIR following intracranial stimulation.Before that, transient failures to recognize faces and facial hallucinations during stimulation of the fusiform gyrus had been reported in a few patients, as part of recording investigations with subdural grids of electrodes (ElecrocorticoGraphy, ECoG; Allison et al., 1994; Puce et al., 1999).Moreover, Vignal et al.(2000) had reported face specific perceptual changes during right prefrontal stimulation of a single case with intracerebral electrodes, and Mundel et al.(2003) had described a patient who suddenly saw all faces as being similar upon stimulation of the lateral portion of the right middle fusiform gyrus. However, in all these reported cases, the stimulation sites were more anterior than the IOG, and there was no relationship established with the cortical face network as defined in fMRI.Moreover, there was no evidence of normal FIR ability outside of stimulation as defined with neuropsychological tests.In contrast, KV's performance in face recognition, and in FIR in particular, was stringently evaluated, with scores within the normal range or even among the highest for most tests, and typical qualitative indexes of face inversion and composite face effects (Jonas et al., 2012).Thus, although KV, as all of these stimulated cases obviously, cannot be defined as a neurologically typical individual, the effect of stimulation on her right IOG/OFA provided the first clear case of transient prosopagnosia following intracranial stimulation.

Once again, it is the work on PS that motivated my colleagues to contact me about KV's case, even though like many researchers they were initially skeptical about my view of a non-hierarchical organization of the neural basis of human face recognition.I helped them interpret their case, complete the neuropsychological testing on face recognition and describe the case of KV.Unfortunately, as often experienced with single case reports, we struggled to convince reviewers of the originality of the case and the strengths of the findings (for obvious reasons, it is difficult to collect a large number of trials in many different conditions in such clinical cases, and you cannot add any at the revision stage of a paper), which led to a substantial delay in the publication. When KV's case was finally published in July 2012, it was rapidly eclipsed by the publication a few months later - in a higher profile journal - of the case of Parvizi et al.(2012) reporting face distortion following intracranial right FFA stimulation.Yet, there was nothing original in Parvizi et al.(2012)'s case report, neither in term of the stimulated region causing face hallucinations (Allison et al., 1994, 1999; Mundel et al., 2003) nor the correspondence with a fMRI-defined face-selective region that we had reported a few months earlier.Most importantly, contrary to a wide interpretation[12] of this case, Parvizi

[12] e.g., https://sm.stanford.edu/archive/stanmed/2013spring/article10.html; https://www.cogneurosociety.org/seizures_faces_parvizi/.

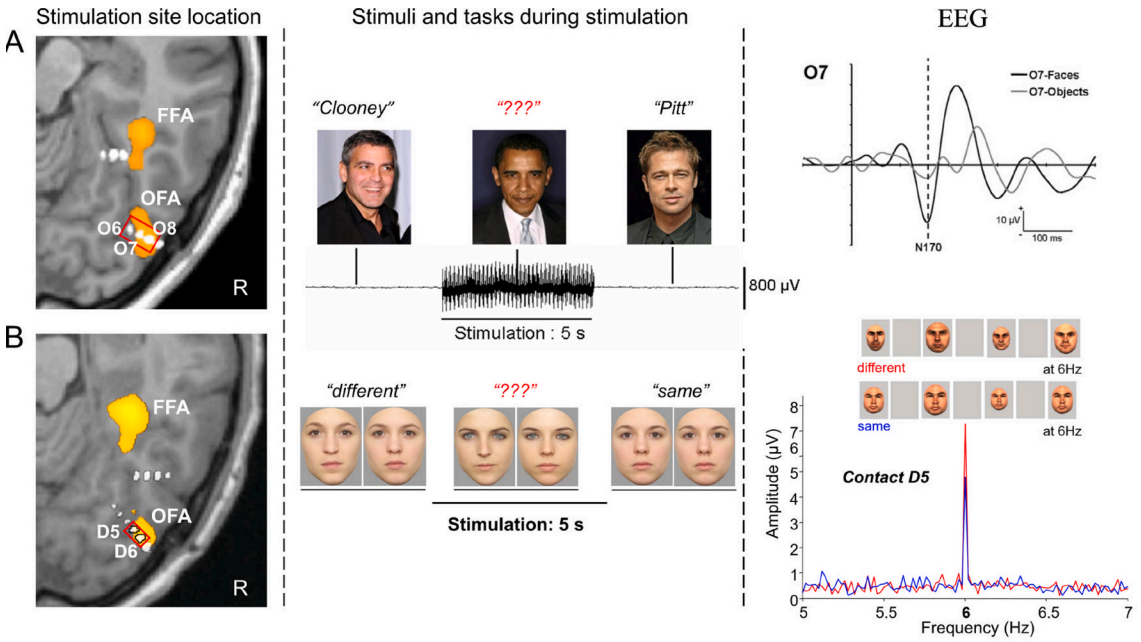


Fig.20. Stimulating the right IOG induces transient FIR impairment (subject KV).A. From Jonas et al.(2012).**B.** Jonas et al.(2014).In both studies, the left panel shows the fMRI face-selective activations in the right VOTC (axial slices) with the SEEG electrodes superimposed (white dots); the middle panel shows the stimuli presented during the stimulation procedure; the right panel shows EEG recordings during the presentation of faces and objects in a standard ERP protocol (A) or a FPVS paradigm measuring sensitivity to face identity (B).In Jonas et al.(2012), the eloquent contacts O6, O7 and O8 (in the red rectangle) are located in the right face-selective IOG (OFA) as shown by fMRI and face-selective ERPs recorded on these contacts.Stimulation of these contacts induced a transient inability to recognize famous faces.In Jonas et al.(2014), stimulating two contacts located within the right face selective IOG (D5 and D6) evoked a transient inability to discriminate unfamiliar face identities.During SEEG, KV was shown with a FPVS adaptation paradigm measuring sensitivity to face identity at a fast rate of 6 Hz, with either identical faces or different faces (Rossion and Boremanse, 2011).The largest difference for different versus same faces for upright faces was found on the eloquent contact D5 (right panel shows responses to different and same faces at 6 Hz in the frequency domain).(For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

et al.(2012) 's patient did not show prosopagnosia: his experience of facial distortion was limited to the face of the experimenter, and he showed no impairment at matching pictures of unfamiliar faces for their identity during intracranial stimulation (see Jonas and Rossion, 2021).

In the past decade, a substantial number of cases with similar face distortion experiences, or generic face recognition impairment, following right FFA/LatMidFG stimulation have been reported, with no effect found reported upon stimulation of the corresponding region of the left hemisphere[13] (Rangarajan et al., 2014; Schalk et al., 2017; Jonas et al., 2018; Schrouff et al., 2020; see Chong et al., 2013; Keller et al., 2017 for generic face recognition impairment).However, technically, no case of transient prosopagnosia due to intracranial stimulation of the (right) FFA has been reported to date (see Jonas and Rossion, 2021 for review).This is somewhat surprising, especially considering the more frequent implantation of electrode contacts (with ECoG or SEEG) in this region as compared to the IOG in epileptic patients.

In contrast, the case of KV with right OFA stimulation has only been replicated so far by another investigation … on herself.About a year after the first SEEG implantation, KV was indeed implanted again with only 3 electrodes in the right occipito-temporal region to narrow the search for the sources of epileptic seizures and perform a standard thermocoagulation procedure to try to suppress her seizures.One electrode was again implanted in the right IOG with electrode contacts in the OFA (Fig.20; see also Jacques et al., 2019 for details).KV was tested even more systematically this time, using a challenging simultaneous unfamiliar face matching task to test for the critical role of the right OFA in FIR independently of name or semantic retrieval impairments.Given KV's excellent FIR ability, faces of different identities were morphed with one another to increase discrimination difficulty (Fig.20; Jonas et al., 2014).KV was presented with 5 pairs successively and, for each pair of faces, had to indicate verbally if the identities were the same or different.Intracerebral OFA stimulation was performed on one random trial out of five, but only when the faces were different (there was no reason to expect identical faces to suddenly look different in identity). Strikingly, while she was almost faultless (and among the best performers) at this task outside of stimulation (Jonas et al., 2014), KV systematically failed at discriminating the different facial identities during right OFA stimulation.

Complementing the electrical stimulation procedure, KV was also tested with a visual stimulation paradigm measuring electrophysiological sensitivity to differences between unfamiliar individual faces (Rossion and Boremanse, 2011).Also strikingly, of all electrode contacts (N = 27) implanted in her brain during the procedure, the largest neural index of FIR, as well as the largest electrophysiological inversion effect, were found on the very same contact in the right OFA leading to transient FIR impairments (Fig.20; Jonas et al., 2014).

Overall, the intracerebral stimulation case of KV provides original and unique support not only for a contribution, as in TMS, but for a *critical* role of the right OFA region in FIR, as supported initially by the case of prosopagnosia PS.Admittedly, the evidence reported on KV has a few limitations.First, even with the 'replication' offered by the second implantation in KV, it is a single case, and it may remain so for some time considering the rarity of intracranial implantations in this region.Unlike TMS studies, the number and variety of trials that can be tested in such cases is limited by clinical constraints.Second, while electrical stimulation with intracerebral contacts is focal, as shown by the absence of effects on neighboring electrode contacts for instance (Jonas et al., 2012, 2014), it is highly likely that upon right OFA stimulation, neural activity in other face-selective regions of the network such as the FFA and more

[13] With the exception of one left handed subject in Rangarajan and Parvizi (2016) and one in Schrouff et al., 2020); see Bukowski et al.(2013) for the role of handedness in face recognition lateralization.

anterior regions is also disrupted (see Jonas and Rossion, 2021).Hence, as for TMS evidence, and whether one advocates a hierarchical or non-hierarchical cortical face network, the effect of intracerebral stimulation in the right OFA cannot be solely attributed to interruption of neural activity in this region.

8.5.3. What is the crucial role of the right OFA alone in face identity recognition?

While all these studies now converge to show a significant contribution of face-selective activity in the right IOG to human face (identity) recognition, with very little if any evidence of a contribution of the homologous region in the left hemisphere, an outstanding question is whether a lesion of the right IOG alone, either directly (i.e., interruption of local function) or indirectly (through interruption of critical processes in connected regions) can cause prosopagnosia.In truth, answering question is more important for clinical purposes than for fundamental research.As noted above in section 3, given her additional cortical lesion of the left middle fusiform gyrus, overlapping with face-selective and high-level face identity neural activity in normal individuals, PS's case cannot be used to make this claim.TMS over the right IOG/OFA in neurotypical individuals cannot clarify this issue either because the disruption of FIR remains modest and inconsistent across tasks and stimuli with this technique.Also, TMS combined with fMRI indicates that the effects of stimulation can propagate to interfere with processing in connected regions, even to face-selective regions of the other hemisphere (Solomon-Harris et al., 2016) in ways that are different than the effect of a focal stable lesion.Even if direct intracranial electrical stimulation may be more focal and lead to more spectacular impairment of the FIR function, the technique suffers from the same limitation in that the effects of stimulation cannot be solely attributed to the stimulated focal point but may spread to distant brain regions of a network (Borchers et al., 2012; Jonas and Rossion, 2021).

For the first time, the well-defined cortical surgery of patient SP, limited to the right IOG and removing all face-selective activity recorded pre-surgery in this region (Weiner et al., 2016, Fig.10) suggested that a lesion of the right IOG alone was *not* sufficient to cause prosopagnosia.In fact, SP's FIR performance was unaffected by the cortical surgery, even though she had difficulties pre-surgery and the contribution of general compensatory factors could not be excluded.

