

# Face Perception

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## **Abstract**

Neurotypical human adults categorize faces – highly complex, socially informative visual stimuli – accurately, rapidly, and automatically, at both generic and individual levels. This defines *expertise* in individual face perception, which is domain-specific and may be restricted to neurotypical human adults. Individual face perception expertise is lost in prosopagnosia, that is, a rare category-specific deficit at face individuation following brain damage. Relying on holistic rather than analytic face perception, humans are experts for both familiar and unfamiliar faces, with repeated, meaningful, and variable exposure to an identity strengthening its unique high-level percept. This human expertise is broadly enabled and constrained by genetics, but active experience is vital throughout development. The combination of these two factors leads to an extensive, right-lateralized ventral occipito-temporal cortical network subtending human-specific expertise at individual face perception. A full understanding of human face perception will require the inclusion of key aspects of expertise beyond accuracy, that is, processing time and automaticity, tested with a wide variety of discriminations and generalizations, e.g., with fast periodic visual stimulation, a key paradigm to probe this function.

## Introduction

Faces emerged through evolution about 500 million years ago, as bridges between the central nervous system and the environment (McNeill, 2000). A face can be described as a collection of sensory receptors positioned together in proximity to the brain, enabling appropriate and rapid reactions to the external world. In humans, the face evolved to have importance for social functioning, conveying both quickly changeable information, for example, emotion from the expression, the direction of attention from the position of the head and gaze, and the state of health from the skin tone—and relatively invariant information, such as age, sex, race, attractiveness, and personality traits (Bruce & Young, 1998; Sheehan & Nachman, 2014; Todorov, 2017).

The face, undoubtedly, holds a special place in cognitive neuroscience research, having become probably the most widely studied stimulus (Calder, Rhodes, Johnson, & Haxby, 2011). Why? Besides being ecologically meaningful, the face is a highly frequent and familiar stimulus, especially in modern societies and the age of (social) media. Further, faces form a rich visual category, including a wide range of physically variable face exemplars (**Figure 1A**). At the individual level, the face is also complex, containing multiple nameable features (eyes, mouth, nose...) and sources of variation, in terms of shape, texture and color. Hence, the face is an ideal stimulus to investigate the bases of perception in a modality that is dominant in the human species: vision.

At a neural level, human face perception has been associated with *specific* visual recognition processes since the proposal of a face-specific recognition deficit following brain damage, i.e., prosopagnosia (Bodamer, 1947). Lesion analysis of prosopagnosia (Meadows, 1974; Sergent & Signoret, 1992), as well as neuroimaging and intracranial recordings of human face perception (since Sergent, Ohta, & Macdonald, 1992 and Allison et al., 1994, respectively), have shown that a large, right-lateralized, expanse of the cerebral cortex is involved in this function. Face perception research is therefore important for understanding the general organization of human brain function, including hemispheric lateralization.

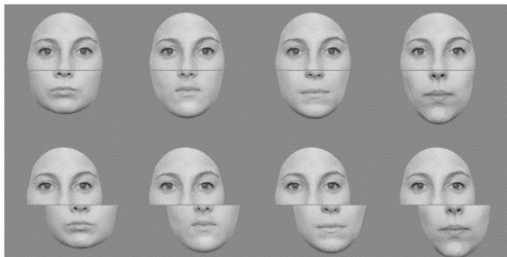
### A) Face perception: Generic



### B) Face perception: Individual



### C) Holistic face perception



### D) Neural substrates



**Figure 1.** **A)** The human brain perceives stimuli as faces under a wide variety of viewing conditions, sometimes with little or no shared features. Understanding the nature of such generic face categorization (i.e., discrimination from nonface objects and generalization across variable face exemplars) requires going beyond sensory, quantifiable, low-level information from the visual stimulus and incorporating memory of the category in the process. **B)** Individual face perception can be understood as a more specific function than generic face perception but similarly requiring categorization: discrimination—here from various unfamiliar faces—and generalization across variable viewing conditions. **C)** The composite face illusion (adapted from Rossion, 2013) illustrates how face perception goes beyond the given sensory information, taking advantage of matches to holistic facial memories derived through experience. All four top halves (above the narrow gap) are physically identical. Yet aligned (top row; compare with misaligned below) with distinct bottom halves (all of different identities), they are perceived as being different. **D,** Inflated segmented brains showing typical locations of face-selective regions in humans (from Weiner & Grill-Spector, 2015) and macaques (from Tsao, Moeller, & Freiwald, 2008), plotted to a common scale. Up to six regions have been labeled in the macaque STS, whereas humans have regions in both the STS (labeled 4, 5, and 6) and the VOTC (1, 2, 3, 7).

