



What can we learn about human individual face recognition from experimental studies in monkeys?

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ABSTRACT

Typical human adults recognize numerous individuals from their faces accurately, rapidly and automatically, reaching a level of expertise at individual face recognition that is important for the quality of their social interactions. A non-human species of primates, the rhesus monkey, has been used for decades as a model of human face processing, in particular for understanding the neural basis of individual face recognition. However, despite responding specifically to faces behaviourally and neurally, this species, as well as other Old World and New World monkeys, is remarkably poor at individuating faces of conspecifics. Following extensive conditioning, monkeys only achieve moderate performance at individual face matching tasks where image-based cues are available. Contrary to humans, monkeys do not show a systematic inversion effect in such tasks, or an advantage for matching face pictures of familiar versus unfamiliar individuals, indicating that they do not rely on qualitatively similar individual face recognition processes as humans. These observations concur with the characteristics of the rhesus monkey cortical face processing system, which lacks two critical aspects for human expertise at individual face recognition: a distinct ventral face-selective pathway and a right hemispheric specialization. While the rhesus monkey brain is undoubtedly an informative non-human model for studying the neural basis of social behaviour and visual cognition, it does not provide an adequate model of human individual face recognition. More generally, this review urges for caution when drawing direct inferences across species without sufficient homologies in behaviour and anatomico-functional landmarks.

1. Introduction

In a number of social animal species, recognition of other individuals is fundamental for social interactions (Tibbetts & Dale, 2007). In humans, individual recognition is thought to be based primarily on the face, which is clearly visible during most interactions and shows elevated phenotypic and genetic interindividual variability compared to other parts of the body (Sheehan & Nachman, 2014). Despite this variability, individual faces are very similar from one another in their overall visual configuration. Hence, since most humans live in large societies and many individuals need to be recognized for adequate social interactions, individual face recognition (IFR) is a very challenging function for the human brain. Despite this challenge, people are generally able to recognize individuals from their face with high accuracy, rapidly (i.e., often at a glance) and automatically (i.e., without explicit instructions to do so) (e.g., Barragan-Jason, Besson, Ceccaldi, &

Barbeau, 2013; Hsiao & Cottrell, 2008; Gobbini et al., 2013; Ramon, Caharel, & Rossion, 2011). Individual faces can also be recognized under occlusion or severely degraded conditions (Bachmann, 1991; Burton, Wilson, Cowan, & Bruce, 1999; Sinha, 2002). Humans also encode a seemingly unlimited number of individual faces in memory for short or long periods of time throughout their whole life naturally, i.e., without formal training (Bahrick, Bahrick, & Wittlinger, 1975). For these reasons, typical human adults are generally considered to be experts at IFR (Carey, 1992; McKone, Kanwisher, & Duchaine, 2007; Rossion, 2018; Schwaninger, Carbon, & Leder, 2003; Tanaka, 2001; Young & Burton, 2018).

Understanding the neural basis of human IFR, a function which relies on the most refined processes of perception and memory in the dominant visual modality, is a major scientific goal. In neuroimaging studies, the perception of face stimuli selectively (i.e., differentially with respect to other object shapes) activates a number of regions of the

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visual cortex, in particular in the inferior side of the brain, i.e. the Ventral Occipito-Temporal Cortex (VOTC; Gao, Gentile, & Rossion, 2018; Grill-Spector, Weiner, Kay, & Gomez, 2017; Haxby, Hoffman, & Gobbini, 2000; Rossion, Hanseeuw, & Dricot, 2012; Sergent, Otha, & MacDonald, 1992; Zhen et al., 2015). Focal damage to these regions, in particular in the right hemisphere, can cause *prosopagnosia*, a severe and specific breakdown of the ability to recognize individual faces, which cannot be explained by low-level visual deficits, a general (i.e., multimodal) recognition problem, or intellectual deficiencies (Bodamer, 1947; Davies-Thompson, Pancaroglu, & Barton, 2014; Hecaen & Angelergues, 1962; Meadows, 1974; Rossion, 2014; Sergent & Signoret, 1992). Electrical intracarotid stimulation applied to these right hemispheric VOTC regions can cause specific distortions of the face percept (Jonas et al., 2012; Rangarajan, Hermes, Foster, Weiner, & Jacques, 2014) and a transient selective inability to behaviourally recognize or discriminate between pictures of individual faces (Jonas et al., 2012, 2014, 2015). Likewise, transcranial magnetic stimulation (TMS) applied over the most posterior region of this network, i.e., the right inferior occipital gyrus, can lead to difficulties in individual face matching tasks (Pitcher, Walsh, Yovel, & Duchaine, 2007) or even in encoding facial identities in long-term memory (Ambrus, Windel, Burton, & Kovács, 2017). Neuroimaging studies of the healthy brain have also shown, using functional MR-adaptation (Grill-Spector & Malach, 2001), that these VOTC regions are sensitive to differences between different facial identities: their response is generally reduced to the repeated presentation of identical as compared to different facial identities (e.g., Davies-Thompson, Gouw, & Andrews, 2009; Gauthier et al., 2000; Gentile & Rossion 2014; Grill-Spector & Malach, 2001; Schiltz & Rossion, 2006). However, it is generally assumed that a full understanding of the neural mechanisms of human expertise at IFR requires complementary neural measures at lower levels of brain organization than cortical networks and local regions, all the way down to the level of single neurons.

This is where rhesus monkeys have served as a nonhuman primate model, potentially bridging what we learn from human lesion studies and neuroimaging to activity at the level of the single cell. Non-human primates have been used for studies of the neural mechanisms of cognition for over 80 years (Jacobsen, 1936) under the assumption that this will improve our understanding of the human brain (Passingham, 2009). A variety of species have been used, but by far the most commonly used primates are macaques (*Macaca*), a genus of several species including the rhesus monkey (*Macaca mulatta*). The rhesus monkey, one of the best-known species of Old World monkeys, is considered by many neuroscientists as the best model of the human visual system, suitable to understand not only low-level visual processes but the most complex mechanisms of visual object recognition (DiCarlo, Zoccolan, & Rust, 2012).