As briefly mentioned in section 3, we recently had the opportunity to perform a similar study in KV who, many years later after the SEEG implantations, finally also underwent cortical surgery of the right IOG in an attempt to remove her persistent epileptic seizures.Given that KV excelled at FIR and her right IOG/OFA was functional as shown with the intracerebral stimulation studies, her case was potentially even more interesting than SP's.In addition to additional behavioral data collection, KV performed two fMRI sessions with the optimal frequency-tagging face localizer, also measuring sensitivity to face individuation with a rapid adaptation paradigm (Gao et al., 2018; Gao et al., 2019, Fig.16).This time, we were only able to perform one fMRI session

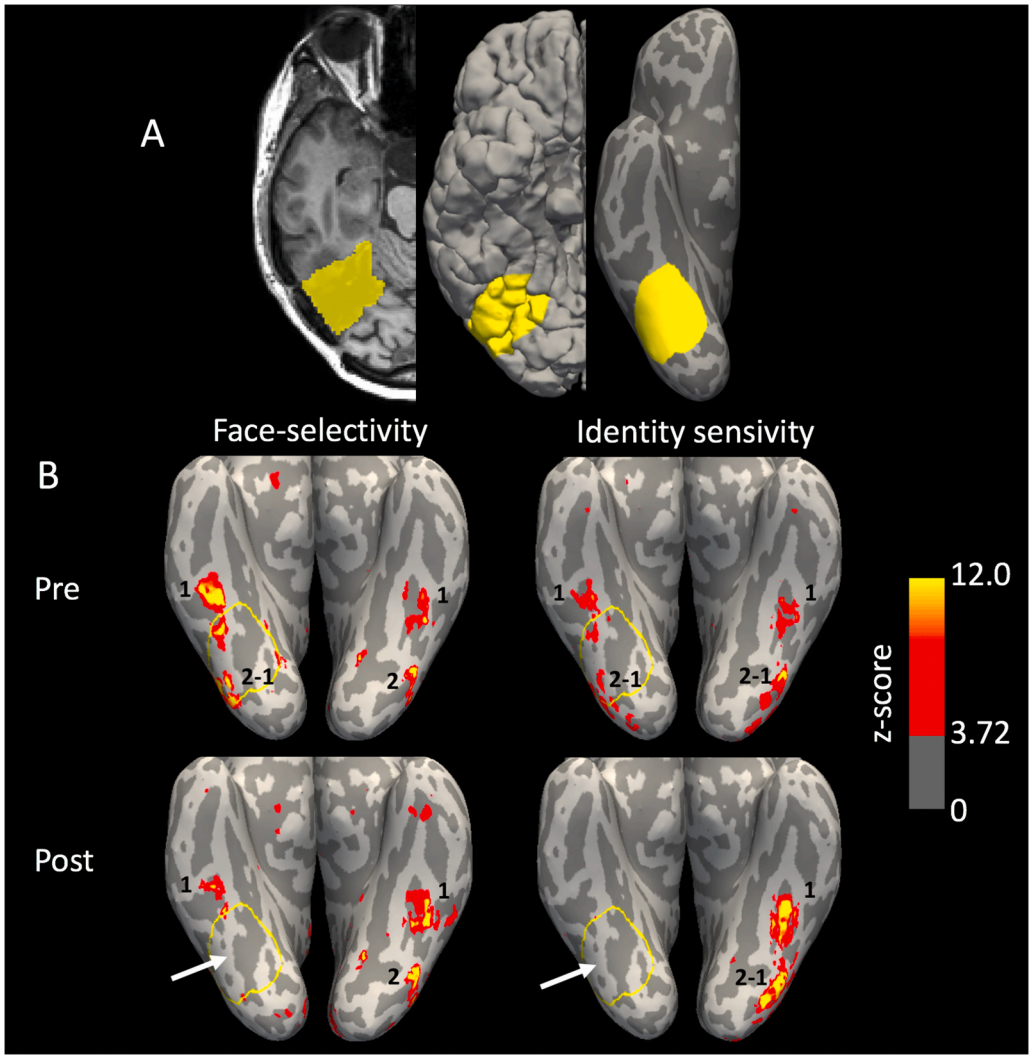


Fig.21. A. Reconstruction of IOG cortical surgery of patient KV.Left, post-session MRI T1 with the resected region highlighted; middle and right: resection mapped onto the cortical surface of pre-session T1.**B.**Face-selective and face identity sensitivity (as measured as in Gao et al., 2019, Fig.15) in a pre-surgery session and post-surgery.Despite the removal of face-selective activity in the right IOG and posterior fusiform gyrus (2–1), face-selectivity is found anteriorly in the middle fusiform gyrus (1), in a location corresponding to the mFus-faces cluster, although there is no response to differences between facial identities in this region.In both experiments, note the substantial increase of activity in the homologous regions of the left hemisphere, which has now become dominant in KV's brain (analyses and illustrations made by Xiaoqian Yan; from Yan, Volfart et al., in preparation).

post-surgery, after about a year.

KV's cortical surgery concerned the right IOG (Fig.21A), effectively removing all face-selective activity in this region, but also in the posterior fusiform gyrus (pFus-faces).Interestingly, the magnitude of the face-selective response in the section of the right middle fusiform gyrus preserved by the cortical resection (mFus-faces) dropped by about 50% (Fig.21B), thus supporting a contribution of inputs from the ipsilateral IOG and pFus-faces to this more anterior face-selective cluster.Yet, the preservation of about half of face-selective activity in this region is also completely in line with the evidence of direct inputs from EVC to mFus-faces (Finzi et al., 2021, Fig.14).

In the few days and weeks following her cortical surgery, KV complained of difficulties at FIR, but described them as relatively mild. However, as tested 5 weeks after the surgery, her pre-surgery high score at unfamiliar face matching (BFRT-c, Rossion and Michel, 2018) had dropped by 10 points (i.e., from 47 to 37/54) and her response times had more than doubled.After a few months, she had no subjective complaints of difficulties at recognizing familiar faces and she performed in the normal range at behavioral tasks requiring to recognize a famous face among three options (a test in which PS performed at chance level, i.e., 33%, see review part I; Volfart et al., in preparation) and was almost flawless and fast at a face identity matching task with natural images of famous or unfamiliar faces (for which PS was also severely impaired as shown in the review part I).

In short, following her extensive right IOG surgery, KV did not become prosopagnosic.Yet, small deficits in unfamiliar face individuation tasks are present and, even a year and a half later, her BFRT-c score and RTs remain in the mild impairment range (for someone with exceptionally good FIR abilities prior to surgery).Interestingly, a fMRI session performed at about 12 months after surgery shows a complete loss of significant face individuation indexes in the face-selective portion of the right middle fusiform gyrus spared by the lesion (as in PS and DF) (Fig.21C).However, strikingly, all face-selective VOTC regions of the left hemisphere now show a large *increase* in face-selectivity and face individuation indexes, as if the intact hemisphere compensated for the loss of function in the RH (Fig.21A).

Several implications can be drawn from these original observations. First, while the right IOG/OFA contributes undoubtedly to FIR, these observations suggest that an isolated lesion of the right IOG (including white matter tracts from EVC to this region), even removing all traces of face-selective activity in this region, may not be sufficient to cause prosopagnosia.Thus, contrary to what I initially thought and suggested about PS's case (Rossion, 2014), it could well be that if her brain damage had only concerned this right IOG region, PS would not have become prosopagnosic.Of course, different individuals, even considering only right-handed subjects, may have different patterns of relative hemispheric dominance for face (identity) recognition (Ettlin et al., 1992; Frässle et al., 2016b; Gao et al., 2018; see also Corrivetti et al., 2017). While KV showed robust bilateral VOTC face-selective activity prior to her surgery (Fig.21), PS's network might have been strongly right lateralized prior to brain damage.Supporting this possibility, even considering that her largest (VOTC) lesion concerned the right hemisphere, PS's remaining cortical face network is in fact extremely right lateralized (e.g., at the level of the STS, anterior OTS and even prefrontal cortex; Fig.16B), and it might well have been the case prior to brain damage.These comparisons across single cases therefore also suggest that, similarly to assessment of language lateralization (Htet et al., 2021), the prognosis of any cortical surgery for FIR should be made based on a priori definition and characterization of the degree of lateralization of the cortical face network with fMRI.

Second, beyond category-selectivity, sensitivity to face identity in middle fusiform gyrus, at least in the anterior cluster usually defined as mFus-faces, indeed seems to require ipsilateral OFA/pFus (i.e., the left hemisphere is not sufficient; Fig.21B), strengthening again the proposal of a critical role at this level of reentrant interactions between the two regions to rapidly refine a face identity representation (Rossion, 2008).

Third, another interesting and original implication of the effect of cortical surgery on KV's case is that impairment at FIR can be, at least partly, compensated quite rapidly after brain damage, with the spared hemisphere increasing its ability to recognize a face as a category and a distinct identity (Fig.21B and C).Again, this is only one very recent observation, made in a relatively young individual patient and following a "clean" surgery procedure, without hemorrhages and other complications, so that one should remain very careful to generalize such findings.Importantly, if we did not have pre-surgery measures of KV's FIR ability, or if we had not been able to measure her behavior shortly after the surgery, we would conclude at this stage that she is in the normal range at this function, and thus that the resected regions were not involved and/or important in this function (for her).

Fourth and finally, the comparison of the spectacular effects of intracerebral right IOG stimulation in patient KV (i.e., systematic transient prosopagnosia, often with a change in perceptual experience; Jonas et al., 2012; Jonas et al., 2014) with the very mild effect observed after cortical resection of a region that encompasses the eloquent electrode contact shows that intracranial electrical stimulation does not mimic the effect of a stable cortical lesion of the stimulated region (Borchers et al., 2012; Jonas and Rossion, 2021).While a stable focal lesion may undoubtedly modify and prevent typical processes in other regions of a connected network (as also shown with KV for the loss of sensitivity to face identity in mFus-faces), it does not *dynamically* interfere with function in this network as is the case with direct electrical stimulation.

9. Summary, conclusions and perspectives

In summary, what have we learned about the neural basis of human face recognition from our extensive series of studies of PS's prosopagnosia? How did her case study directly inspired and constrained neurofunctional models of human face recognition? How did her case study also *indirectly*, i.e., through neural studies performed on normal participants and other clinical cases, contributed to improving our knowledge at this level? And how can we reconcile finding at the neural level with what we learned about PS's prosopagnosia and human face recognition from behavioral studies as described in part I of the review of the case?

9.1. The critical role of the right IOG in human face identity recognition

Before the first PS case report, there was undoubtedly a disproportionate emphasis on the right fusiform gyrus in the field of human face recognition.This emphasis can be traced back to the early proposal of a critical contribution of posterior occipito-temporal structures of the right hemisphere to prosopagnosia (Hecaen and Angelergues, 1962).As mentioned in the first review on the neural basis of the clinical condition, lesions of the fusiform gyrus (and right matter tracts around that region) were often confirmed in autopsied reported cases (Meadows, 1974).Subsequently, in what is still the most cited review on prosopagnosia, published 40 years ago, Damasio et al.(1982) also underscored the critical role of the fusiform gyrus in this condition.Yet, this influential review (see also Damasio et al., 1982) was wrong in claiming that the visual recognition impairment in prosopagnosia was not specific to faces (see Rossion, 2018a and part I of this review) and that it was always caused by bilateral (occipito-temporal) lesions (see Fig.3).In retrospect, Damasio's third error was to fail to acknowledge the key role of the right IOG, rather emphasizing, in addition to the fusiform gyrus, a critical role of the lingual and parahippocampal gyri in causing prosopagnosia (Damasio et al., 1982).In reality, there is little evidence that populations of neurons in these latter two structures play a (critical) category-specific role in human face recognition.

With the advent of (functional) neuroimaging studies of face recognition in the early 1990s, the focus shifted once again to the right fusiform gyrus (Sergent et al., 1992; Kanwisher et al., 1997; McCarthy et al.,

1997).Yet, face-selective potentials were also recorded intracranially in the lateral IOG at about the same time (Allison et al., 1994, 1999) and, within a few years, neuroimaging studies using PET or fMRI also noticed right lateralized face-selective activity in the IOG (Puce et al., 1996; Halgren et al., 1999; Haxby et al., 1999; Gauthier et al., 2000; Rossion et al., 2000), this activity being sufficiently reliable to be tentatively incorporated as an early processing stage in early neurofunctional models of human face recognition (Haxby et al., 2000).

While PS was certainly not the first reported neurological patient with FIR impairment following right IOG damage, she was a clear case of prosopagnosia, i.e., with a category-selective disorder at face identity recognition, with a predominant right IOG lesion.Hence, her case report drew attention to the necessary role of the right IOG in human face recognition, especially since there was no face-selective activation in this region (i.e., no OFA; Rossion et al., 2003) and PS's right (middle) fusiform gyrus was left structurally intact.The overlap of lesions in a number of reported cases of prosopagnosia a few years later appeared to confirm the critical role of this right IOG region (Bouvier and Engel, 2006), but it is the case of PS that undoubtedly inspired the series of TMS studies exploring the critical role of the right OFA in FIR (Pitcher, 2009, 2021).It also attracted the interest of clinicians and researchers to the first observation of a case of transient prosopagnosia during intracranial stimulation, patient KV, with the eloquent stimulation contact located inside the right IOG/OFA (Fig.20; Jonas et al., 2012; see Jonas and Rossion, 2021 for review).While all these studies converge to show a significant contribution of face-selective activity in the right IOG (i.e., right OFA) to human face (identity) recognition, the following cortical surgery of the right IOG in patient KV nevertheless suggests that removal of this region unilaterally causes long-term difficulties at FIR, but may not be sufficient to cause prosopagnosia if anterior face-selective regions (i.e., FFA complex and more anterior regions of the VATL) as well as the left VOTC remain intact (Fig.21).