### Face Perception Emerges from Recognition

In (neuro)cognitive models of vision, perception is commonly considered to be the processing that leads to the formation of visual representations—that is, neural images of the external world. Perception is thought to precede *recognition*, when correctly formed perceptual representations are associated with representations stored in memory. Although this dissociation between perception and recognition is widely used in face perception research (e.g., the distinction between a *structural encoding stage* and *face*

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*recognition units* in the influential Bruce & Young [1986] model; see also Duchaine & Yovel, 2015; Haxby, Hoffman, & Gobbini, 2000; Jiang et al., 2006), it is not supported by empirical evidence (e.g., by a clear dissociation between perceptual and mnesic forms of prosopagnosia; Farah, 1990/2004; Gainotti, 2013) and causes a series of difficulties, such as understanding why *perceptual tasks* (e.g., the simultaneous matching of individual face images) are performed better with familiar than unfamiliar faces (Bruce et al., 2001).

Most importantly, it causes a fracture between *different levels* of face perception: discerning that a visual stimulus is a face is considered a *perceptual* task (face detection), while identifying somebody's face as that of a specific individual is considered a *recognition* task (**Figure 1A and 1B**). These two levels are often taken to be neurofunctionally distinct and even to have opposing demands: that face detection requires extracting "what is common to faces," while individual recognition requires extracting "differences between faces" (Tsao & Livingstone, 2008). However, being able to tell that a face is a face (generic face perception) requires both *discrimination* (i.e., providing a selective response to faces) and *generalization* (i.e., providing the same response to different faces). In the same vein, recognizing someone's identity (individual face perception) requires both *discrimination* (from other faces) and *generalization* (across various views of the same face). Therefore, in a coherent theoretical framework, a facial identity should be considered as a category (Burton et al., 2016; **Figure 1B**).

In this theoretical framework, perception arises through matching low-level (i.e., sensory, unconscious) information to high-level (categorical) representations in memory. This matching corresponds to *categorization*, that is, *recognition*, of the visual environment. In this view, *perception* does not precede recognition but is the *subjective experience that emerges from this process*. We consider this framework to be essential for understanding the nature of human face perception and its neural basis.

## Human expertise

Behavioral, eye movement, and electrophysiological studies in humans have shown that widely variable natural stimuli are perceived as faces extremely accurately, rapidly (shortly after 100 milliseconds), and automatically (without intentionality) (Crouzet, Kirchner, & Thorpe, 2010; Hershler et al., 2010;

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Rossion, 2014a). These characteristics, applied across a wide range of discriminations and generalizations, define the *expertise* of neurotypical human adults at generic face perception. However, human's level of expertise is arguably best expressed when considering the challenge of *individual* face perception.

Every human face is unique in its morphological characteristics, and modern human societies are characterized by the presence of numerous familiar and unfamiliar individuals, augmented with (social) media. Since individual faces are similar in their overall visual configuration, the human visual system is formidably challenged to successfully individuate people by their faces. Nevertheless, a combination of this social (over)exposure and biological factors, as discussed below, allow people to recognize familiar individuals from their faces with astounding accuracy, even across changes of viewpoint and expression or under degraded conditions (occlusion, distortion, blurring: V. Bruce, 1982; Burton et al., 1999; Hole et al., 2002; Sinha, 2002). Familiar faces can also be discriminated from unfamiliar faces within a few hundred milliseconds (Caharel, Ramon, & Rossion, 2014; Visconti di Oleggio Catsello & Gobbini, 2015). Additionally, humans naturally (i.e., without formal training) recognize and encode a seemingly unlimited number of individual faces in memory, for short or long periods of time, throughout their lives (Bahrick, Bahrick, & Wittlinger, 1975).