Single neurons responding selectively to faces were found in the macaque infero-temporal (IT) cortex originally by Gross, Rocha-Miranda, and Bender (1972; see Gross, 2008 for a historical review). Further single cell studies performed during the 1980's reported large proportions of these face-selective neurons in the macaque IT, describing their response properties in detail (e.g., Baylis, Rolls, & Leonard, 1985; Bruce, Desimone, & Gross, 1981; Desimone, Albright, Gross, & Bruce, 1984; Perrett, Rolls, & Caan, 1982; for reviews of these early studies, see Desimone, 1991; Rolls, 1992; Perrett, Hietanen, Oram, & Benson, 1992). Following the development of monkey fMRI (Logothetis, Guggenberger, Peled, & Pauls, 1999; Vanduffel, Zhu, & Orban, 2014 for review), several face-selective regions (also called clusters or patches) were subsequently identified in macaque IT (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003), and these regions have since been targeted for the recording of face-selective cells in a few laboratories (e.g., Aparicio, Issa, & DiCarlo, 2016; Chang & Tsao, 2017; Freiwald & Tsao, 2010; Freiwald, Tsao, & Livingstone, 2009; Issa & DiCarlo, 2012; Ohayon, Freiwald, & Tsao, 2012; Taubert, Van Belle, Vanduffel, Rossion, & Vogels, 2015a,b; Tsao, Freiwald, Tootell, &

Livingstone, 2006).

Under the assumption that macaques are typical primates who provide a general model for understanding cortical organization in the human brain, a major objective of this research program is to understand the neural basis of human face processing (e.g., Desimone, 1991; Rolls, 1992; Tovée & Tovée, 1993; Perrett, Oram, & Ashbridge, 1998), in particular of IFR. In this context, early studies, without pre-definition of the regions using fMRI, reported variability in the firing rate of single neurons' in response to images of different individual faces, this variability being proposed as a mechanism for the recognition of individual faces (Baylis et al., 1985; Perrett, Smith, Potter, Mistlin, & Head, 1984; Rolls, 1984, 1992). Specifically, these studies found that each face-selective neuron recorded in the macaque IT does not respond only to one face, but has a different relative response to each of the members of a set of faces. Thus, the hypothesis has been that the firing rate across a *population* of such neurons can convey information about different individuals, i.e., a distributed neural code (Rolls, 1992). Moreover, this information is thought to directly relate to physical properties of the stimuli: faces that are physically similar appear to be represented by similar distributed codes across the neuronal population (Leopold, Bondar, & Giese, 2006; Young & Yamane, 1992). In recent years, this seminal work has been extended to target, and compare, the coding of different individual faces in functionally-defined, face selective regions of macaque IT (Tsao et al., 2006). For instance, a recent study reported that the firing rates of approximately 200 neurons sampled from face-selective regions in two macaque brains could be used to decode visual similarity among 2000 humanoid faces, claiming to make a major breakthrough in understanding the neural code that allows the human brain to recognize individual faces (Chang & Tsao, 2017).

Here, we extend on a brief and specific commentary about this latter piece of work (Rossion & Taubert, 2017) to review three lines of evidence (or lack thereof) challenging the assumptions of this research program, and argue on this basis that electrophysiological recordings in macaques are severely limited in their ability to provide information about the neural basis of human IFR. First, objective behavioral measures in laboratory settings show that macaques and other monkeys are poor at recognizing individual faces, requiring extensive exposure and training with specific images to reach only moderate levels of performance (Section 2). Second, there is no evidence that IFR performance in monkeys is affected by key image manipulations, such as picture-plane inversion, or by the degree of familiarity of the individual faces, indicating that monkeys do not rely on qualitatively similar perceptual processes as humans (Section 3). Third, macaques do not possess a (right lateralized) ventral cortical face network in the occipito-temporal cortex, which is critical in the human species to support expertise at IFR (Section 4). For these reasons, we argue that distributed codes across populations of neurons in the macaque IT for images of different individuals does not inform about the fundamental mechanisms of human IFR (Section 5).

Before getting into the core of the argumentation, we need to clarify three points. First, we define IFR here as *when one individual identifies another according to its individually distinctive facial characteristics*. It is the most precise form of facial recognition (e.g., compared to the recognition of gender, emotional expression, etc.), involving and requiring unique (combination of) cues. In studies of human IFR, pictures of individual faces are (explicitly or incidentally) encoded, to then be subsequently recognized ("recognition tasks"). Alternatively, face pictures are presented briefly one after the other, or even simultaneously, participants being asked to determine if they depict the same person or not. These latter tasks are usually defined as "face matching tasks" or "individual face matching tasks". However, all of these tasks aim at measuring IFR, which corresponds to the matching between two or more stimuli of the same face identity. The tasks generally imply various levels of visual *discrimination* (from other individual faces, i.e. distractors), and *generalization* (across different images of the same

individual).

Second, in human studies, IFR is typically measured with images of *unfamiliar* faces (i.e., faces never seen before), for practical and methodological reasons (i.e., control of stimuli, comparable level of knowledge across participants). While performance at IFR, including matching tasks, is undoubtedly substantially improved for face pictures of familiar as compared to unfamiliar individuals (e.g., Bruce, 1982; Bruce et al., 1999; Bruce, Henderson, Newman, & Burton, 2001), performance with unfamiliar faces is usually good to very good, even in difficult tasks and similarly looking distractors, without any training. Hence, we do not subscribe to the view that typical human adults would lack expertise at IFR for unfamiliar faces (Hancock, Bruce, & Burton, 2000; Megreya & Burton, 2006; Young & Burton, 2018). In fact, one of the most important points to derive from the present review, from our point of view, is to realize that, compared to monkeys, typical human adults indeed demonstrate a high level of expertise when tasked with recognizing unfamiliar faces (Rossion, 2018).

Third, although there are at least 200 species of primates living today (Fleagle, 1999; Purvis, 1995), including nearly 90 species of Old World monkeys, the rhesus monkey is by far the most widely used species, in particular in neurophysiological studies. In fact, in the common parlance of neuroscientists, rhesus monkeys and other macaques are often referred to as simply ‘monkeys’ (Preuss, 2000). Here, therefore, when using the term “monkeys” to refer to neurophysiological studies (e.g., “monkey IT”), we mean *macaque monkeys* (generally rhesus monkeys). However, other species of monkeys, including New World monkeys, have also been included in behavioral experiments. Observations in these studies are informative and are even sometimes referred to by monkey neurophysiologists as if they were directly transposable to rhesus monkeys, or to all monkey species. In this review, when referring to these studies, the specific species of monkeys will be mentioned.