9.2. Why a non-hierarchical human cortical face network?

The case study of PS also provided arguably the first evidence to question the notion of hierarchical (neural) processing in human face recognition research.Yet, admittedly, this hierarchical view is still very much influential and dominant in this area of research (section 7; Fig.12).As discussed above, one reason for that is that there is little understanding of the role of reentrant interactions (often equated/confounded with the notion of cortical feedback, which implies the notion of spatio-temporal hierarchy; see Vezoli et al., 2021) and direct pathways bypassing cortical areas of a putative hierarchy (Grill-Spector et al., 2018).Moreover, at first glance, both reentry and bypassing cortical routes apparently greatly complicate the precise definition of the type of visual representation and computation(s) performed at one stage of a network, and challenge currently influential hierarchically-based DNNs to provide valid information for understanding face and visual object recognition.

According to the view advocated here, face-selectivity from clear views of faces in the human adult brain could be triggered in parallel in different VOTC regions, which would exchange reentrant inputs dynamically to be synchronized in time (i.e., without one performing "computation" on a defined type of representation to send inputs to the other one and receive feedback in return) (e.g., Fig.13).Moreover, in a number of cases, face-selectivity could even emerge first in midfusiform regions (FFA complex) (section 7.2) through direct inputs bypassing the cortical face "hierarchy" (i.e., early visual cortex to mFus-faces; Finzi et al., 2021).Such inputs should not be merely considered as "complementary" or "redundant" with sensory inputs from EVC to the IOG. Instead, there are situations in which these inputs may be absolutely critical, otherwise the visual stimulus would not even be recognized/perceived as a face: e.g., if the stimulus is large, located in the periphery, relatively far away, masked by noise, occlusion, etc., in short, in all contexts in which the perception of a face benefits, or even depends on, a unified integration of parts – holistic representation – across a relatively large facial space.Reentrant connections between the midfusiform regions (FFA complex) and the IOG (OFA) would help generating a finer-grained holistic representation (part I) of a face identity, this representation being "distributed" within the face-selective cortical system (Rossion, 2008, Fig.6).Unfortunately, the presence of such reentrant connections is difficult to establish with currently available methods of investigation in the human brain (although, as demonstrated for a while, their relevance can be tested in biologically plausible computational models of the visual system; e.g., Finkel and Edelman, 1989; Tononi et al., 1992).

Compared to a cortical face network with a fixed number of hierarchical stages, both the notion of distributed representations through reentrant cortical interactions and bypass routes also provide more flexibility and plasticity, and are more compatible with large-scale gradients of sensitivity to functional properties (e.g., a visuo-semantic gradient in the postero-anterior axis; Rossion, 2022b) and genuine interindividual variability in the size, location and even number of face-selective regions in the VOTC (Gao et al., 2022).

9.3. Towards an integrated neurofunctional view?

This briefly sketched neurofunctional view is obviously speculative at this state of knowledge, certainly incomplete, probably incorrect. However, it offers a plausible alternative to a standard but inconsistent view according to which a series of hierarchical stages are required to build perceptual face representations, from parts to wholes, from view-dependent to view-invariant, from face detection to identity, with the outcome of this hierarchy, a putative view-invariant perceptual representation of a face identity, being *then* associated to another representation of that face identity in memory.Instead, according to the present neurofunctional view as described in part I of this review (Rossion, 2022a), the populations of neurons distributed in the VOTC that have learned to fire selectively to faces (and face identities) and form clusters through experience simply constitute our cortical *memories* of faces (i.e., a distributed cortical memory; Fuster, 2009).Face recognition occurs when low-level sensory (i.e., visual) inputs successfully trigger - in parallel - activity of these cortical memories, which are dynamically linked by reentry.Thus, in this framework, *perception* (of a face) is nothing more than the subjective (i.e., conscious) experience of this recognition process (Figure 23 in Rossion, 2022a).Recognition/Perception merely reflects the successful matching of variable sensory inputs to a selective cortical memory built from experience, without involving local computational processes at the level of these neuronal populations.Given that they do not represent a fixed series of computational/representational stages, face-selective neuronal clusters can thus truly vary across individual brains in terms of their size, anatomical location and even their number (Gao et al., 2022).Inspired by the study of the prosopagnosic patient PS and strengthened by converging evidence from multiple sources as described here and in the first part of the review, this alternative neurofunctional view will deserve further development and evaluation beyond single case studies in neuropsychology and cognitive neuroscience in the years to come.

Credit author statement

Bruno Rossion wrote and revised the whole review manuscript.

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References

Allison, T., Ginter, H., McCarthy, G., Nobre, A.C., Puce, A., Luby, M., Spencer, D.D., 1994. Face recognition in human extrastriate cortex. Journal of neurophysiology 71, 821–825.
Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends in cognitive sciences 4, 267–278.
Allison, T., Puce, A., Spencer, D.D., McCarthy, G., 1999. Electrophysiological studies of human face perception.I: Potentials generated in occipitotemporal cortex by face and non-face stimuli. Cerebral cortex 9, 415–430.
Ambrus, G.G., Amado, C., Krohn, L., Kovács, G., 2019. TMS of the occipital face area modulates cross-domain identity priming. Brain structure & function 224, 149–157.
Ambrus, G.G., Dotzer, M., Schweinberger, S.R., Kovács, G., 2017a. The occipital face area is causally involved in the formation of identity-specific face representations. Brain structure & function 222, 4271–4282.
Ambrus, G.G., Windel, F., Burton, A.M., Kovács, G., 2017b. Causal evidence of the involvement of the right occipital face area in face-identity acquisition. NeuroImage 148, 212–218.
Amihai, I., Deouell, L.Y., Bentin, S., 2011. Neural adaptation is related to face repetition irrespective of identity: a reappraisal of the N170 effect. Experimental brain research 209, 193–204.
Andrews, T.J., Schluppeck, D., Homfray, D., Matthews, P., Blakemore, C., 2002. Activity in the fusiform gyrus predicts conscious perception of Rubin's vase-face illusion. NeuroImage 17, 890–901.
Anzellotti, S., Caramazza, A., 2014. The neural mechanisms for the recognition of face identity in humans. Frontiers in psychology 5, 672. https://doi.org/10.3389/fpsyg.2014.00672.
Atkinson, A.P., Adolphs, R., 2011. The neuropsychology of face perception: beyond simple dissociations and functional selectivity. Philosophical transactions of the Royal Society of London.Series B, Biological sciences 366, 1726–1738.
Avidan, G., Behrmann, M., 2009. Functional MRI reveals compromised neural integrity of the face processing network in congenital prosopagnosia. Current biology 19, 1146–1150.
Avidan, G., Tanzer, M., Hadj-Bouziane, F., Liu, N., Ungerleider, L.G., Behrmann, M., 2014. Selective dissociation between core and extended regions of the face processing network in congenital prosopagnosia. Cerebral cortex 24, 1565–1578.
Axelrod, V., Rozier, C., Malkinson, T.S., Lehongre, K., Adam, C., Lambrecq, V., Navarro, V., Naccache, L., 2019. Face-selective neurons in the vicinity of the human fusiform face area. Neurology 92, 197–198.
Barraclough, N.E., Perrett, D.I., 2011. From single cells to social perception. Philosophical transactions of the Royal Society of London.Series B, Biological sciences 366, 1739–1752.
Barton, J.J., 2008. Structure and function in acquired prosopagnosia: lessons from a series of 10 patients with brain damage. Journal of neuropsychology 2, 197–225.
Barton, J.J., Hanif, H., Ashraf, S., 2009. Relating visual to verbal semantic knowledge: the evaluation of object recognition in prosopagnosia. Brain 132, 3456–3466.
Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological Studies of Face Perception in Humans. Journal of cognitive neuroscience 8, 551–565.
Benton, A.L., Van Allen, M.W., 1972. Prosopagnosia and facial discrimination. Journal of the neurological sciences 15, 167–172.
Bergmann, T.O., Varatheeswaran, R., Hanlon, C.A., Madsen, K.H., Thielscher, A., Siebner, H.R., 2021. Concurrent TMS-fMRI for causal network perturbation and proof of target engagement. NeuroImage 237, 118093.
Berman, M.G., Park, J., Gonzalez, R., Polk, T.A., Gehrke, A., Knaffla, S., Jonides, J., 2010. Evaluating functional localizers: the case of the FFA. NeuroImage 50, 56–71.
Bernstein, M., Yovel, G., 2015. Two neural pathways of face processing: A critical evaluation of current models. Neuroscience and biobehavioral reviews 55, 536–546.
Biederman, I., 1987. Recognition-by-components: a theory of human image understanding. Psychol Rev 94, 115–147.
Bona, S., Silvanto, J., Cattaneo, Z., 2018. TMS over right OFA affects individuation of faces but not of exemplars of objects. Neuropsychologia 117, 364–370.
Borghesani, V., Narvid, J., Battistella, G., Shwe, W., Watson, C., Binney, R.J., Sturm, V., Miller, Z., Mandelli, M.L., Miller, B., Gorno-Tempini, M.L., 2019. "Looks familiar, but I do not know who she is": the role of the anterior right temporal lobe in famous face recognition. Cortex; a journal devoted to the study of the nervous system and behavior 115, 72–85.
Bouvier, S.E., Engel, S.A., 2006. Behavioral deficits and cortical damage loci in cerebral achromatopsia. Cerebr.Cortex 16, 183–191.
Bruce, V., Young, A.W., 1986. Understanding face recognition. Br.J.Psychol. 77, 305–327.
Bryant, K., Preuss, T., 2018. A comparative perspective on the human temporal lobe. In: Bruner, E., Ogihara, N., Tanabe, H. (Eds.), Digital Endocasts: from Skulls to Brains, pp. 239–258.
Buckner, R.L., 2013. The cerebellum and cognitive function: 25 years of insight from anatomy and neuroimaging. Neuron 80 (3), 807–815.
Bukowski, H., Dricot, L., Hanseeuw, B., Rossion, B., 2013. Cerebral lateralization of face-sensitive areas in left-handers: only the FFA does not get in right. Cortex 49, 2583–2589.
Bullier, J., 2001. Integrated model of visual processing. Brain research.Brain research reviews 36 (2–3), 96–107.
Busigny, T., Joubert, S., Felician, O., Ceccaldi, M., Rossion, B., 2010. Holistic perception of the individual face is specific and necessary: evidence from an extensive case study of acquired prosopagnosia. Neuropsychologia 48, 4057–4092.
Busigny, T., Rossion, B., 2010a. Acquired prosopagnosia abolishes the face inversion effect. Cortex 46, 965–981.
Busigny, T., Rossion, B., 2010b. Acquired prosopagnosia is not due to a general impairment in fine-grained recognition of exemplars of a visually homogeneous category. Behav.Neurol. 23, 229–231.
Busigny, T., Rossion, B., 2011. Holistic processing impairment can be restricted to faces in acquired prosopagnosia: evidence from the global/local Navon effect. J. Neuropsychol. 5 (Pt 1), 1–14.
Burra, N., Kerzel, D., Ramon, M., 2017. Gaze-cueing requires intact face processing - Insights from acquired prosopagnosia. Brain and cognition 113, 125–132.
Busigny, T., Graf, M., Mayer, E., Rossion, B., 2010a. Acquired prosopagnosia as a face-specific disorder, ruling out the general visual similarity account. Neuropsychologia 48, 2051–2067.
Busigny, T., Joubert, S., Felician, O., Ceccaldi, M., Rossion, B., 2010b. Holistic perception of the individual face is specific and necessary: evidence from an extensive case study of acquired prosopagnosia. Neuropsychologia 48, 4057–4092.
Busigny, T., Mayer, J., Rossion, B., 2013. Prosopagnosia. In: O.Godefroy, Vascular Cognitive Impairment & Dementia.The Behavioral & Cognitive Neurology of Stroke, second ed., pp. 231–246.
Caldara, R., Schyns, P., Mayer, E., Smith, M., Gosselin, F., Rossion, B., 2005. Does prosopagnosia take the eyes out from faces? Evidence for a defect in the use of diagnostic facial information in a brain-damaged patient. J.Cognit.Neurosci. 17, 1652–1666.
Calder, A.J., Young, A.W., 2005. Understanding the recognition of facial identity and facial expression. Nat.Rev.Neurosci. 6, 641–651.
Caramazza, A., McCloskey, M., 1988. The case for single-patient studies. Cogn. Neuropsychol. 5, 517–527.
Carlson, T., Grol, M.J., Verstraten, F.A., 2006. Dynamics of visual recognition revealed by fMRI. Neuroimage 32, 892–905.
Catani, M., Jones, D.K., Donato, R., Ffytche, D.H., 2003. Occipito-temporal connections in the human brain. Brain 126, 2093–2107.
Chance, S.A., Sawyer, E.K., Clover, L.M., et al., 2013. Hemispheric asymmetry in the fusiform gyrus distinguishes Homo sapiens from chimpanzees. Brain Struct.Funct. 218, 1391–1405.
Chong, S.C., Jo, S., Park, K.M., Joo, E.Y., Lee, M.J., Hong, S.C., Hong, S.B., 2013. Interaction between the electrical stimulation of a face-selective area and the perception of face stimuli. Neuroimage 15 (77), 70–76.
Cohen, A.L., Soussand, L., Corrow, S.L., Martinaud, O., Barton, J.J.S., Fox, M.D., 2019. Looking beyond the face area: lesion network mapping of prosopagnosia. Brain 142, 3975–3990.
Cohen Kadosh, K., Walsh, V., Cohen Kadosh, R., 2011. Investigating face-property specific processing in the right OFA. Soc.Cognit.Affect Neurosci. 6, 58–65.
Collins, J.A., Koski, J.E., Olson, I.R., 2016. More than meets the eye: the merging of perceptual and conceptual knowledge in the anterior temporal face area. Front.Hum. Neurosci. 10, 2016.
Collins, C.E., Turner, E.C., Sawyer, E.K., Reed, J.L., Young, N.A., Flaherty, D.K., Kaas, J. H., 2016. Cortical cell and neuron density estimates in one chimpanzee hemisphere. Proc.Natl.Acad.Sci.U.S.A. 113, 740–745.
Connor, C.E., 2010. Neuroscience.A new viewpoint on faces. Science 330, 764–765.
Conway, B.R., 2018. The organization and operation of inferior temporal cortex. Annual review of vision science 4, 381–402.
Corrivetti, F., Herbet, G., Moritz-Gasser, S., Duffau, H., 2017. Prosopagnosia Induced by a Left Anterior Temporal lobectomy Following a Right Temporo-occipital Resection in a Multicentric Diffuse Low-Grade Glioma. World neurosurgery 97, 756.e1–756.e5.
Crone, N.E., Miglioretti, D.L., Gordon, B., Lesser, R.P., 1998. Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis.II.Event-related synchronization in the gamma band. Brain 121, 2301–2315.
Crouzet, S.M., Kirchner, H., Thorpe, S.J., 2010. Fast saccades toward faces: face detection in just 100 ms. J.Vis. 10 (4), 1–17. https://doi.org/10.1167/10.4.16.
Cusimano, M., 2015. Bond villain fails neuroanatomy. Nature 528, 479.
Dalrymple, K.A., Oruç, I., Duchaine, B., Pancaroglu, R., Fox, C.J., Iaria, G., Handy, T.C., Barton, J.J., 2011. The anatomic basis of the right face-selective N170 in acquired prosopagnosia: a combined ERP/fMRI study. Neuropsychologia 49, 2553–2563.
Damasio, A.R., Damasio, H., Van Hoesen, G.W., 1982. Prosopagnosia: anatomic basis and behavioral mechanisms. Neurology 32, 331–341.
Davies-Thompson, J., Gouws, A., Andrews, T.J., 2009. An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. Neuropsychologia 47, 1627–1635.
Davies-Thompson, J., Andrews, T.J., 2012. Intra- and interhemispheric connectivity between face-selective regions in the human brain. J.Neurophysiol. 108, 3087–3095.
Decramer, T., Premereur, E., Zhu, Q., Van Paesschen, W., van Loon, J., Vanduffel, W., Taubert, J., Janssen, P., Theys, T., 2021. Single-unit recordings reveal the selectivity of a human face area. J.Neurosci. 41, 9340–9349.