In sum, although the capacity of the human brain to individuate faces must be better evaluated and documented by systematic quantitative research (see Summary and Perspectives), these observations suggest that neurotypical human adults can indeed be considered as *experts* at individual face perception (Carey, 1992; McKone, Kanwisher, & Duchaine, 2007; Rossion, 2018b; Tanaka, 2001; Young & Burton, 2018). To illustrate this level of expertise, we compare neurotypical adults' performance to two kinds of non-experts, other animal species and patients with prosopagnosia.

### ***Non-human species***

Behavioral studies have shown that non-human species, such as sheep (Peirce, Leigh, & Kendrick, 2001), fish (Wang & Takeuchi, 2017), or even wasps (Sheehan & Tibbetts, 2011), can discriminate pictures of (conspecific) individual faces, drawing parallels to human performance. However, the face individuation performance of nonhuman species often follows long operant-conditioning procedures and, despite a small

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number of individual exemplars, remains relatively modest (Rossion & Taubert, 2019). Moreover, successful performance at such tasks appears to be based on low-level image characteristics (with limited across-image generalization) and/or external traits (e.g., antennae for wasps or ears for sheep; see respective references above).

Importantly, this limited ability also holds for the species often considered the best model for the human visual system: the macaque monkey. Macaques, as well as other monkey species (Pokorny & de Waal, 2009), are in fact quite poor at behavioral face individuation tasks (Parr, Heintz, & Pradhan, 2008; Rossion & Taubert, 2019). Moreover, monkeys do not rely on qualitatively similar processes as humans. That is, they fail to show a decrease of performance with stimulus (picture-plane) inversion (C. Bruce, 1982; Rossion & Taubert, 2019), one of the most compelling effects in human studies (Rossion, 2008), and rely primarily on external features (Parr et al., 2008). These observations raise questions as to the appropriateness of the macaque as a model for the neural basis of human (individual) face perception (Rossion & Taubert, 2019). More generally, humans may be the only species to naturally use the face as the primary source of information for individuation (as opposed to smell, vocalization, body appearance, and so on; Sheehan & Nachman, 2014), reaching an expertise at this function that is unparalleled in the animal world.

### ***Prosopagnosia: a category-specific individuation impairment***

Another non-expert system is demonstrated by prosopagnosia, a rare inability to individuate faces following brain damage in a neurotypically-developed face perception system (not to be confused with *prosopdysgnosia* or *developmental/congenital prosopagnosia*, which is a difficulty individuating faces of developmental origin; Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006; McConachie, 1976). Prosopagnosia is a massive impairment in recognizing both faces encountered before and after brain damage (i.e., it is both a retrograde and anterograde recognition deficit), which cannot be accounted for by low-level sensory deficits and/or intellectual deficiencies. Most importantly, it is a *category-specific* individual recognition disorder: cases of prosopagnosia are able to recognize nonface objects correctly and rapidly (Bodamer, 1947; Busigny et al., 2010; Rossion, 2018a).

Prosopagnosia appears to be caused by a failure to match sensory inputs to damaged, high-level, neural regions responding selectively to faces (see Neuro-functional Substrates). Prosopagnosia is therefore a (visual) *recognition* disorder, which necessarily implies impairment at face *perception*. This is why, despite decades of research, there is no evidence for a clear-cut distinction between perceptual (“apperceptive”) and mnesic (“associative”) forms of prosopagnosia (Farah, 1990/2004; Gainotti, 2013).

Interestingly, despite their impaired individual face perception, patients with prosopagnosia are generally capable of generic face perception, which does not require detailed internal representations (Liu-Shuang, Torfs, & Rossion, 2016). They can also discriminate pictures of unfamiliar faces well above the chance level (e.g., Busigny et al., 2010; Sergent & Signoret, 1992) and even learn to individuate face pictures (Sergent & Signoret, 1992); in fact, they perform better than nonhuman species at such tasks. However, unlike neurotypical human adults, their performance is slow, effortful, and limited in generalization. This shows the importance of going beyond a “can/can’t do” criterion for measuring observers’ levels of expertise at (individual) face perception.