2. Are monkeys experts at individual face recognition?

Many animals living in social groups have a face – a body part usually at the front, which emerged over half a billion years ago in sea creatures and has evolved as a biological interface between the central nervous system and the environment (Bruce & Young, 1998; McNeill, 2000). A face is collection of sensory receptors whereby animals can gather information about the world around them (via sight, sound, smell, etc.) and react appropriately. Since the primary purpose of the face is not to signal identity, it does not necessarily follow that all social animals with a face will depend on facial structure to recognize conspecifics. Signalling identity is, therefore, a secondary function that needs to be confirmed, empirically, on a species-by-species basis. For instance, evidence suggests that neither penguins nor seals rely on facial morphology, but rather on sound vocalizations, to recognize individual conspecifics (Insley, 2000; Jouventin, Aubin, & Lengagne, 1999, respectively). In contrast, the potential queens of a single species of wasp, *P. fuscatus*, do rely on diagnostic facial marks to recognize individuals (Sheehan & Tibbetts, 2008, 2011), but this recognition is limited to 6–10 familiar individuals. Other wasp species, with a less complex social structure, are not able to perform individual recognition of conspecifics based on the face (Sheehan & Tibbetts, 2011). Hence, while having a face is a necessary condition for IFR, it is not a *sufficient* condition in the animal world. Rather, the extent to which a species relies on facial structure ought to reflect the ecological demands of the species’ society (i.e., *is it important to distinguish groups or individuals within a society? Are all individuals familiar or is there a mixture of familiar and unfamiliar individuals, changing regularly? How many individuals comprise a functional society? What types of signals are readily available to individuate conspecifics?*). In this section, we argue that there is little evidence to support the assumption that rhesus monkeys and other monkeys rely primarily on facial information to individuate conspecifics, and certainly not to the same extent and level of expertise as

humans.

We start by acknowledging that a number of experiments have shown that rhesus monkeys can learn to recognize individual faces of (unfamiliar) conspecifics following operant conditioning (Bruce, 1982; Parr, Winslow, & Hopkins, 1999; Parr, Winslow, Hopkins, & deWaal, 2000; Parr, Heintz, & Pradhan, 2008; Parr & Heintz, 2008; Rosenfeld & Van Hoesen, 1979; Vermeire & Hamilton, 1998; see also Micheletta et al., 2015 in crested macaques). Capuchins, a species of New World monkey, are also able to learn to individuate faces (Pokorný & de Waal 2009a; Pokorný, Webb, & de Waal, 2011; Talbot, Leverett, & Brosnan, 2016). These studies are often cited as evidence that “*monkeys, like humans, are able to use faces to recognize individuals*” (e.g., Parr et al., 1999; Pokorný & de Waal, 2009a; see also Leopold & Rhodes, 2010) or, in monkey physiology studies investigating IFR, that “*faces are important for primates*” (e.g., Chang & Tsao, 2017; Meyers, Borzello, Freiwald, & Tsao, 2015). However, if anything, a careful analysis of these behavioral experiments serve to demonstrate that rhesus monkeys do not possess a good natural ability to recognize individual faces.

Indeed, in order to learn to discriminate two pictures of different individual faces (e.g., Bruce, 1982), or to match strictly identical pictures of faces against a distractor face, rhesus monkeys need hundreds of trials to achieve a satisfactory level of performance (e.g., 80%, Parr et al., 1999, 2000, 2008; Parr & Heintz 2008; Rosenfeld & Van Hoesen, 1979; Vermeire & Hamilton, 1998; Fig. 1A). In these studies, the exact same pairs of face images have to be presented repeatedly, with relatively few pairs used (e.g., 4 pairs of individual faces to discriminate in Bruce, 1982; 10–15 pairs in the studies of Parr and colleagues). Capuchins also take hundreds or thousands of trials to achieve a modest level of performance at similar tasks (50–60%; Pokorný & de Waal 2009a; Pokorný et al., 2011; see Fig. 1B–D; see also Talbot et al., 2016, with 72% of performance reached before transfer). Importantly, this slow acquisition rate and moderate level of performance are not due to difficulty in task acquisition. Indeed, monkeys in these experiments have usually been well trained at the tasks with other stimuli such as clip arts. Moreover, after the majority of a group of monkeys achieves a satisfactory level of performance with a set of face images, the introduction of novel images of the same individuals, or images of new individuals, into the task often leads to a significant drop in performance (Parr et al., 2000; Pokorný & de Waal 2009a; Pokorný et al., 2011; Fig. 1B to D; about 30%–45% in Talbot et al., 2016). In sum, following operant conditioning, monkeys can learn to recognize specific images of faces but this alone should not be taken as evidence of a naturally developed ability to individuate conspecific faces, let alone a comparable level of IFR expertise as demonstrated in humans.

As a matter of fact, human adults who specifically lose this expertise following brain damage, i.e. patients with prosopagnosia (Bodamer, 1947), are nevertheless also able to successfully learn specific images of individual faces (e.g., Caldara et al., 2005; Sergent & Signoret, 1992: 10 individuals with two images per individual, 100% performance after 2–3 h of training). These patients with prosopagnosia are also able to match identical images of faces with at least 80% performance (e.g., the first 6 items of the Benton Facial Recognition Test, BFRT, Benton & Van Allen, 1968; see Rossion & Michel, 2018), although they take significantly longer than typical individuals (e.g., Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010). In fact, many patients with prosopagnosia can also, albeit relatively slowly, match individual faces across head rotation changes well above chance level (e.g., Delvenne, Seron, Coyette, & Rossion, 2004; Sergent & Signoret, 1992).