Deffke, I., Sander, T., Heidenreich, J., Sommer, W., Curio, G., Trahms, L., Lueschow, A., 2007. MEG/EEG sources of the 170-ms response to faces are co-localized in the fusiform gyrus. Neuroimage 35, 1495–1501.
Degelder, B., Rouw, R., 2001. Beyond localisation: a dynamical dual route account of face recognition. Acta Psychol. 107, 183–207.
De Renzi, E., Faglioni, P., Grossi, D., Nichelli, P., 1991. Apperceptive and associative forms of prosopagnosia. Cortex 27, 213–221.
Delvenne, J.F., Seron, X., Coyette, F., Rossion, B., 2004. Evidence for perceptual deficits in associative visual (prosop)agnosia: a single-case study. Neuropsychologia 42, 597–612.
DiCarlo, J.J., Cox, D.D., 2007. Untangling invariant object recognition. Trends Cognit. Sci. 11, 333–341.
DiCarlo, J.J., Zoccolan, D., Rust, N.C., 2012. How does the brain solve visual object recognition? Neuron 73, 415–434.
Dricot, L., Sorger, B., Schiltz, C., Goebel, R., Rossion, B., 2008. The roles of "face" and "non-face" areas during individual face perception, evidence by fMRI, adaptation in a brain-damaged prosopagnosic patient. Neuroimage 40, 318–332.
Dubois, J., de Berker, A.O., Tsao, D.Y., 2015. Single-unit recordings in the macaque face patch system reveal limitations of fMRI MVPA. J.Neurosci.: the official journal of the Society for Neuroscience 35, 2791–2802.
Dubois, S., Rossion, B., Schiltz, C., Bodart, J.-M., Dejardin, S., Michel, C., Bruyer, R., Crommelinck, M., 1999. Effect of familiarity on the processing of human faces. Neuroimage 9, 278–289.
Duchaine, B., Yovel, G., 2015. A revised neural framework for face processing. Annual Review of Vision Science 1, 293–416.
Duncan, K.J., Pattamadilok, C., Knierim, I., Devlin, J.T., 2009. Consistency and variability in functional localisers. Neuroimage 46, 1018–1026.
Edelman, G.M., 1978. Group selection and phasic reentrant signaling: a theory of higher brain function. In: Schmitt, F.O. (Ed.), The Mindful Brain. MIT Press, Cambridge.
Edelman, G.M., Gally, J.A., 2013. Reentry: a key mechanism for integration of brain function. Front.Integr.Neurosci. 7, 63.
Eger, E., Henson, R.N., Driver, J., Dolan, R.J., 2007. Mechanisms of top-down facilitation in perception of visual objects studied by fMRI. Cerebr.Cortex 17, 2123–2133.
Eick, C.M., Kovacs, G., Rostalski, S.M., Rohrig, L., Ambrus, G.G., 2020. The occipital face area is causally involved in identity-related visual-semantic associations. Brain Struct.Funct. 225, 1483–1493.
Elbich, D.B., Molenaar, P.C.M., Scherf, K.S., 2019. Evaluating the organizational structure and specificity of network topology within the face processing system. Hum.Brain Mapp. 40 (9), 2581–2595.
Esterman, M., Yantis, S., 2010. Perceptual expectation evokes category-selective cortical activity. Cerebr.Cortex 20, 1245–1253.
Ettlin, T.M., Beckson, M., Benson, D.F., Langfitt, J.T., Amos, E.C., Pineda, G.S., 1992. Prosopagnosia: a bihemispheric disorder. Cortex 28, 129–134.
Evans, J.J., Heggs, A.J., Antoun, N., Hodges, J.R., 1995. Progressive prosopagnosia associated with selective right temporal lobe atrophy.A new syndrome? Brain 118 (Pt 1), 1–13.
Ewbank, M.P., Henson, R.N., Rowe, J.B., Stoyanova, R.S., Calder, A.J., 2013. Different neural mechanisms within occipitotemporal cortex underlie repetition suppression across same and different-size faces. Cerebr.Cortex 23, 1073–1084.
Fairhall, S.L., Ishai, A., 2007. Effective connectivity within the distributed cortical network for face perception. Cerebr.Cortex 17, 2400–2406.
Fan, X., Wang, F., Shao, H., Zhang, P., He, S., 2020. The bottom-up and top-down processing of faces in the human occipitotemporal cortex. Elife 9, 1–21.
Fang, F., He, S., 2005. Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. Neuron 45 (5), 793–800.
Farah, M.J., 1990. Visual Agnosia: Disorders of Object Recognition and what They Tell Us about Normal Vision. MIT Press, Cambridge.
Farivar, R., Blanke, O., Chaudhuri, A., 2009. Dorsal-ventral integration in the recognition of motion-defined unfamiliar faces. J.Neurosci. 29, 5336–5342.
Felleman, D.J., Van Essen, D.C., 1991. Distributed hierarchical processing in the primate cerebral cortex. Cerebr.Cortex 1, 1–47.
Finkel, L.H., Edelman, G.M., 1989. Integration of distributed cortical systems by reentry: a computer simulation of interactive functionally segregated visual areas. J. Neurosci. 9, 3188–3208.
Finzi, D., Gomez, J., Nordt, M., Rezai, A.A., Poltoratski, S., Grill-Spector, K., 2021. Differential spatial computations in ventral and lateral face-selective regions are scaffolded by structural connections. Nat.Commun. 12, 2278.
Fiset, D., Blais, C., Royer, J., Richoz, A.R., Dugas, G., Caldara, R., 2017. Mapping the impairment in decoding static facial expressions of emotion in prosopagnosia. Soc. Cognit.Affect Neurosci. 1;12 (8), 1334–1341.
Formisano, E., Goebel, R., 2003. Tracking cognitive processes with functional MRI, mental chronometry. Curr.Opin.Neurobiol. 13, 174–181.
Fox, C.J., Iaria, G., Barton, J.J., 2008. Disconnection in prosopagnosia and face processing. Cortex 44, 996–1009.
Frässle, S., Paulus, F.M., Krach, S., Jansen, A., 2016a. Test-retest reliability of effective connectivity in the face perception network. Hum.Brain Mapp. 37, 730–744.
Frässle, S., Paulus, F.M., Krach, S., Schweinberger, S.R., Stephan, K.E., Jansen, A., 2016b. Mechanisms of hemispheric lateralization: asymmetric interhemispheric recruitment in the face perception network. Neuroimage 124, 977–988.
Freiwald, W.A., 2020. Social interaction networks in the primate brain. Curr.Opin. Neurobiol. 65, 49–58.
Freiwald, W.A., Tsao, D.Y., 2010. Functional compartmentalization and viewpoint generalization within the macaque face-processing system. Science 330, 845–851.
Freiwald, W., Duchaine, B., Yovel, G., 2016. Face processing systems: from neurons to real-world social perception. Annu.Rev.Neurosci. 39, 325–346.
Friston, K.J., Li, B., Daunizeau, J., Stephan, K.E., 2003. Network discovery with DCM. Neuroimage 56, 1202–1221.
Furl, N., Henson, R.N., Friston, K.J., Calder, A.J., 2015. Network Interactions Explain Sensitivity to Dynamic Faces in the Superior Temporal Sulcus. Cerebral cortex 25, 2876–2882.
Fuster, J.M., 2009. Cortex and memory: emergence of a new paradigm. J.Cognit. Neurosci. 21, 2047–2072.
Fysh, M.C., Ramon, M., 2022. Accurate but inefficient: Standard face identity matching tests fail to identify prosopagnosia. Neuropsychologia 165, 108119.
Gao, X., Gentile, F., Rossion, B., 2018. Fast periodic stimulation (FPS): a highly effective approach in fMRI brain mapping. Brain Struct.Funct. 223, 2433–2454.
Gao, X., Vuong, Q.C., Rossion, B., 2019. The cortical face network of the prosopagnosic patient PS with fast periodic stimulation in fMRI. Cortex 119, 528–542.
Gao, X., Wen, M., Sun, M., Rossion, B., 2022. A Genuine Interindividual Variability in Number and Anatomical Localization of Face-Selective Regions in the Human Brain. Cerebral cortex, bhab519.
Gauthier, I., Tarr, M.J., Moylan, J., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. The fusiform "face area" is part of a network that processes faces at the individual level. J. Cognit.Neurosci. 12, 495–504.
Gentile, F., Ales, J., Rossion, B., 2017. Being BOLD: the neural dynamics of face perception. Hum.Brain Mapp. 38, 120–139.
Gilaie-Dotan, S., Malach, R., 2007. Sub-exemplar shape tuning in human face-related areas. Cerebr.Cortex 17, 325–338.
Gilaie-Dotan, S., Gelbard-Sagiv, H., Malach, R., 2010a. Perceptual shape sensitivity to upright and inverted faces is reflected in neuronal adaptation. Neuroimage 50, 383–395.
Gilaie-Dotan, S., Silvanto, J., Schwarzkopf, D.S., Rees, G., 2010b. Investigating representations of facial identity in human ventral visual cortex with transcranial magnetic stimulation. Frontiers in human neuroscience 4, 50. https://doi.org/10.3389/fnhum.2010.00050.
Gobbini, M.I., Haxby, J.V., 2007. Neural systems for recognition of familiar faces. Neuropsychologia 45, 32–41.
Goesaert, E., Op de Beeck, H.P., 2013. Representations of facial identity information in the ventral visual stream investigated with multivoxel pattern analyses. J.Neurosci. 33, 8549–8558.
Goffaux, V., Peters, J., Haubrechts, J., Schiltz, C., Jansma, B., Goebel, R., 2011. From coarse to fine? Spatial and Temporal dynamics of cortical face processing. Cerebr. Cortex 21, 467–476.
Golarai, G., Ghahremani, D.G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J.L., Gabrieli, J.D.E., Grill-Spector, K., 2007. Differential development of high-level visual cortex correlates with category-specific recognition memory. Nat.Neurosci. 10, 512–522.
Golarai, G., Liberman, A., Grill-Spector, K., 2017. Experience shapes the development of neural substrates of face processing in human ventral temporal cortex. Cerebr.Cortex 27, 1229–1244.
Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. Trends Neurosci. 15, 20–25.
Goodale, M., Milner, D., 2013. Sight Unseen: an Exploration of Conscious and Unconscious Vision, second ed. Oxford University Press.
Grill-Spector, K., Malach, R., 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol. 107, 293–321.
Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends Cognit.Sci. 10, 14–23.
Grill-Spector, K., Weiner, K.S., Kay, K., Gomez, J., 2017. The functional neuroanatomy of human face perception. Annual Review of Vision Science 3, 167–196.
Grill-Spector, K., Weiner, K.S., Gomez, J., Stigliani, A., Natu, V.S., 2018. The functional neuroanatomy of face perception: from brain measurements to deep neural networks. Interface focus 8, 20180013.
Groen, I., Silson, E.H., Pitcher, D., Baker, C.I., 2021. Theta-burst TMS of lateral occipital cortex reduces BOLD responses across category-selective areas in ventral temporal cortex. Neuroimage 230, 117790.
Gross, C., 1999. Brain, Vision, Memory: Tales in the History of Neuroscience. MIT Press.
Gross, C.G., Bender, D.B., Rocha-Miranda, C.E., 1969. Visual receptive fields of neurons in inferotemporal cortex of the monkey. Science (New York, N.Y.) 166, 1303–1306.
Gross, C.G., Rocha-Miranda, C.E., Bender, D.B., 1972. Visual properties of neurons in inferotemporal cortex of the macaque. J.Neurophysiol. 35, 96–111.
Grossi, D., Soricelli, A., Ponari, M., Salvatore, E., Quarantelli, M., Prinster, A., Trojano, L., 2014. Structural connectivity in a single case of progressive prosopagnosia: the role of the right inferior longitudinal fasciculus. Cortex 56, 111–120.
Grüsser, O.-J., Landis, T., 1991. Visual Agnosias and Other Disturbances of Visual Perception and Cognition. CRC Press, Boca Raton, 1991.
Gschwind, M., Pourtois, G., Schwartz, S., Van De Ville, D., Vuilleumier, P., 2012. White-matter connectivity between face-responsive regions in the human brain. Cerebr. Cortex 22, 1564–1576.
Halgren, E., Dale, A.M., Sereno, M.I., Tootell, R.B.H., Marinkovic, K., Rosen, B., 1999. Location of human face-selective cortex with respect to retinotopic areas. Hum.Brain Mapp. 7, 29–37.
Halgren, E., Raij, T., Marinkovic, K., Jousmaki, V., Hari, R., 2000. Cognitive response profile of the human fusiform face area as determined by MEG. Cerebr.Cortex 10, 69–81.
Harris, A.M., Aguirre, G.K., 2007. Prosopagnosia.*Current Biology* 17, R7–R8.
Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends Cognit.Sci. 4, 223–233.