### **Holistic Face Perception**

How are faces perceived? According to an *analytic view*, the face percept is built from the perception of independent face parts, such as the eyes, nose, mouth, and so on. The definition of parts is problematic, as it can be performed in a myriad of ways: feature-based (e.g., by cutting out rectangles around the eyes, the nose, and the mouth), halves (top/bottom or left/right), surface/shape, Gabor jets, or apertures or “bubbles” in response classification techniques and more. Although these parts are thought to be ultimately integrated into a global face percept, this face percept is thought to be equivalent to the sum of its parts (Gold, Mundy, & Tjan, 2012) so that the parts’ respective contributions can be studied and defined independently. However, visual illusions such as the composite face illusion, in which identical top face halves are aligned with differing bottom face halves, produce the impression of different top face halves (**Figure 1C**).

Such illusions therefore provide compelling evidence that facial parts are mandatorily perceived interactively or interdependently of one another—that is, holistically (Rossion, 2013; Tanaka & Farah, 1993;



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Young, Hellawell, & Hay, 1987). The importance of holistic face perception is supported by its disruption following stimulus inversion (Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987) and in cases of prosopagnosia (Rossion, 2014b; Van Belle et al., 2010). Despite such observations, holistic perception is not fully embraced in scientific research, probably because it is very difficult to understand in neurocomputational terms (Spillman, 1999; but see Biederman & Kalocsai, 1997; Tan & Poggio, 2016).

### **Perception of familiar and unfamiliar faces**

Individual faces encoded in (long-term) memory—that is, familiar faces—are more easily individuated than unfamiliar faces, both in old/new recognition (V. Bruce, 1982) and simultaneous matching tasks (Bruce et al., 2001). Thus, although pictures of unfamiliar faces offer experimental advantages in terms of stimulus control, findings from these studies need to be carefully interpreted and may not fully extend to familiar face perception. Nevertheless, behavioral experiments show that without any task training, typical human adults remain very good at simultaneous or delayed unfamiliar face-matching tasks, even in difficult tasks requiring high levels of generalization across substantial changes in size, head orientation, and lighting conditions with many similar-looking distractors (Megreya & Burton, 2006; Rossion & Michel, 2018). Moreover, the perception of unfamiliar facial identities is significantly affected by picture-plane inversion (Rossion, 2008), against the claim of reliance on low-level information for unfamiliar face perception (Megreya & Burton, 2006). The composite face illusion is also best illustrated with pictures of unfamiliar faces (**Figure 1C**). In addition, the “other-race” face effect, reflecting a level of expertise specific to experienced facial morphologies, is readily demonstrated with unfamiliar faces (Rossion & Michel, 2011). Electrophysiological studies also show that discrimination of individual unfamiliar faces is fast and automatic across changes—for example, in size and head orientation (Caharel, d’Arripe, & Ramon, 2009; Liu-Shuang, Norcia, & Rossion, 2014).

Thus, contrary to a recently expressed view limiting expertise to familiar faces (Young & Burton, 2018), we posit that neurotypical human adults are experts even with unfamiliar faces. However, an initial individual face percept is labile and will be registered as a distinct (dynamic) category in the brain only when it is seen repeatedly, variably, and meaningfully, and is thus associated with contextual, affective, and

semantic information in the brain of the observer. This exposure will also greatly expand the range of generalization ability for individuation of that face. Interestingly, the resulting advantage in individuation tasks for familiar over unfamiliar faces is found neither in patients with prosopagnosia (for obvious reasons) nor in macaque monkeys (Micheletta et al., 2015; Rossion & Taubert, 2019), so that it may be considered as an additional marker of human expertise at individual face perception.