In typical human adults, natural (i.e., untrained) performance at unfamiliar face matching (with or without a brief delay between images) is excellent even across head orientation changes, a transformation preserving critical pigmentation cues (Laguerre, Dormal, Biervoys, Kuefner, & Rossion, 2012; Rossion & Michel, 2018). In fact, it is only when having to find a single unfamiliar face across substantial changes of viewing conditions, in particular lighting direction variations, and among many similar unfamiliar distractors that individual

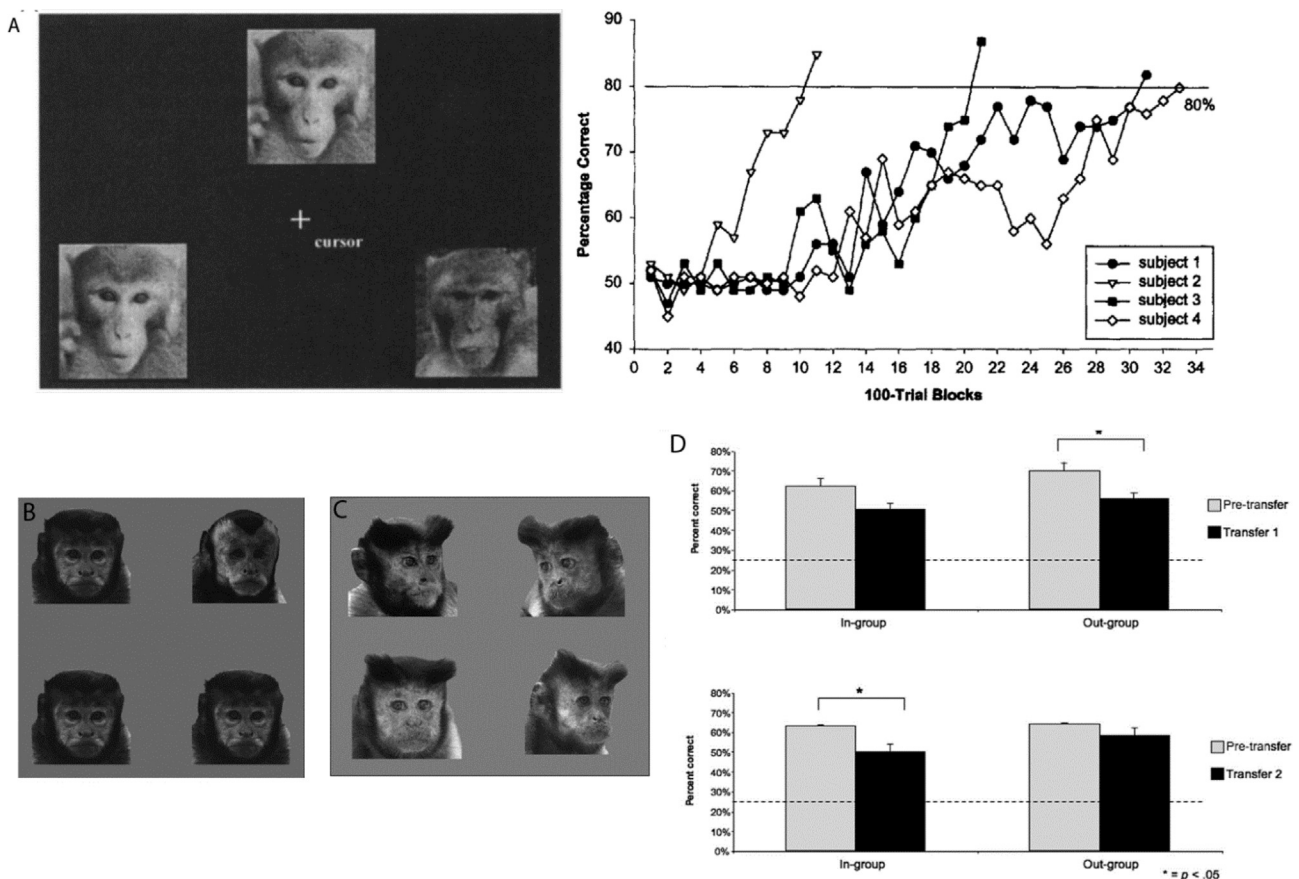


Fig. 1. A. Left. Example of a sequential 2AFC or match-to-sample task used in the studies of Parr and colleagues (Parr et al., 2000; 2008) in which a target face is presented on top, and disappears when the monkey contacts it with a cursor driven by a joystick. After the target face is contacted, it is cleared from the monitor, and the two comparison stimuli appear below. In some versions of the task, the target face remains on the screen. Note that the two images to match are strictly identical. Right. Results of 4 macaques tested at this trivial task with blocks of 100 trials, showing that they need between 1100 and 3300 trials to reach criterion (> 80% performance). Introducing a new image set after reaching criterion leads to a significant drop of performance, even though the task still requires a simple image comparison. B. Example of a discrimination learned pre-transfer in the studies of Pokorny and de Waal (2009a) and Pokorny et al. (2011), where the odd individual Capuchin monkey on the top right has to be selected by the subject (image adapted from Pokorny et al., 2011). C. Example of a Transfer 1 task in which different views of the individuals are presented; the odd monkey individual is on the top left corner. Note that although the task may appear difficult, this odd individual face image could be easily selected based on its much darker hair covering the face and the higher global contrast. C. Examples of performance obtained in such tasks by 5 Capuchin monkeys. Note that even after extensive training, performance does not exceed 60% for the exact same images (Pre-Transfer). Moreover, unlike humans, Capuchins do not perform better with ingroup (familiar) faces than outgroup (i.e. unfamiliar) faces at the face matching task (see section 3).

face matching performance in humans drops to about 70–80%, i.e., a performance level that is sometimes defined as *low*, “*highly inaccurate*” or even “*remarkably poor*” for human standards (e.g., Bruce et al., 1999; Hancock et al., 2000; Megreya & Burton, 2006, 2008; Megreya, White, & Burton, 2011; White, Kemp, Jenkins, Matheson, & Burton, 2014; Young & Burton, 2018). However, with familiar faces, including faces that are briefly familiarized, performance is close to ceiling at the first attempt (Megreya & Burton, 2006). On the basis of their limited ability at much simpler tasks as described above and illustrated in Fig. 1, monkeys could not even be tested in such extremely challenging conditions as tested with humans in the latter studies: they would not be able to perform above chance level, even with unlimited time.