Hauk, O., Rice, G.E., Volfart, A., Magnabosco, F., Ralph, M., Rossion, B., 2021. Face-selective responses in combined EEG/MEG recordings with fast periodic visual stimulation (FPVS). NeuroImage 242, 118460.
Haxby, J.V., Gobbini, I., 2011. Distributed neural systems for face perception. In: Calder, Andy, Rhodes, Gillian, Johnson, Mark, Jim Haxby (Eds.), Oxford Handbook of Face Perception. Oxford University Press, p. 93—110.
Haxby, J.V., Ungerleider, L.G., Clark, V.P., Schouten, J.L., Hoffman, E.A., Martin, A., 1999. The effect of face inversion on activity in human neural systems for face and object perception. Neuron 22, 189–199.
Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science 293, 2425–2430.
Hay, D.C., Young, A.W., 1982. The human face. In: Ellis, A.W. (Ed.), Normality and Pathology in Cognitive Functions. Academic Press, London, pp. 173–202.
Hecaen, H., Angelergues, R., 1962. Agnosia for faces (prosopagnosia). Arch.Neurol. 7, 92–100.
Henriksson, L., Mur, M., Kriegeskorte, N., 2015. Faciotopy-A face-feature map with face-like topology in the human occipital face area. Cortex; a journal devoted to the study of the nervous system and behavior 72, 156–167.
Henson, R.N., 2016. Repetition suppression to faces in the fusiform face area: a personal and dynamic journey. Cortex; a journal devoted to the study of the nervous system and behavior 80, 174–184.
Herbet, G., Zemmoura, I., Duffau, H., 2018. Functional Anatomy of the Inferior Longitudinal Fasciculus: From Historical Reports to Current Hypotheses. Frontiers in neuroanatomy 12, 77.
Herculano-Houzel, S., 2016. The Human Advantage: A New Understanding of How Our Brain Became Remarkable. MIT Press, Cambridge (Massachusetts).
Hermann, P., Grotheer, M., Kovács, G., Vidnyánszky, Z., 2017. The relationship between repetition suppression and face perception. Brain imaging and behavior 11, 1018–1028.
Hershler, O., Golan, T., Bentin, S., Hochstein, S., 2010. The wide window of face detection. J.Vis. 10 (10), 21. https://doi.org/10.1167/10.10.21.
Hesse, J.K., Tsao, D.Y., 2020. The macaque face patch system: a turtle's underbelly for the brain. Nat.Rev.Neurosci. 21, 695–716.
Heywood, C.A., Cowey, A., 1992. The role of the 'face-cell' area in the discrimination and recognition of faces by monkeys. Philos.Trans.R.Soc.Lond.B Biol.Sci. 335, 31–38, 8.
Hochstein, S., Ahissar, M., 2002. View from the top: hierarchies and reverse hierarchies in the visual system. Neuron 36, 791–804.
Htet, N.N., Pizarro, R., Nair, V.A., Chu, D.Y., Meier, T., Tunnell, E., Rutecki, P., Hermann, B., Meyerand, E.M., Prabhakaran, V., 2021. Comparison of language and memory lateralization by functional MRI and wada test in epilepsy. Frontiers in neurology and neuroscience research 2, 100009.
Hubel, D.H., Wiesel, T.N., 1962. Receptive fields, binocular interaction and functional architecture in the cat visual cortex. J.Physiol.(Lond.) 160, 106–154.
Hubel, D.H., Wiesel, T.N., 2005. Brain and Visual Perception: the Story of a 25-year Collaboration. Oxford University Press US.
Hulten, P., 1987. The Arcimboldo Effect. Thames and Hudson, London.
Hung, C.C., Yen, C.C., Ciuchta, J.L., Papoti, D., Bock, N.A., Leopold, D.A., Silva, A.C., 2015. Functional mapping of face-selective regions in the extrastriate visual cortex of the marmoset. J.Neurosci.: the official journal of the Society for Neuroscience 35, 1160–1172.
Hupé, J.M., James, A.C., Payne, B.R., Lomber, S.G., Girard, P., Bullier, J., 1998. Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. Nature 394, 784–787.
Ishai, A., 2008. Let's face it: it's a cortical network. Neuroimage 40, 415–419.
Issa, E.B., DiCarlo, J.J., 2012. Precedence of the eye region in neural processing of faces. J.Neurosci. 32 (47), 16666–16682.
Itier, R.J., Taylor, M.J., 2004. Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. Neuroimage 21, 1518–1532.
Jacques, C., d'Arripe, O., Rossion, B., 2007. The time course of the face inversion effect during individual face discrimination. J.Vis. 7, 3. https://doi.org/10.1167/7.8.3.
Jacques, C., Jonas, J., Maillard, L., Colnat-Coulbois, S., Koessler, L., Rossion, B., 2019. The inferior occipital gyrus as a major cortical source of the face-evoked N170: evidence from simultaneous scalp and intracerebral human recordings. Hum.Brain Mapp. 40, 1403–1418.
Jacques, C., Rossion, B., Volfart, A., Brissart, H., Colnat-Coulbois, S., Maillard, L., Jonas, J., 2020. The neural basis of rapid unfamiliar face individuation with human intracerebral recordings. Neuroimage 117174.
Jacques, C., Rossion, B., 2009. The initial representation of individual faces in the right occipito-temporal cortex is holistic: electrophysiological evidence from the composite face illusion. J.Vis. 11;9 (6), 1–16, 8.
James, T.W., Culham, J., Humphrey, G.K., Milner, A.D., Goodale, M.A., 2003. Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. Brain : J.Neurol. 126, 2463–2475.
James, T.W., Humphrey, G.K., Gati, J.S., Menon, R.S., Goodale, M.A., 2000. The effects of visual object priming on brain activation before and after recognition. Curr.Biol. 10, 1017–1024.
Jansari, A., Miller, S., Pearce, L., Cobb, S., Sagiv, N., Williams, A.L., Tree, J.J., Hanley, J. R., 2015. The man who mistook his neuropsychologist for a popstar: when configural processing fails in acquired prosopagnosia. Frontiers in human neuroscience 9, 390. https://doi.org/10.3389/fnhum.2015.00390.
Jiang, F., Badler, J., Righi, G., Rossion, B., 2015. Category search speeds up face-selective fMRI responses in a non-hierarchical cortical face network. Cortex 66, 69–80.
Jiang, F., Blanz, V., Rossion, B., 2011b. Holistic processing of shape cues in face identification: evidence from face inversion, composite faces and acquired prosopagnosia. Visual Cognition 19, 1003–1034.
Jiang, F., Dricot, L., Righi, G., Tarr, M.J., Goebel, R., Weber, J., Rossion, B., 2011. Face categorization in visual scenes may start in a higher order area of the right fusiform gyrus, evidence from dynamic visual stimulation in neuroimaging. J.Neurophysiol. 106, 2720–2736.
Jiang, X., Rosen, E., Zeffiro, T., Vanmeter, J., Blanz, V., Riesenhuber, M., 2006. Evaluation of a shape-based model of human face discrimination using FMRI and behavioral techniques. Neuron 50, 159–172.
Jonas, J., Rossion, B., 2021. Intracerebral electrical stimulation to understand the neural basis of human face identity recognition. Eur.J.Neurosci. 54, 4197–4211.
Jonas, J., Descoins, M., Koessler, L., Colnat-Coulbois, S., Sauvee, M., Guye, M., Vignal, J.-P., Vespignani, H., Rossion, B., Maillard, L., 2012. Focal electrical intracerebral stimulation of a face-sensitive area causes transient prosopagnosia. Neuroscience 222, 281–288.
Jonas, J., Rossion, B., Krieg, J., Koessler, L., Colnat-Coulbois, S., Vespignani, H., Jacques, C., Vignal, J.P., Brissart, H., Maillard, L., 2014. Intracerebral electrical stimulation of a face-selective area in the right inferior occipital cortex impairs individual face discrimination. Neuroimage 99, 487–497.
Jonas, J., Brissart, H., Hossu, G., Colnat-Coulbois, S., Vignal, J.P., Rossion, B., Maillard, L., 2018. A face identity hallucination (palinopsia) generated by intracerebral stimulation of the face-selective right lateral fusiform cortex. Cortex 99, 296–310.
Kadipasaoglu, C.M., Conner, C.R., Baboyan, V.G., Rollo, M., Pieters, T.A., Tandon, N., 2017. Network dynamics of human face perception. PLoS One 12, e0188834.
Kanwisher, N., 2017. The quest for the FFA and where it led. J.Neurosci. 37, 1056–1061.
Kanwisher, N., 2000. Domain specificity in face perception. Nat.Neurosci. 3, 759–763.
Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical area specialized for the perception of faces. Phil.Trans.R.Soc.B 361, 2109–2128.
Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area a module in human extrastriate cortex specialized for face perception. J.Neurosci. 17, 4302–4311.
Kanwisher, N., Tong, F., Nakayama, K., 1998. The effect of face inversion on the human fusiform face area. Cognition 68, B1–B11.
Keller, C.J., Davidesco, I., Megevand, P., Lado, F.A., Malach, R., Mehta, A.D., 2017. Tuning face perception with electrical stimulation of the fusiform gyrus. Hum.Brain Mapp. 38, 2830–2842.
Kesssler, R., Rusch, K., Wende, K., Schuster, V., Jansen, A., 2021. Revisiting the effective connectivity within the distributed cortical network for face perception. Neuroimage 1, 100045.
Khuvis, S., Yeagle, E.M., Norman, Y., Grossman, S., Malach, R., Mehta, A.D., 2021. Face-selective units in human ventral temporal cortex reactivate during free recall. J. Neurosci. 41, 3386–3399.
Kleinschmidt, A., Cohen, L., 2006. The neural bases of prosopagnosia and pure alexia: recent insights from functional neuroimaging. Curr.Opin.Neurol. 19, 386–391.
Klink, P.C., Dagnino, B., Gariel-Mathis, M.A., Roelfsema, P.R., 2017. Distinct feedforward and feedback effects of microstimulation in visual cortex reveal neural mechanisms of texture segregation. Neuron 95, 209–220 e3.
Kravitz, D.J., Saleem, K.S., Baker, C.I., Ungerleider, L.G., Mishkin, M., 2013. The ventral visual pathway: an expanded neural framework for the processing of object quality. Trends Cognit.Sci. 17, 26–49.
Kriegeskorte, N., Formisano, E., Sorger, B., Goebel, R., 2007. Individual faces elicit distinct response patterns in human anterior temporal cortex. Proc.Natl.Acad.Sci.U. S.A. 104, 20600–20605.
Lafer-Sousa, R., Conway, B.R., Kanwisher, N.G., 2016. Color-biased regions of the ventral visual pathway lie between face- and place-selective regions in humans, as in macaques. J.Neurosci. 36, 1682–1697.
Landis, T., Cummings, J.L., Christen, L., Bogen, J.E., Imhof, H.G., 1986. Are unilateral right posterior cerebral lesions sufficient to cause prosopagnosia? Clinical and radiological findings in six additional patients. Cortex 22, 243–252.
LeCun, Y., Bengio, Y., Hinton, G., 2015. Deep learning. Nature 521, 436–444.
Leopold, D.A., Bondar, I.V., Giese, M.A., 2006. Norm-based face encoding by single neurons in the monkey inferotemporal cortex. Nature 442, 572–575.
Levy, I., Hasson, U., Avidan, G., Hendler, T., Malach, R., 2001. Center-periphery organization of human object areas. Nat.Neurosci. 4, 533–539.
Lissauer, H., 1890. Ein Fall von Seelenblindheit nebst einem beitrage zue Theorie derselben. Archiv fur Psychiatrie und Nervenkrankheiten 21, 22–270. English translation by Jackson, M.Cognitive Neuropsychology 1988, 5, 157-192.
Liu-Shuang, J., Torfs, K., Rossion, B., 2016. An objective electrophysiological marker of face individualisation impairment in acquired prosopagnosia with fast periodic visual stimulation. Neuropsychologia 83, 100–113.
Liu, J., Harris, A., Kanwisher, N., 2002. Stages of processing in face perception: an MEG study. Nat.Neurosci. 5, 910–916.
Logothetis, N.K., 2008. What we can do and what we cannot do with fMRI. Nature 453, 869–878.
Lohse, M., Garrido, L., Driver, J., Dolan, R.J., Duchaine, B.C., Furl, N., 2016. Effective connectivity from early visual cortex to posterior occipitotemporal face areas supports face selectivity and predicts developmental prosopagnosia. J.Neurosci. 36, 3821–3828.
Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P. J., Brady, T.J., Rosen, B.R., Tootell, R.B., 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc.Natl.Acad. Sci.U.S.A. 92, 8135–8139.
Mandler, G., 1980. Recognizing: the judgment of previous occurrence. Psychol.Rev. 87, 252–271.