## **Genetics and experience throughout development**

To what extent is human face perception genetically predetermined and to what extent does it arise due to visual experience? The complex interplay between these factors prevents them from being neatly disentangled, especially in the case of this naturally developed expertise in the human species. For example, developmental difficulties at individual face recognition may run in families (Susilo & Duchaine, 2013), and monozygotic twins' performance at face recognition tests are more strongly correlated than dizygotic twins' performance (Wilmer et al., 2010), leading to claims that genetics largely determines face recognition. However, genetics could affect both specific and general functions essential for learning to individuate faces throughout development. Thus, while genetics certainly influences the neural development (from epigenetics through nervous system development to cytoarchitectonic and functional neural organization) required for face recognition, experience appears to be necessary or instrumental throughout the developmental time course.

The extent to which the visually unexperienced human newborn's brain exhibits selective responses to faces is debated (Johnson et al., 1991; Simion et al., 2003). Perhaps supported by an innate bias to look at the general structural characteristics present in faces (e.g., "top-heavy patterns": Simion et al., 2003), infants receive an enormous amount of exposure to faces (Sugden, Mohamed-Ali, & Moulson, 2014) and look preferentially at face stimuli per se after a few months of age (Chien, 2011). Four-to-six-month-old infants already show a specific neural response to variable natural images of faces compared to objects, even for single-glanced faces (de Heering & Rossion, 2015). Experience also leads to the *fine-tuning* of individual facial discrimination abilities; at nine months of age, infants show lower performance at discriminating nonexperienced than frequently experienced faces (e.g., other-species faces: Pascalis, de

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Haan, & Nelson, 2002; “other-race” human faces: Kelly et al., 2007). Other studies have illustrated that the type of experience that infants have with faces matters: active experience increases performance more than passive experience (Scott & Monesson, 2010). Nevertheless, even after nine years of age a predominant exposure to “other-race” faces can reverse such an early selection in discrimination ability (Sangrigoli & de Schonen, 2004). Thus, experience as well as genetics appears to be necessary and influential.

Overall, these studies show that the early encounter between a biological system and the environment *selects* a specific relevant type of facial morphology for perceptual *learning* (rather than *narrowing*). Indeed, individual face perception continues to develop until adulthood, but whether this is due to the progressive maturation of face perception specifically or is explained by more general cognitive development is debated (Crookes & McKone, 2009). Neuroimaging investigations show that the topology of face-selective regions in the posterior ventral occipitotemporal cortex (VOTC) is mature by age seven, but the spatial extent and degree of face selectivity continue to develop into adulthood, supporting a selective development of the function (Golarai, Liberman, & Grill-Spector, 2017).