In sum, far from matching humans, monkeys required to individuate images of conspecific faces do not appear to perform better than other animal species, such as sheep (Kendrick, da Costa, Leigh, Hinton, & Peirce, 2001), wasps (Sheehan & Tibbetts, 2011) or fish (Wang & Takeuchi, 2017) similarly trained to recognize individual faces of conspecifics, or even to recognize individual human faces (e.g., bees, Dyer, Neumeyer, & Chittka, 2005; fish, Newport, Wallis, Reshitnyk, & Siebeck, 2016; sheep, Knolle, Gonçalves, & Morton, 2017). They also perform well below human patients with prosopagnosia. The implication is that an intact set of specialized cortical face regions, or even a

primate cortex, is not needed to accomplish these IFR tasks above chance level. In other words, successful performance at IFR after extensive training in monkeys (and other animal species) does not provide evidence that this species reaches a comparable level of expertise as humans and rely on comparable neurofunctional processes.

To avoid the issue of (over)training, a number of paradigms have been used in which macaque monkeys are required to habituate to a given unfamiliar face (i.e., the adapting stimulus). After looking at the adapting stimulus for a prolonged period of time, these studies report a viewing preference for a novel individual face over the adapting face, which is taken as evidence of successful IFR (Dahl, Logothetis, & Hoffman, 2007; Dufour, Pascalis, & Petit, 2006; Gothard, Erickson, & Amaral, 2004; Gothard, Brooks, & Peterson, 2009; Pascalis and Bachevalier, 1998; Sugita, 2008; see also Neiwirth, Hassett, & Sylvester, 2007 in Tamarins). Unfortunately, IFR performance cannot be quantified with this paradigm, which simply reports a significant viewing preference (after adaptation). Moreover, although human adults can be tested in such tasks also (e.g., Pascalis, de Haan, & Nelson, 2002; Scott, Shannon, & Nelson, 2005), they may have no interest in spending more time looking at a novel or adapting stimulus in such habituation/novelty paradigms, which makes it difficult to obtain meaningful comparable datasets in humans to evaluate monkeys’

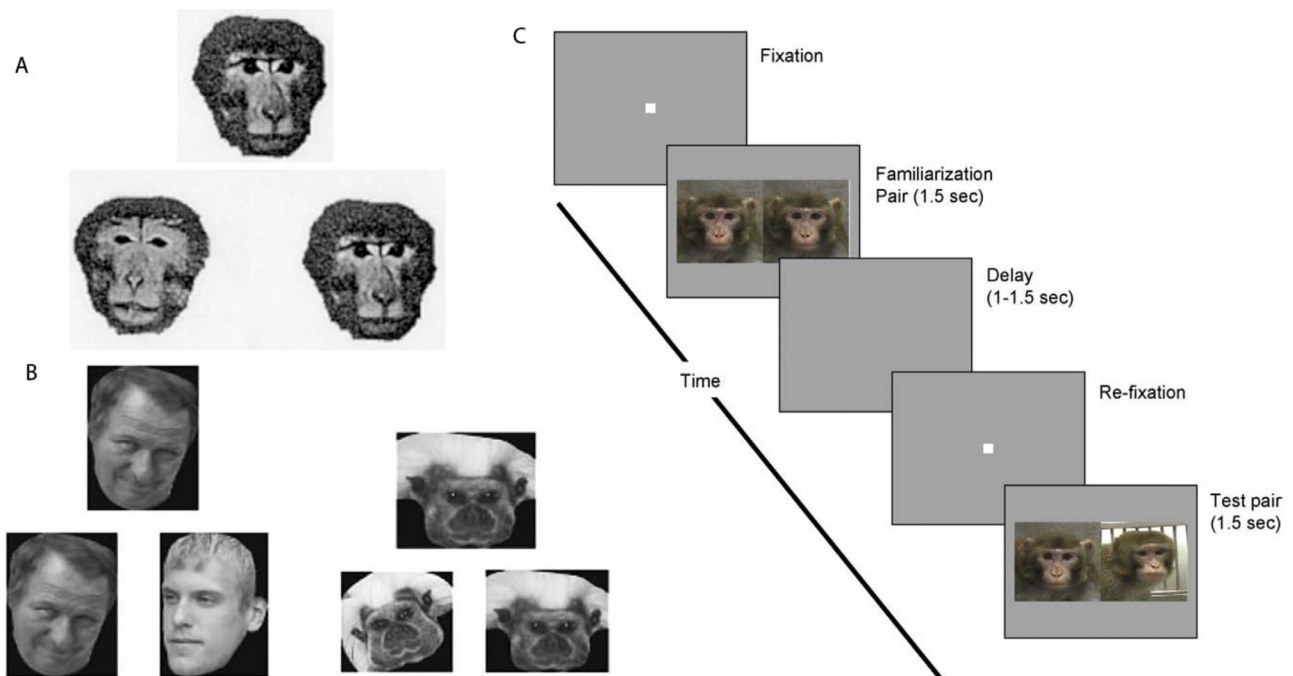


Fig. 2. Examples of images used in studies using the habituation/novelty paradigm to test monkeys' IFR ability. A. Example of images from [Pascalis and Bachevalier \(1998\)](#), with the habituation stimulus on top, followed by the two images at the bottom. Viewing preference for the novel item may have nothing to do with face identity but can be based on obvious low-level image cues. Moreover, head orientation and gaze direction differ between the two faces. B. Example images used by [Neiworth et al. \(2007\)](#) to test Tamarin monkeys' preference for novel human or Tamarin faces. In all cases, targets and distractors differ in terms of many cues beyond face identity. C. Example of an habituation/novelty trial used by [Gothard et al. \(2004\)](#), who showed longer eye gaze fixations on the novel face image presented after habituation. Again, many cues differ between these images, even outside of the faces displayed, seriously weakening claims in these studies that on the basis of a preferred response to a non-habituated stimulus, monkeys are able to perform IFR without training.

performance. Most importantly, although viewing preferences in such adaptation paradigms have generally been taken as evidence that monkeys are naturally able to individuate faces of conspecifics, these studies are confounded by repetition of the exact same images ([Fig. 2](#)). Hence, a significant viewing preference may reflect the recognition of an individual depicted in an image, or some other process such as the exogenous allocation of attention to low-level image cues. For example, when the exact same images are used to habituate and test monkeys' preferential looking, the distractor images will be more novel irrespective of the individual they depict (i.e., both low-level image cues and a whole host of socially relevant signals such as head orientation or eye gaze direction can signal novelty; [Fig. 2](#)).