Marotta, J.J., Genovese, C.R., Behrmann, M., 2001. A functional MRI study of face recognition in patients with prosopagnosia. Neuroreport 13, 1581–1587.
Marr, D., 1982. Vision: A Computational Investigation into Human Representation and Processing of Visual Information. Freeman, San Francisco.
Marr, D., Nishihara, H.K., 1978. Representation and recognition of the spatial organization of three-dimensional shapes. Proceedings of the Royal Society of London.Series B, Biological sciences 200, 269–294.
Mazard, A., Schiltz, C., Rossion, B., 2006. Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex. Neuropsychologia 44, 912–922.
McCarthy, G., Puce, A., Belger, A., Allison, T., 1999. Electrophysiological studies of human face perception.II: Response properties of face-specific potentials generated in occipitotemporal cortex. Cerebral cortex 9, 431–444.
McCarthy, G., Puce, A., Gore, J., Allison, T., 1997. Face-specific processing in the human fusiform gyrus. J.Cognit.Neurosci. 9, 605–610.
Meadows, J.C., 1974. The anatomical basis of prosopagnosia. J.Neurol.Neurosurg. Psychiatr. 37, 489–501.
Meyers, E.M., Borzello, M., Freiwald, W.A., Tsao, D., 2015. Intelligent information loss: the coding of facial identity, head pose, and non-face information in the macaque face patch system. J.Neurosci.: the official journal of the Society for Neuroscience 35 (18), 7069–7081.
Miller, K.J., Leuthardt, E.C., Schalk, G., Rao, R.P.N., Anderson, N.R., Moran, D.W., Miller, J.W., Ojemann, J.G., 2007. Spectral changes in cortical surface potentials during motor movement. J.Neurosci. 27, 2424–2432.
Miller, J.A., Voorhies, W.I., Li, X., Raghuram, I., Palomero-Gallagher, N., Zilles, K., Sherwood, C.C., Hopkins, W.D., Weiner, K.S., 2020. Sulcal morphology of ventral temporal cortex is shared between humans and other hominoids. Sci.Rep. 10, 17132.
Milner, A.D., Perrett, D.I., Johnston, R.S., Benson, P.J., Jordan, T.R., Heeley, D.W., Bettucci, D., Mortara, F., Mutani, R., Terazzi, E., 1991. Perception and action in 'visual form agnosia. Brain 114 (Pt 1B), 405–428.
Mooney, C.M., 1956. Closure with negative after-images under flickering light. Can.J. Psychol. 10, 191–199.
Mumford, D., 1992. On the computational architecture of the neocortex.II.The role of cortico-cortical loops. Biol.Cybern. 66, 241–251.
Mundel, T., Milton, J.G., Dimitrov, A., Wilson, H.W., Pelizzari, C., Uftring, S., Torres, I., Erickson, R.K., Spire, J.P., Towle, V.L., 2003. Transient inability to distinguish between faces: electrophysiologic studies. J.Clin.Neurophysiol. 20, 102–110, 2003.
Mur, M., Ruff, D.A., Bodurka, J., Bandettini, P.A., Kriegeskorte, N., 2010. Face-identity change activation outside the face system: "release from adaptation" may not always indicate neuronal selectivity. Cerebr.Cortex 20, 2027–2042.
Nasr, S., Tootell, R.B., 2012. Role of fusiform and anterior temporal cortical areas in facial recognition. Neuroimage 63, 1743–1753.
Nestor, A., Plaut, D.C., Behrmann, M., 2011 Jun 14. Unraveling the distributed neural code of facial identity through spatiotemporal pattern analysis. Proc.Natl.Acad.Sci. U.S.A. 108 (24), 9998–10003.
Nestor, A., Plaut, D.C., Behrmann, M., 2011b. Unraveling the distributed neural code of facial identity through spatiotemporal pattern analysis. Proc.Natl.Acad.Sci.U.S.A. 108, 9998–10003.
Nordt, M., Gomez, J., Natu, V.S., Rezai, A.A., Finzi, D., Kular, H., Grill-Spector, K., 2021. Cortical recycling in high-level visual cortex during childhood development. Nat. Human Behav. 5, 1686–1697.
O'Craven, K.M., Downing, P.E., Kanwisher, N., 1999. fMRI evidence for objects as the units of attentional selection. Nature 401, 584–587.
O'Toole, A.J., Roark, D.A., Abdi, H., 2002. Recognizing moving faces: a psychological and neural synthesis. Trends Cognit.Sci. 6, 261–266.
Orban de Xivry, J.-J., Ramon, M., Lefèvre, P., Rossion, B., 2008. Reduced fixation on the upper area of personally familiar faces following acquired prosopagnosia. J. Neuropsychol. 2, 245–268.
Parvizi, J., Jacques, C., Foster, B.L., Witthoft, N., Rangarajan, V., Weiner, K.S., Grill-Spector, K., 2012. Electrical stimulation of human fusiform face-selective regions distorts face perception. The Journal of neuroscience 32, 14915–14920.
Passingham, R., 2009. How good is the macaque monkey model of the human brain? Curr.Opin.Neurobiol. 19, 6–11.
Peelen, M.V., Downing, P.E., 2005. Selectivity for the human body in the fusiform gyrus. J.Neurophysiol. 93, 603–608.
Peelen, M.V., Lucas, N., Mayer, E., Vuilleumier, P., 2009a. Emotional attention in acquired prosopagnosia. Soc.Cognit.Affect Neurosci. 4, 268–277.
Peelen, M.V., Fei-Fei, L., Kastner, S., 2009b. Neural mechanisms of rapid natural scene categorization in human visual cortex. Nature 460, 94–97.
Perrett, D.I., Rolls, E.T., Caan, W., 1982. Visual neurones responsive to faces in the monkey temporal cortex. Exp.Brain Res. 47, 329–342.
Perrett, D.I., Smith, P.A., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., Jeeves, M. A., 1985. Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc.Roy.Soc.Lond.B Biol.Sci. 223, 293–317.
Phillips, P.J., Yates, A.N., Hu, Y., Hahn, C.A., Noyes, E., Jackson, K., Cavazos, J.G., Jeckeln, G., Ranjan, R., Sankaranarayanan, S., Chen, J.C., Castillo, C.D., Chellappa, R., White, D., O'Toole, A.J., 2018. Face recognition accuracy of forensic examiners, superrecognizers, and face recognition algorithms. Proc.Natl.Acad.Sci.U. S.A. 115 (24), 6171–6176.
Pickering, E.C., Schweinberger, S.R., 2003. N200, N250r, and N400 event-related brain potentials reveal three loci of repetition priming for familiar names. J.Exp.Psychol. Learn.Mem.Cogn. 29 (6), 1298–1311.
Pitcher, D., 2009. TMS Studies of the Occipital Face Area. Doctoral thesis. University of London.
Pitcher, D., 2021. Face Processing and TMS.Oxford Handbook of Transcranial Stimulation, second ed.
Pitcher, D., Ungerleider, L.G., 2021. Evidence for a third visual pathway specialized for social perception. Trends Cognit.Sci. 25, 100–110.
Pitcher, D., Walsh, V., Duchaine, B., 2011. The role of the occipital face area in the cortical face perception network. Exp.Brain Res. 209, 481–493.
Pitcher, D., Walsh, V., Yovel, G., Duchaine, B., 2007. TMS evidence for the involvement of the right occipital face area in early face processing. Curr.Biol. 17, 1568–1573.
Pitcher, D., Garrido, L., Walsh, V., Duchaine, B.C., 2008. Transcranial magnetic stimulation disrupts the perception and embodiment of facial expressions. J. Neurosci. 28, 8929–8933.
Pitcher, D., Duchaine, B., Walsh, V., 2014. Combined TMS and FMRI reveal dissociable cortical pathways for dynamic and static face perception. Curr.Biol. 24, 2066–2070.
Pitcher, D., Goldhaber, T., Duchaine, B., Walsh, V., Kanwisher, N., 2012. Two critical and functionally distinct stages of face and body perception. J.Neurosci. 32, 15877–15885.
Preuss, T.M., 2000. Taking the measure of diversity: comparative alternatives to the model-animal paradigm in cortical neuroscience. Brain, behavior and evolution 55, 287–299.
Price, C.J., Friston, K.J., 1999. Scanning patients with tasks they can perform. Hum.Brain Mapp. 8, 102–108.
Prieto, E.A., Caharel, S., Henson, R., Rossion, B., 2011. Early (N170/M170) face-sensitivity despite right lateral occipital brain damage in acquired prosopagnosia. Front.Hum.Neurosci. 5, 138. Epub.
Puce, A., Allison, T., McCarthy, G., 1999. Electrophysiological studies of human face perception.III: effects of top-down processing on face-specific potentials. Cerebr. Cortex 9 (5), 445–458.
Puce, A., Allison, T., Asgari, M., Gore, J.C., McCarthy, G., 1996. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. J.Neurosci. 16, 5205–5215.
Puce, A., Allison, T., Gore, J.C., McCarthy, G., 1995. Face-sensitive areas in human extrastriate cortex studied by functional MRI. J.Neurophysiol. 74, 1192–1199.
Pyles, J.A., Verstynen, T.D., Schneider, W., Tarr, M.J., 2013. Explicating the face perception network with white matter connectivity. PLoS One 8 (4), e61611.
Quadflieg, S., Todorov, A., Laguesse, R., Rossion, B., 2012. Normal face-based judgments of social characteristics despite severely impaired holistic face processing. Vis. Cognit. 20, 865–882.
Quek, G.L., Rossion, B., Liu-Shuang, J., 2021. Critical information thresholds underlying generic and familiar face categorisation at the same face encounter. Neuroimage 243, 118481.
Rajimehr, R., Young, J.C., Tootell, R.B., 2009. An anterior temporal face patch in human cortex predicted by macaque maps. Proc.Natl.Acad.Sci.U.S.A. 106, 1995–2000.
Ramon, M., Rossion, B., 2010. Impaired processing of relative distances between features *and* of the eye region in acquired prosopagnosia—two sides of the same holistic coin? Cortex 46, 374–389.
Ramon, M., Busigny, T., Gosselin, F., Rossion, B., 2016. All new kids on the block? Impaired holistic processing of personally familiar faces in a kindergarten teacher with acquired prosopagnosia. Visual Cognition 24, 321–355.
Ramon, M., Busigny, T., Rossion, B., 2010. Impaired holistic processing of unfamiliar individual faces in acquired prosopagnosia. Neuropsychologia 48, 933–944.
Ramon, M., Sokhn, N., Lao, J., Caldara, R., 2018. Decisional space determines saccadic reaction times in healthy observers and acquired prosopagnosia. Cognitive neuropsychology 35, 304–313.
Ramon, M., Vizioli, L., Liu-Shuang, J., Rossion, B., 2015. The neural microgenesis of personally familiar face recognition. Proceedings of the National Academy of Science USA 112, E4835–E4844.
Ramon, M., Busigny, T., Gosselin, F., Rossion, B., 2016. All new kids on the block? Impaired holistic processing of personally familiar faces in a kindergarten teacher with acquired prosopagnosia. Vis.Cognit. 24, 321–355.
Rangarajan, V., Parvizi, J., 2016. Functional asymmetry between the left and right human fusiform gyrus explored through electrical brain stimulation. Neuropsychologia 83, 29–36.
Rangarajan, V., Hermes, D., Foster, B.L., Weiner, K.S., Jacques, C., Grill-Spector, K., Parvizi, J., 2014. Electrical stimulation of the left and right human fusiform gyrus causes different effects in conscious face perception. J.Neurosci. 34, 12828–12836.
Rao, R.P., Ballard, D.H., 1999. Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nat.Neurosci. 2, 79–87.
Rice, G.E., Watson, D.M., Hartley, T., Andrews, T.J., 2014. Low-level image properties of visual objects predict patterns of neural response across category-selective regions of the ventral visual pathway. J.Neurosci. 34, 8837–8844.
Richoz, A.R., Jack, R.E., Garrod, O.G., Schyns, P.G., Caldara, R., 2015. Reconstructing dynamic mental models of facial expressions in prosopagnosia reveals distinct representations for identity and expression. Cortex 65, 50–64.
Riddoch, M.J., Johnston, R.A., Bracewell, R.M., Boutsen, L., Humphreys, G.W., 2008. Are faces special? A case of pure prosopagnosia. Cognitive neuropsychology 25, 3–26.
Riesenhuber, M., Poggio, T., 1999. Hierarchical models of object recognition in cortex. Nat.Neurosci. 2, 1019–1025.
Righart, R., Andersson, F., Schwartz, S., Mayer, E., Vuilleumier, P., 2010. Top-down activation of fusiform cortex without seeing faces in prosopagnosia. Cerebral cortex 20, 1878–1890.
Roelfsema, P.R., Lamme, V.A., Spekreijse, H., Bosch, H., 2002. Figure-ground segregation in a recurrent network architecture. J.Cognit.Neurosci. 14, 525–537.
Rolls, E.T., 1992. Neurophysiological mechanisms underlying face processing within and beyond the temporal cortical visual areas. Phil.Trans.Roy.Soc.Lond. 335, 11–21.
Rossion, B., 2008. Constraining the cortical face network by neuroimaging studies of acquired prosopagnosia. Neuroimage 40, 423–426.