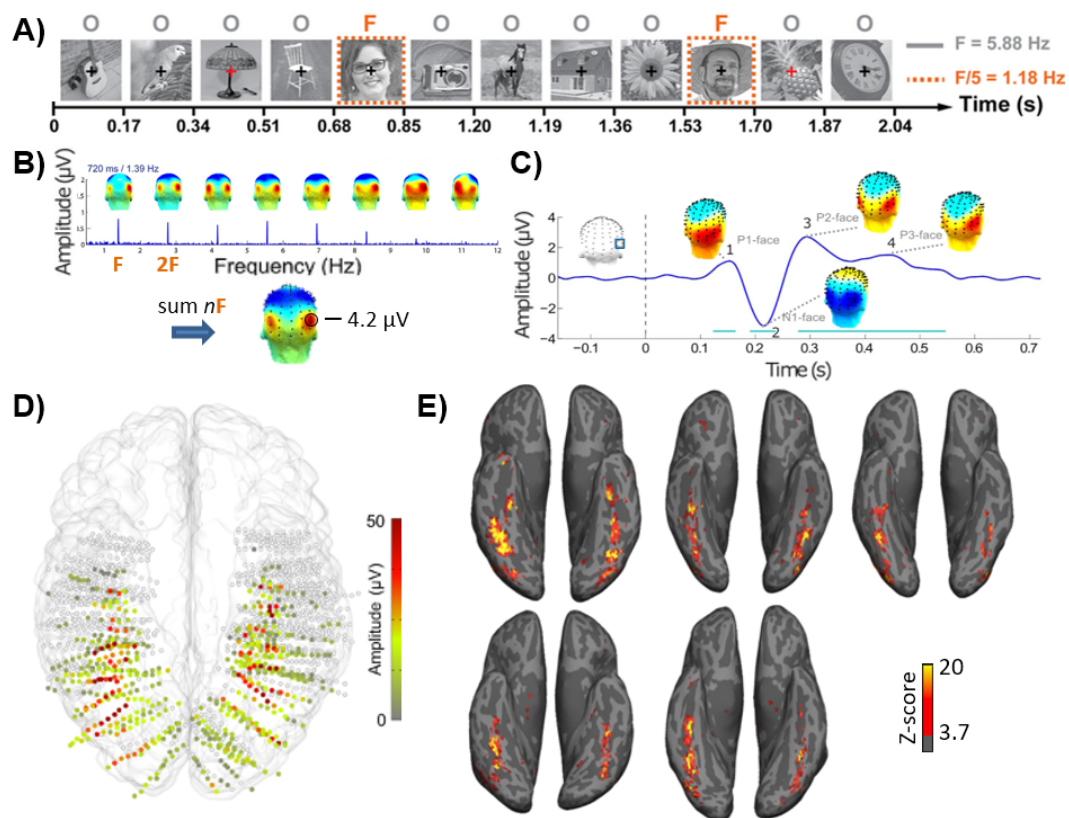
To summarize, although the notion of expertise has been around for decades in the field of face perception (Carey, 1992; Diamond & Carey, 1986), it is generally conflated with the view that expertise arises from visual experience without genetic constraints and that it could be developed in a similar way for various kinds of nonface stimuli learned during development or even in adulthood (Diamond & Carey, 1986; Gauthier & Tarr, 1997). In this vein, “acquired” domain-general expertise has often been radically opposed to “innate” domain-specific expertise (McKone, Kanwisher, & Duchaine, 2007). Instead, current evidence suggests that neurotypical human adults possess a *domain-specific expertise* in (individual) face perception, emerging from both genetic factors and experience.

## **Neuro-functional substrates**

The neural bases of human individual face perception were first hinted at by patients presenting with prosopagnosia, i.e., after lesions to the VOTC, in particular the right fusiform gyrus (Meadows, 1974; Sergent & Signoret, 1992). Since the mid-1990s, functional magnetic resonance imaging (fMRI) studies have

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identified clusters of voxels (of a few cubic millimeters) that respond significantly more to pictures of faces than nonface objects, especially along the VOTC (in particular, the lateral fusiform gyrus) and the superior temporal sulcus, or STS (e.g., for reviews, see Duchaine & Yovel, 2015; Grill-Spector et al., 2017; Haxby, Hoffman, & Gobbini, 2000; **Figure 1D**). More broadly distributed face-selective neural populations have been suggested from direct, invasive intracranial electroencephalographic recordings performed for clinical purposes (Allison et al., 1994). However, spatial clustering of face-selective responses, with a peak of activity in the right lateral fusiform gyrus, have also been reported in electrocorticography (Jacques et al., 2016) as well as with depth (i.e., intracerebral) electrodes with a frequency-tagging approach (for a review, see Jonas et al., 2016; Rossion et al., 2018; **Figure 2**).



**Figure 2.** **A)** A fast periodic visual stimulation (FPVS) categorization paradigm (adapted from Rossion et al., 2015): stimuli are presented at a fast rate, 5.88 images per second (Hz), with faces appearing here as every fifth stimulus—that is, at 5.88 Hz / 5 = 1.18 Hz. Selective responses to faces are thus “tagged” at 1.18 Hz, under severe time constraints (one fixation per image), automatically (i.e., without an explicit perception task), and with variable stimuli ensuring ecological validity. **B,** Scalp electroencephalogram responses recorded in the amplitude spectrum at the presentation rate of faces (F) and its harmonics—that is, 2F, 3F, and so on, plotted from an occipitotemporal region indicated below. To quantify the response, these harmonics are baseline corrected and summed (Retter & Rossion, 2016). **C,** These selective responses to faces can also be represented in the time domain. This reveals at least four face-selective deflections, onset after about 100 ms and persisting for over 400 ms. **D,** Intracerebral depth electrode contacts’ face-selective amplitudes are shown from a large sample of participants (N = 28; from Jonas et al., 2016). **E,** The ventral surfaces of individual human brains showing the wide variability, across five individuals, in their face-selective fMRI activation obtained with the same type of paradigm (data unsmoothed; Gao, Gentile, & Rossion, 2018). While these differences in terms of the spatial extent and number of clusters may be due to individual anatomy interacting with fMRI signal capture, they may reflect genuine (behaviorally relevant) interindividual differences.