In summary, there is little empirical support for the claim that monkeys can naturally recognize individual faces of conspecifics, let alone approach human-like expertise at this function. Note that this conclusion arises even without considering speed of recognition, which is an important factor in human studies (i.e., to distinguish between typical observers and patients with prosopagnosia performing individual face matching tasks; e.g., [Davidoff & Landis, 1990](#); [Delvenne et al., 2004](#); see [Rossion & Michel, 2018](#)). It is also important to mention that studies showing rhesus monkeys' ability to select familiar dominant monkeys based on face images only ([Deaner, Khera, & Platt, 2005](#)) do not provide solid evidence for their ability to actually recognize these individuals, since macaques can also extract such information from pictures of unfamiliar conspecifics ([Micheletta et al., 2015](#), in crested macaques). More generally, many species have badges of status (i.e., reliable subsets of signals of quality that reveal information about an individual's size and dominance) that can be readily decoded from the body, including the face. For instance, a species of wasps showing no evidence of IFR, *Polistes dominulus*, nevertheless relies on facial patterns to predict body size and social dominance (e.g., [Tibbetts & Dale, 2004](#)). In humans, signals of dominance can be readily extracted from the face of unfamiliar individuals ([Todorov, Baron, &](#)

[Oosterhof, 2008](#)), and social judgments of faces that are correlated across people can be achieved even in the absence of a good ability to recognize individual faces ([Quadflieg, Todorov, Laguesse, & Rossion, 2012](#); [Rezlescu, Susilo, Barton, & Duchaine, 2014](#); [Todorov & Duchaine, 2008](#)).

We suggest there are at least three reasons for which monkeys, in particular rhesus macaques, might find the tasks measuring IFR challenging. First, although the perceptual world of the rhesus monkey, like humans and many other primates, is dominated by vision, the human societies in which we live are characterized very differently from those formed by groups of rhesus monkeys. Rhesus monkeys' society is generally comprised of a smaller number of individuals (a historical trend exaggerated in the conditions of monkeys raised in captivity and hosted in research laboratories), and they are organized around relative stable hierarchies based on relatedness to dominant females. Human society, on the other hand, is characterised by the presence of numerous individuals and fission–fusion dynamics, i.e., a tendency to change the number of individuals over time. Second, although human faces are extremely variable morphologically, even within a genetically homogeneous group ([Sheehan & Nachman, 2014](#)), individual monkey faces, in particular those of macaques, may not necessarily vary substantially, and thus convey reliable (i.e., invariant) signals for identity. This could be because there is no need to individuate many individuals or because, unlike for humans ([Sheehan & Nachman, 2014](#)), there are other readily recognizable cues from the body shape or the voice that can be used to rapidly recognize the necessary limited number of individuals. Third, and more generally, although monkeys are diurnal – like us – and are closely related to humans from a phylogenetic perspective (certainly more so than other mammals, including rodents), one cannot assume continuity across the primate order in all facets of visual cognition and cortical organization ([Preuss, 2000](#)). In fact, as discussed in the next section, the available evidence rather indicates that monkeys lack both the cognitive and neural specializations that support human IFR.

3. Cognitive specialization

A large body of scientific literature has concluded repeatedly that human recognition of individual exemplars differs qualitatively for faces and nonface stimuli (Farah, Wilson, Drain, & Tanaka, 1998; McKone et al., 2007; Rossion, 2008). In this section, we review studies that have investigated the same cognitive specializations in nonhuman primates.

3.1. Face inversion

In humans, there is a large drop of performance at individual face recognition tasks when pictures of faces are presented upside-down: this effect is typically about 20% in behavioral studies, and is much larger for faces than nonface objects (Yin, 1969). It has been replicated for 50 years across a wide variety of tasks (e.g., old/new recognition and matching tasks) and variables (accuracy rates or RTs) (for reviews, see Farah et al., 1998; Rossion, 2008; 2009) and is arguably the strongest and most reliable effect found in the field of human face recognition. Strikingly, there is no evidence of such an inversion cost in macaques tested with conspecific faces in the same kinds of IFR tasks described in the previous section (Bruce, 1982; Rosenfeld and Van Hoesen, 1979; see also Gothard et al., 2004; Phelps and Roberts, 1994; Wright & Roberts, 1996). Note that rhesus monkeys are perfectly able to detect the difference between an upright and inverted face image and, under unrestricted viewing conditions, they do prefer to look at upright than inverted images of faces (Adachi, Chou, & Hampton, 2009; Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003; Tomonaga, 1994). Importantly, rhesus monkeys do not have a prehensile tail, nor any specific adaptation for suspensory behaviour or arboreal locomotion such as brachiation. They live predominately on the ground, like humans; thus there is no particular reason to believe that they are exposed as often to inverted as upright faces.

It is important to note that investigation of the face inversion effect in macaque monkeys is often described as having yielded mixed results in the scientific literature (as reviewed in Dahl, Rasch, Tomonaga, & Adachi, 2013; Leopold & Rhodes, 2010). We argue that this ambiguity stems from three causes. First, while some studies consider an inversion effect in monkeys to be the mere preference for upright faces over inverted faces (Tomonaga, 1994), others relate it better performance for upright faces in a face/nonface detection task (Perrett, Mistlin, et al., 1988), or differences in eye movement exploration between upright and inverted faces (Dahl, Wallraven, Bulthoff, & Logothetis, 2009; Guo et al., 2003). However, none of these are dependent measures of *individuation* of faces, the critical function at stake. Instead these outcomes point to a viewing preference for visual stimuli presented in the cardinal (upright) orientation, better face categorization (i.e., face detection) when stimuli are upright compared to when they are turned upside down, or, finally, a reliable eye movement pattern for upright faces which could reflect an efficient strategy for extracting any number of socially relevant signals (e.g., expression, gender/attractiveness, gaze direction, health, kinship etc.). In sum, if these studies were testing human subjects, they would not meet the burden of proof required for making inferences about IFR.