Rossion, B., 2009. Clarifying the functional neuro-anatomy of face perception by single-case neuroimaging studies of acquired prosopagnosia. In: Harris, L., Jenkins, M. (Eds.), Cortical Mechanisms of Vision. Cambridge University Press.
Rossion, B., 2013. The composite face illusion: a whole window into our understanding of holistic face perception. Vis.Cognit. 21, 139–253.
Rossion, B., 2014. Understanding face perception by means of prosopagnosia and neuroimaging. Front.Biosci. 308–317, 6.
Rossion, B., 2018. Damasio's error-Prosopagnosia with intact within-category object recognition. J.Neuropsychol. 12, 357–388.
Rossion, B., Jacques, C., 2008. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. Neuroimage 39, 1959–1979.
Rossion, B., 2022a. Twenty years of investigation with the case of prosopagnosia PS to understand human face identity recognition. Part I: Function (in press).
Rossion, B., 2022b. What makes us human? Face Identity Recognition. In: Garcia, A., Ibanez, A. (Eds.), Routledge Handbook of Neurosemiotics. Routledge (in press).
Rossion, B., Boremanse, A., 2011. Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. J.Vis. 11 (2), 1–21, 16.
Rossion, B., Jacques, C., 2011. In: Luck, S., Kappenman, E. (Eds.), The N170: Understanding the Time-Course of Face Perception in the Human Brain.The Oxford Handbook of ERP Components. Oxford University Press, pp. 115–142.
Rossion, B., Caharel, S., 2011. ERP evidence for the speed of face categorization in the human brain, disentangling the contribution of low-level visual cues from face perception. Vis.Res. 51, 1297–1311.
Rossion, B., Lochy, A., 2022. Is Human Face Recognition Lateralized to the Right Hemisphere Due to Neural Competition with Left Lateralized Visual Word Recognition? A Critical Review. Brain Structure and Function 227, 599–629.
Rossion, B., Michel, C., 2018. Normative data for accuracy and response times at the computerized Benton Facial Recognition Test (BFRT-c). Behav.Res.Methods 50, 2442–2460.
Rossion, B., Taubert, J., 2019. What can we learn about human individual face recognition from experimental studies in monkeys? Vis.Res. 157, 142–158.
Rossion, B., Retter, T.L., 2020. Face perception. In: Poeppel, D., Gazzaniga, M.S., Mangun, G. (Eds.), The Cognitive Neurosciences, sixth ed., pp. 129–139 ch.11.
Rossion, B., Delvenne, J.-F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., Guerit, J.-M., 1999. Spatio-temporal brain localization of the face inversion effect. Biol.Psychol. 50, 173–189.
Rossion, B., Dricot, L., Devolder, A., Bodart, J.M., Crommelinck, M., De Gelder, B., Zoontjes, R., 2000. Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. J.Cognit.Neurosci. 12, 793–802.
Rossion, B., Schiltz, C., Robaye, R., Pirenne, D., Crommelinck, M., 2001. How does the brain discriminate familiar and unfamiliar faces: a PET study of face categorical perception. J.Cognit.Neurosci. 13, 1019–1034.
Rossion, B., Caldara, R., Seghier, M., Schuller, A.M., Lazeyras, F., Mayer, E., 2003. A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. Brain 126, 2381–2395.
Rossion, B., Kaiser, M.D., Bub, D., Tanaka, J.W., 2009. Is the loss of diagnosticity of the eye region a common feature of acquired prosopagnosia? J.Neuropsychol. 3, 69–78.
Rossion, B., Dricot, L., Goebel, R., Busigny, T., 2011. Holistic face categorization in higher-level cortical visual areas of the normal and prosopagnosic brain: towards a non-hierarchical view of face perception. Front.Hum.Neurosci. 4, 225. https://doi.org/10.3389/fnhum.2010.00225.
Rossion, B., Hanseeuw, B., Dricot, L., 2012. Defining face perception areas in the human brain: a large-scale factorial fMRI face localizer analysis. Brain Cognit. 79, 138–157.
Ruff, C.C., Driver, J., Bestmann, S., 2009. Combining TMS and fMRI: from "virtual lesions" to functional-network accounts of cognition. Cortex 45, 1043–1049.
Sadeh, B., Podlipsky, I., Zhdanov, A., Yovel, G., 2010. Event-related potential and functional MRI measures of face-selectivity are highly correlated: a simultaneous ERP-fMRI investigation. Hum.Brain Mapp. 31, 1490–1501.
Sadr, J., Sinha, P., 2004. Object recognition and random image structure evolution. Cognit.Sci. 28, 259–287.
Sawamura, H., Orban, G.A., Vogels, R., 2006. Selectivity of neuronal adaptation does not match response selectivity: a single-cell study of the FMRI adaptation paradigm. Neuron 49, 307–318.
Schalk, G., Kapeller, C., Guger, C., Ogawa, H., Hiroshima, S., Lafer-Sousa, R., Saygin, Z. M., Kamada, K., Kanwisher, N., 2017. Facephenes and rainbows: causal evidence for functional and anatomical specificity of face and color processing in the human brain. Proc.Natl.Acad.Sci.U.S.A. 114, 12285–12290.
Schapiro, A.C., McClelland, J.L., Welbourne, S.R., Rogers, T.T., Lambon Ralph, M.A., 2013. Why bilateral damage is worse than unilateral damage to the brain. J.Cognit. Neurosci. 25, 2107–2123.
Scherf, K.S., Luna, B., Avidan, G., Behrmann, M., 2011. What" precedes "which": developmental neural tuning in face- and place-related cortex. Cerebr.Cortex 21, 1963–1980.
Schiltz, C., Rossion, B., 2006. Faces are represented holistically in the human occipito-temporal cortex. Neuroimage 32, 1385–1394.
Schiltz, C., Sorger, B., Caldara, R., Ahmed, F., Mayer, E., Goebel, R., Rossion, R., 2006. Impaired face discrimination in acquired prosopagnosia is associated with abnormal response to individual faces in the right middle fusiform gyrus. Cerebr.Cortex 4, 574–586.
Schmahmann, J.D., Guell, X., Stoodley, C.J., Halko, M.A., 2019. The theory and neuroscience of cerebellar cognition. Annu.Rev.Neurosci. 42, 337–364.
Schrouff, J., Raccah, O., Baek, S., Rangarajan, V., Salehi, S., Mourão-Miranda, J., Helili, Z., Daitch, A.L., Parvizi, J., 2020. Fast temporal dynamics and causal relevance of face processing in the human temporal cortex. Nat.Commun. 11 (1), 656.
Schwarz, L., Kreifelts, B., Wildgruber, D., Erb, M., Scheffler, K., Ethofer, T., 2019. Properties of face localizer activations and their application in functional magnetic resonance imaging (fMRI) fingerprinting. PLoS One 14, e0214997.
Schwarzlose, R.F., Baker, C.I., Kanwisher, N., 2005. Separate face and body selectivity on the fusiform gyrus. J.Neurosci. 25, 11055–11059.
Schweinberger, S.R., Neumann, M.F., 2016. Repetition effects in human ERPs to faces. Cortex; a journal devoted to the study of the nervous system and behavior 80, 141–153. https://doi.org/10.1016/j.cortex.2015.11.001.
Sergent, J., 1986. Microgenesis of face perception. In: Ellis, H.D., Jeeves, M.A., Newcombe, F., Young, A.M. (Eds.), Aspects of Face Processing. Martinus Nijhoff, Dordrecht, pp. 17–33.
Sergent, J., 1988a. Face perception and the right hemisphere. In: Weiskrantz, L. (Ed.), Thought without Language, vols.108–131. Clarendon Press, Oxford, 1988.
Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing.A, positron emission tomography study. Brain 115, 15–36.
Sergent, J., Signoret, J.-L., 1992. Varieties of functional deficits in prosopagnosia. Cerebr. Cortex 2, 375–388.
Serre, T., 2016. Models of visual categorization. Wiley interdisciplinary reviews. Cognitive science 7, 197–213.
Serre, T., Oliva, A., Poggio, T., 2007. A feedforward architecture accounts for rapid categorization. Proc.Natl.Acad.Sci.U.S.A. 104, 6424–6429.
Shallice, T., 1979. Case-study approach in neuropsychological research. J.Clin. Neuropsychol. 1, 183–211.
Simon, S.R., Khateb, A., Darque, A., Lazeyras, F., Mayer, E., Pegna, A.J., 2011. When the brain remembers, but the patient doesn't: converging fMRI and EEG evidence for covert recognition in a case of prosopagnosia. Cortex 47, 825–838.
Sliwinska, M.W., Bearpark, C., Corkhill, J., McPhillips, A., Pitcher, D., 2020. Dissociable pathways for moving and static face perception begin in early visual cortex: evidence from an acquired prosopagnosic. Cortex 130, 327–339.
Solomon-Harris, L.M., Mullin, C.R., Steeves, J.K.E., 2013. TMS to the 'occipital face area' affects recognition but not categorization of faces. Brain Cognit. 83, 245–251.
Solomon-Harris, L.M., Rafique, S.A., Steeves, J.K., 2016. Consecutive TMS-fMRI reveals remote effects of neural noise to the "occipital face area. Brain Res. 1650, 134–141.
Sorger, B., Goebel, R., Schiltz, C., Rossion, B., 2007. Understanding the functional neuroanatomy of acquired prosopagnosia. Neuroimage 35, 836–852.
Sporns, O., Tononi, G., Edelman, G.M., 1991. Modeling perceptual grouping and figure-ground segregation by means of active reentrant connections. Proc.Natl.Acad.Sci.U. S.A. 88, 129–133.
Steeves, J.K., Culham, J.C., Duchaine, B.C., Pratesi, C.C., Valyear, K.F., Schindler, I., Humphrey, G.K., Milner, A.D., Goodale, M.A., 2006. The fusiform face area is not sufficient for face recognition: evidence from a patient with dense prosopagnosia and no occipital face area. Neuropsychologia 44, 594–609.
Steeves, J., Dricot, L., Goltz, H., Sorger, B., Peters, J., Milner, D., Goodale, M.-A., Goebel, R., Rossion, B., 2009. Abnormal face identity coding in the middle fusiform gyrus of two brain-damaged prosopagnosic patients. Neuropsychologia 47, 2584–2592.
Tanaka, J.W., Farah, M., 1993. Parts and wholes in face recognition. Q.J.Exp.Psychol. 46, 225–245.
Tarr, M.J., Gauthier, I., 2000. FFA: a flexible fusiform area for subordinate-level visual processing automatized by expertise. Nat.Neurosci. 3, 764–769.
Taubert, J., Japee, S., Murphy, A.P., Tardiff, C.T., Koele, E.A., Kumar, S., Leopold, D.A., Ungerleider, L.G., 2020. Parallel processing of facial expression and head orientation in the macaque brain. J.Neurosci. 40, 8119–8131.
Taubert, J., Van Belle, G., Vanduffel, W., Rossion, B., Vogels, R., 2015. Neural correlate of the thatcher face illusion in a monkey face-selective patch. J.Neurosci. 35 (27).
Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., Kanwisher, N., 2000. Response properties of the human fusiform face area. Cogn.Neuropsychol. 17 (1), 257–280.
Tong, F., Nakayama, K., Vaughan, J.T., Kanwisher, N., 1998. Binocular rivalry and visual awareness in human extrastriate cortex. Neuron 21 (4), 753–759.
Tononi, G., Sporns, O., Edelman, G.M., 1992. Reentry and the problem of integrating multiple cortical areas: simulation of dynamic integration in the visual system. Cerebr.Cortex 2, 310–335.
Tovee, M.J., 1998. Face processing, getting by with a little help from its friends. Curr. Biol. 8, R317–R320.
Tranel, D., Vianna, E., Manzel, K., Damasio, H., Grabowski, T., 2009. Neuroanatomical correlates of the Benton facial recognition test and judgment of line orientation test. J.Clin.Exp.Neuropsychol. 31, 219–233.
Tsantani, M., Kriegeskorte, N., Storrs, K., Williams, A.L., McGettigan, C., Garrido, L., 2021. Ffa and ofa encode distinct types of face identity information. J.Neurosci. 41 (9).
Tsao, D.Y., Livingstone, M.S., 2008. Mechanisms of face perception. Annu.Rev.Neurosci. 31, 411–437.
Tsao, D.Y., Freiwald, W.A., Tootell, R.B., Livingstone, M.S., 2006. A, cortical area consisting entirely of face-selective cells. Science 311, 670–674.
Tsao, D.Y., Moeller, S., Freiwald, W.A., 2008. Comparing face patch systems in macaques and humans. Proc.Natl.Acad.Sci.U.S.A. 105, 19514–19519.
Ullman, S., 2007. Object recognition and segmentation by a fragment-based hierarchy. Trends Cognit.Sci. 11, 58–64.
Ungerleider, L.G., Mishkin, M., 1982. Two cortical visual systems. In: Ingle, D.J., Goodale, M.A., Mansfield, R.J.W. (Eds.), Analysis of visual behavior. MIT Press, Cambridge, pp. 549–586.
Van Belle, G., de Graef, P., Verfaillie, K., Busigny, T., Rossion, B., 2010a. Whole not hole: expert face recognition requires holistic perception. Neuropsychologia 48, 2609–2620.