While the human VOTC network has been associated with invariant aspects of faces, in particular individual face perception, the more dorsal STS network is thought to be critical for the perception of dynamic aspects of faces, such as eye gaze direction, head orientation and facial expression (as in monkeys: Heywood & Cowey, 1992; humans: Allison, Puce, & McCarthy, 2000). In humans, more recent models have

emphasized the dissociation between form and motion as the primary functional division between the ventral system along the VOTC and the dorsal system that goes through the STS, respectively (Bernstein & Yovel, 2015).

In terms of time course, event-related potential (ERP) studies have reported several face-selective electrophysiological components, the most prominent and well-studied of which is undoubtedly the N170 (Bentin et al., 1996), a marker of conscious (individual) face perception (Rossion, 2014a). However, more recent studies isolating face-selective responses in a rapid train of nonface stimuli have shown that electrophysiological face-selective responses devoid of low-level visual confounds emerge about 100 ms after stimulus onset and persist for over 400 ms (Retter & Rossion, 2016).

A hallmark of human face perception is that the right hemisphere is more functionally active than the left; again, this has been evidenced by both direct (Bentin et al., 1996; Jonas et al., 2016; Rossion, 2014a;) and indirect (neuroimaging) neural measurements (Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & Macdonald, 1992), as well as by behavioral studies with divided visual field presentations in split-brain or normal observers (Parkin & Williamson, 1987) and with transcranial magnetic stimulation (Pitcher et al., 2007). Importantly, a right hemisphere lesion is both necessary and sufficient to cause prosopagnosia in right-handed individuals (Sergent & Signoret, 1992). The factors causing this right lateralization, which is specific to the human species (e.g., it is absent in macaques) remain largely unknown. While it has been proposed that this is due to competition from visual language acquisition (reading) taking place primarily in the left VOTC (Behrmann & Plaut, 2015), generic face perception is right lateralized as early as 4-6 months of age, well before reading acquisition (de Heering & Rossion, 2015), casting doubt on this view.

Neurofunctional models of face perception have been generated with modular roles attributed to clusters of voxels in the VOTC and STS, referred to as *face-selective areas* (Duchaine & Yovel, 2015; Haxby, Hoffman, & Gobbini, 2000). In the original models, such clusters were thought to be hierarchically spatially organized, with perceptual and mnemonic information ordered along a posterior to anterior axis along VOTC areas (Haxby, Hoffman, & Gobbini, 2000). However, neuroimaging studies of brain-damaged patients with prosopagnosia (Rossion et al., 2003) and time-resolved fMRI (Jiang et al., 2011) have instead shown a

nonhierarchical organization, forcing the revision of these models (Duchaine & Yovel, 2015). Studies using fMRI with a higher spatial resolution have dissociated the face-selective cluster in the fusiform gyrus (“Fusiform Face Area” [FFA]: Kanwisher, McDermott, & Chun, 1997) into several subclusters, such as the pFus-faces/FFA-1 and mFus-faces/FFA-2, and have linked them to cytoarchitectonically distinct regions (Grill-Spector et al., 2017; Weiner & Grill-Spector, 2012). However, in general there is great interindividual variability in the number of spatially dissociable face-selective regions and their extent throughout the cortex (Gao, Gentile, & Rossion, 2018; **Figure 2E**). Whether this interindividual variability in the number and exact localization of face-selective regions is due to the measurement noise of functionally defined regions that are generalizable anatomically across people or is genuine (and potentially related to behavioral differences in face perception) remains unknown.