The second cause of ambiguity in the literature concerns operant conditioning: some studies report a modest inversion effect in individuation tasks only after training monkeys extensively with upright faces, and then comparing performance for these *specific* stimuli at upright (trained) and inverted (untrained) orientations (Overman & Doty, 1982; Vermeire & Hamilton, 1998). Because this design confuses the face inversion effect with general learning biases, it is generally acknowledged that these studies do not provide evidence of a behavioral face inversion effect in monkeys (Bruce, C., 1982; Dahl et al., 2013; Vermeire and Hamilton, 1998).

A third source of ambiguity is the nature of matching tasks used. A number of studies have reported significant face inversion effects in

two-alternative forced-choice tasks requiring a subject to discriminate between two face stimuli (Fig. 1; Parr, 2011; Parr et al., 1999, 2000, 2008; Parr & Heintz, 2008). In these tasks, a picture is presented to the monkeys during the initial encoding phase (the “sample”) and is followed by a “match-distractor stimulus pair” (i.e., one picture would be the correct match and the other the incorrect distractor). The potential problem with these tasks is that in the inverted conditions, the picture-plane orientation of the sample and the match-distractor pair differs by 180 degrees, whereas in the upright condition, all three stimuli are presented at the same orientation. As others have put it (Dahl et al., 2013), this paradigm (which is not used in human studies) therefore measures a “face rotation effect” rather than a “face inversion effect”. Hence, unsurprisingly, in these studies, “rotation effects” are found for other stimuli tested in monkeys, such as human and chimpanzee faces or pictures of automobiles (Parr et al., 1999), with no evidence of a larger effect for conspecific faces. Based on this lack of specificity and other findings, Parr et al. (2008) in fact concluded that rhesus monkeys lack human-like expertise for faces. The same limitation applies to studies measuring a “face rotation effect” in a habituation/novelty paradigm (*rhesus monkeys*, Gothard, et al., 2009; *Tamarins*, Neiwirth et al., 2007, Fig. 2B).

In summary, although monkeys perceive the difference between upright and inverted faces, have a clear preference for upright faces, and are typically exposed to many more upright than upside-down faces in typical living conditions, as well as in experiments, they do not present with an advantage at *individuating* conspecific faces at upright over inverted orientations. This observation represents a striking difference with human performance in terms of the cognitive specializations thought to govern IFR (Rossion, 2008).

3.2. The composite face effect

In humans, the composite face effect has been used as an index of mandatory integration of facial parts into a unified representation of the individual face (“holistic face perception”; Young, Hellawell, & Hay, 1987; see Murphy, Gray, & Cook, 2017; Rossion, 2013 for reviews). This effect is based primarily on a visual illusion: identical top halves of (unfamiliar) faces are perceived as being different when they are aligned with different bottom halves; this illusion disappearing when the two halves are misaligned, or when the faces are presented upside-down (Fig. 3). This composite face illusion shows that an individual face part (here the top half) cannot be perceived independently of the other parts (here the bottom half), as if the face processing system automatically fused the face parts into a single percept. Based on this illusion, many behavioral studies have designed matching paradigms in which human observers make mistakes and/or show prolonged responses times (RTs) at matching identical top halves of unfamiliar faces associated with different bottom halves. This effect is generally strong and reliable, although many versions of this paradigm in terms of stimuli and parameters have been used and can also lead to spurious effects (or absence of effects, see Rossion, 2013 for an extensive and critical review of the composite face effect).

Taubert and Parr (2009) compared the performance of rhesus monkeys and spider monkeys (a New World primate species where members form societies governed by fission–fusion dynamics) in a matching task involving composite face stimuli. Both species were initially trained to attend only to the top half of the sample stimulus using face-like shapes. This was a lengthy process with a small number of stimuli and the inferences drawn from this study depend on the assumption that the subjects could generalize from round shapes to real photographs of faces. Nonetheless the authors found differences in the response profile of both species, with evidence of a composite effect emerging independently of visual expertise. For example, rhesus monkeys only exhibited a composite effect for gorilla faces.

In Taubert, Qureshi, and Parr (2012), the authors were careful not to train rhesus monkeys with test stimuli and to measure a control

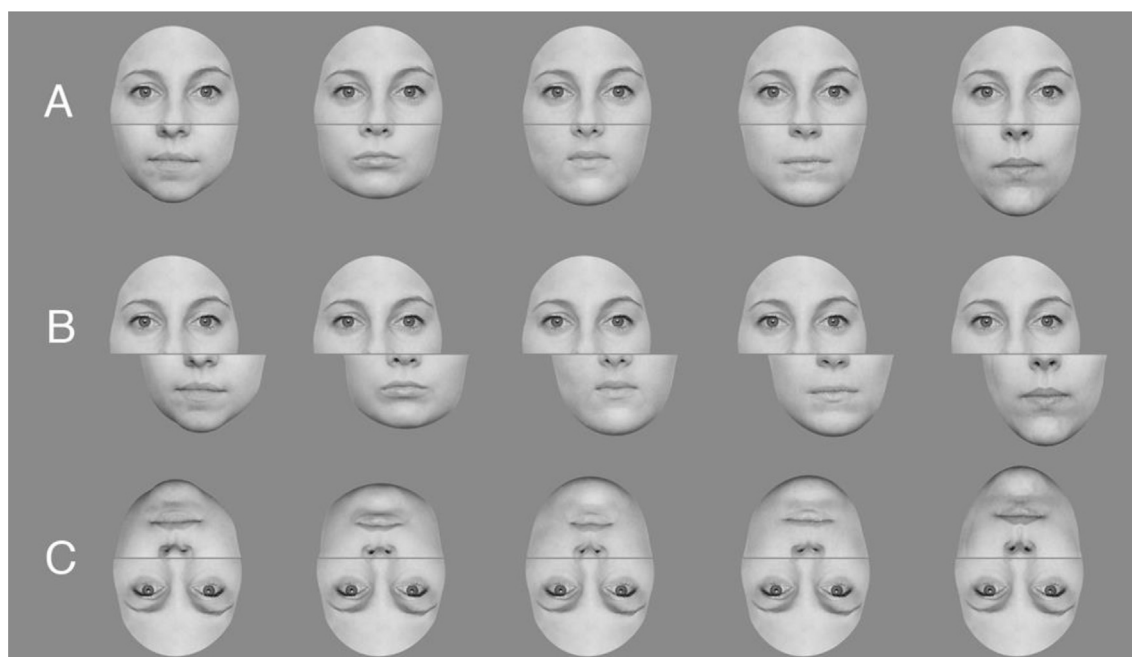


Fig. 3. The composite face illusion (adapted from Rossion, 2013). A. All 5 top halves (above the thin line) are physically identical. Yet, when they are aligned with distinct bottom halves (all of different identities, neutral expression, taken under the same lighting conditions), they are perceived as being different. B. If the bottom halves differ but are spatially misaligned with the top halves, one has no difficulties in perceiving the top face halves as being indeed identical. C. Same as in A but the display has been vertically flipped, showing inverted faces. All 5 “top” halves (here at the bottom of the display below the thin line) are physically identical and one does not see them as being different.