Van Belle, G., Lefèvre, P., Laguesse, R., Busigny, T., de Graef, P., Verfaillie, K., Rossion, B., 2010b. Feature-based processing of personally familiar faces in prosopagnosia: evidence from eye gaze-contingency. Behav.Neurol. 23, 255–257.
Van Belle, G., Lefevre, P., Rossion, B., 2015. Face inversion and acquired prosopagnosia reduce the size of the perceptual field of view. Cognition 136, 403–408.
Vezoli, J., Magrou, L., Goebel, R., Wang, X.J., Knoblauch, K., Vinck, M., Kennedy, H., 2021. Cortical hierarchy, dual counterstream architecture and the importance of top-down generative networks. Neuroimage 225, 117479.
Vignal, J.P., Chauvel, P., Halgren, E., 2000. Localised face processing by the human prefrontal cortex: stimulation-evoked hallucinations of faces. Cogn.Neuropsychol. 17, 281–291.
Wang, Y., Metoki, A., Smith, D.V., Medaglia, J.D., Zang, Y., Benear, S., Popal, H., Lin, Y., Olson, I.R., 2020. Multimodal mapping of the face connectome. Nat.Human Behav. 4, 397–411.
Walther, D.B., Koch, C., 2007. Attention in hierarchical models of object recognition. Prog.Brain Res. 165, 57–78.
Weiner, K.S., Grill-Spector, K., 2010. Sparsely-distributed organization of face and limb activations in human ventral temporal cortex. Neuroimage 52, 1559–1573.
Weiner, K.S., Grill-Spector, K., 2012. The improbable simplicity of the fusiform face area. Trends Cognit.Sci. 16, 251–254.
Weiner, K.S., Grill-Spector, K., 2013. Neural representations of faces and limbs neighbor in human high-level visual cortex: evidence for a new organization principle. Psychol.Res. 77, 74–97.
Weiner, K.S., Grill-Spector, K., 2015. The evolution of face processing networks. Trends Cognit.Sci. 19, 240–241.
Weiner, K.S., Zilles, K., 2016. The anatomical and functional specialization of the fusiform gyrus. Neuropsychologia 83, 48–62.
Weiner, K.S., Gomez, J., 2021. Third visual pathway, anatomy, and cognition across species. Trends Cognit.Sci. 25, 548–549.
Weiner, K.S., Barnett, M.A., Lorenz, S., Caspers, J., Stigliani, A., Amunts, K., Zilles, K., Fischl, B., Grill-Spector, K., 2017. The cytoarchitecture of domain-specific regions in human high-level visual cortex. Cerebr.Cortex 27, 146–161.
Weiner, K.S., Jonas, J., Gomez, J., Maillard, L., Brissart, H., Hossu, G., Jacques, C., Loftus, D., Colnat-Coulbois, S., Stigliani, A., Barnett, M.A., Grill-Spector, K., Rossion, B., 2016. The face-processing network is resilient to focal resection of human visual cortex. J.Neurosci. 36, 8425–8440.
Whitwell, R.L., Milner, A.D., Goodale, M.A., 2014. The two visual systems hypothesis: new challenges and insights from visual form agnosic patient DF. Front.Neurol. 5, 255. https://doi.org/10.3389/fneur.2014.00255.
Wiese, H., Tüttenberg, S.C., Ingram, B.T., Chan, C., Gurbuz, Z., Burton, A.M., Young, A. W., 2019. A robust neural index of high face familiarity. Psychol.Sci. 30, 261–272.
Yan, X., Rossion, B., 2020. A robust neural familiar face recognition response in a dynamic (periodic) stream of unfamiliar faces. Cortex 132, 281–295.
Young, A.W., Hellawell, D., Hay, D.C., 1987. Configurational information in face perception. Perception 16, 747–759.
Yovel, G., 2016. Neural and cognitive face-selective markers: an integrative review. Neuropsychologia 83, 5–13.
Yovel, G., Kanwisher, N., 2005. The neural basis of the face inversion effect. Curr.Biol. 15, 2256–2262.
Yovel, G., Freiwald, W.A., 2013. Face recognition systems in monkey and human: are they the same thing? F1000Prime Rep 5, 10.
Yue, X., Cassidy, B.S., Devaney, K.J., Holt, D.J., Tootell, R.B., 2011. Lower-level stimulus features strongly influence responses in the fusiform face area. Cerebr.Cortex 21, 35–47.
Zemmoura, I., Burkhardt, E., Herbet, G., 2021. The inferior longitudinal fasciculus: anatomy, function and surgical considerations. J.Neurosurg.Sci. https://doi.org/10.23736/S0390-5616.21.05391-1.
Zhen, Z., Yang, Z., Huang, L., Kong, X., Wang, X., Dang, X., Huang, Y., Song, Y., Liu, J., 2015. Quantifying interindividual variability and asymmetry of face-selective regions: a probabilistic functional atlas. Neuroimage 113, 13–25.
Zhu, Q., Zhang, J., Luo, Y.L., Dilks, D.D., Liu, J., 2011. Resting-state neural activity across face-selective cortical regions is behaviorally relevant. J.Neurosci. 31, 10323–10330.
Zilles, K., Palomero-Gallagher, N., Amunts, K., 2013. Development of cortical folding during evolution and ontogeny. Trends Neurosci. 36, 275–284.