Recent years have seen a rise in fMRI studies attempting to “decode” the representations of (unfamiliar) individual faces in the cortical face network in order to localize and define the nature of individual face representations. However, the results of these studies are often inconsistent and describe relatively weak effects potentially driven by image-based cues (Guntupalli, Wheeler, & Gobbini, 2017; Kriegeskorte et al., 2007; Nestor, Plaut, & Behrmann, 2011). In contrast, fMR-adaptation studies (Grill-Spector & Malach, 2001), which are based on reduced fMRI signal to repeated facial identities as compared to different stimuli, have measured more consistent changes of activity during individual face discrimination in face-selective VOTC regions (Davies-Thompson, Gouws, & Andrews, 2009; Gauthier et al., 2000). Their findings are generally in agreement with studies of prosopagnosia and electrical brain stimulation in these regions (Jonas et al., 2012; Parvizi et al., 2012; Rossion, 2014b for review).

In line with the present theoretical framework, we suggest that a number of tightly interconnected face-selective clusters in the VOTC holds memories of (individual) faces, carved from the lifetime brain-environment interaction. Specific activity in these regions, triggered from low-level sensory inputs, leads to both generic and individual face recognition/perception, with the former temporally preceding the latter.

Neuroimaging studies show inconsistent differences in the amplitude (or pattern) of responses to familiar and unfamiliar faces across VOTC face-selective regions (Gobbini & Haxby, 2007; Natu & O’Toole,

2011; Visconti di Oleggio Castello et al., 2017), which is surprising given the role of these regions in causing prosopagnosia (Jonas et al., 2012; Rossion, 2014b; Sergent & Signoret, 1992). This could be due to contrasting effects in neuroimaging (e.g., larger fMR-adaptation effects for repeated familiar than unfamiliar faces, compensated by much richer associations to semantic information for familiar faces). It is also likely that familiarity effects will be revealed at smaller levels of organization (e.g., the strengthening of connections among groups of neurons, such as cortical columns or minicolumns) as well as shorter time scales in future studies, providing neural mechanisms for individual recognition of familiar faces.

### Summary and Perspectives

In this chapter, we proposed a theoretical framework considering the perception of faces to *arise* from recognition, that is, from matching sensory inputs with high-level, face-selective, holistic representations, mainly in the VOTC. Moreover, we advocate reintegrating the notion of neurotypical human adult's *expertise* in the study of face perception, as a domain-specific expertise arising from both genetic and experiential factors. This expertise in individual face perception—even for unfamiliar faces—is striking in comparison with non-expert populations, that is, other animal species and patients with prosopagnosia; additional non-expert populations could include infants, children and, arguably, artificial systems (if they are probed with valid measures of face recognition; see O'Toole et al., 2018; Philips & O'Toole, 2014; Scheirer et al., 2014). Importantly, such an emphasis on expertise highlights neurotypical human adults' extraordinary ability at (individual) face perception and encourages research into this complex function's origins and substrates.

We suggest operationalizing expertise not only in terms of accuracy, but also processing time and automaticity, across variable discriminations/generalizations of face stimuli. To this end, face perception could be measured with fast periodic visual stimulation , or FPVS (Retter & Rossion, 2016; Rossion, 2014a). In a recent FPVS categorization paradigm, a within-category stimulus (e.g., faces) appears as a “frequency-tagged” proportion of periodically-presented across-category stimuli (e.g., nonface objects; Rossion et al., 2015; ; **Figure 2A**). Importantly for capturing *categorization* responses, i.e., *recognition* responses in our theoretical framework, this approach can readily incorporate a large amount of variable discriminations



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and generalizations, with ecologically valid natural stimuli (see **Figure 2A**). Automaticity is required when the process of interest is measured implicitly, e.g., while naïve participants perform an orthogonal task. Additionally, when stimuli are presented in succession at relatively fast rates (e.g. about 6 Hz in **Figure 2A**), processing time of each stimulus is restricted. Moreover, FPVS can be advantageously applied (i.e., with high sensitivity and objectivity) to a variety of recording techniques, including human (intracerebral) electrophysiology, and fMRI (**Figure 2B-D**). We thus propose that FPVS will allow the isolation of high-level processes from low-level sensory biases, while incorporating the key notions of accuracy, processing time, and automaticity, that define human face perception expertise.

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