condition where the exogenous bottom halves of the faces were not presented. They found a small composite effect for rhesus macaques driven by only 4 of the 6 subjects in the sample. In both papers the smaller effect sizes and the greater inter-subject differences for rhesus macaques as compared to humans was explained by differences in social structure and cognitive specializations (Taubert, Qureshi, et al., 2012; Taubert & Parr 2009).

Dahl et al. (2007) claimed to have overcome the limitations of trained effect tasks, instead using a “rebound” habituation effect as a proxy for the composite face effect in rhesus monkeys. The design was reasonably straightforward; when a stimulus is repeated, exchanging the bottom half of a face produced less rebound (in terms of eye movement exploration) in the misaligned condition than in the corresponding aligned condition. This result was interpreted as reflecting the perception of a novel identity in the top half of the face in the aligned condition (which is largely consistent with the theory behind the composite face effect in humans, see Rossion, 2013, and with evidence of such decreases in habituation in composite face tasks used in fMRI or EEG; Jacques and Rossion, 2009; Schiltz & Rossion, 2006, respectively). Unfortunately, unless one relies on gaze-contingent constraints for instance (Van Belle, de Graef, Verfaillie, Busigny, & Rossion, 2010), eye movement exploration is not well-suited to capture holistic (i.e., undissociable in parts) encoding of an individual face in composite face paradigms (e.g., no difference in eye gaze fixations between aligned and misaligned faces; De Heering, Rossion, Turati, & Simion, 2008).

Moreover, Dahl et al. (2007)’s finding suffers from a major shortcoming: in their study, the misaligned stimuli were not centered on the upper part of the monkey faces. That is, the critical region to compare between aligned and misaligned conditions (upper part) was not located at the same position on the images, being left lateralized relative to the centre in the misaligned trials only. Hence, if monkeys in that study looked more on the centre of the overall stimulus, there made fewer fixations on the eyes, independently of perceiving a novel face, for misaligned trials. Supporting this interpretation, the authors found a main effect of misalignment already in adaptation trials, where both top parts of the faces were novel. Importantly, there was no control

condition to exclude a general effect of “misalignment”. Since monkeys would have been trained to fixate on a screen (usually centrally) and, further, they are used to stimuli (and objects in the natural environment) being whole and not disassembled, “less rebound” in misaligned trials could easily reflect a neophobic response to a strange stimulus or a reluctance to explore facial features displaced from the centre of the screen.

In sum, studies of the composite effect are in line with the lack of inversion effect in monkeys and do not provide further evidence that this species perceive individual faces holistically, a key process behind human expertise at individual face recognition.

3.3. Lack of advantage in matching familiar as compared to unfamiliar faces

Another clear index thought to characterize face individuation in humans is the strong advantage found for pictures of familiar over unfamiliar individuals. This advantage has been found not only in old/new recognition tasks (e.g., Bruce, 1982) but also in individual face matching tasks, in particular when the pictures to match vary in head orientation and/or lighting direction (e.g., Burton et al., 1999; Bruce et al., 2001; Megreya & Burton, 2006). Although (untrained) human performance at unfamiliar face matching tasks even in extremely difficult conditions is usually very good (e.g., 70–80% accuracy in 1/10 matching tasks with different target images, similar distractors, and catch trials with absent targets, Megreya & Burton, 2006) some authors have even claimed, on the basis of the advantage found for familiar faces, that human expertise at IFR would concern only familiar faces (Young & Burton, 2018; but see Rossion, 2018).

Strikingly, the only study – to our knowledge – that compared familiar and unfamiliar face matching in macaques failed to find any advantage for familiar faces (Micheletta et al., 2015). In that study, three monkeys performed a 2AFC task requiring to match simultaneously presented different images of the same target face against a distractor individual face. The monkeys, who had been extensively trained at the task with other stimuli including identical images of

faces, reached only a correct level of performance overall for such task (about 75%). However, there was no advantage for pictures of highly familiar as compared to unfamiliar individuals. The species tested was crested macaques, who are phylogenetically closely related to rhesus macaques but are considered as more socially tolerant (Duboscq et al., 2013).

Studies in Capuchin monkeys, a species of new world monkey which is also referred to by monkey physiologists as providing evidence that primates, in general, are uniquely adept at extracting information from faces, including identity (e.g., Meyers et al., 2015), have provided mixed results on this issue. In the first study of Capuchin monkeys that explicitly tested this hypothesis, the individual face matching task was performed even slightly better when the conspecifics face stimuli were unfamiliar (i.e., monkeys raised separately from the tested subjects) than when they were familiar (i.e., monkeys raised in the same group for many years; Pokorný and de Waal, 2009a; Fig. 1B). In a more recent study, performance did not differ either between in-group and out-group faces in a 4AFC simultaneous face matching task (Talbot et al., 2016). However, monkeys were visually familiar with the out-group individuals, and performance for these two groups of faces was better than for a completely unfamiliar set of faces. Although the authors took these findings as evidence of a familiarity effect in individual face matching in Capuchins, in the absence of a cross-over interaction between the subjects tested and the stimulus sets, this difference in performance easily be due to physical differences in stimulus sets (i.e., a larger physical homogeneity between the unfamiliar face pictures). Moreover, in that study, despite having been extensively trained at the task with clip arts and identical face images, Capuchins took more than 10,000 trials on average to perform the 4AFC across head orientation changes significantly above chance level, reaching only modest levels of performance overall (i.e., about 45% for familiar faces; see Talbot et al., 2016).

Hence, overall, while performance at matching different pictures of a given individual is superior for familiar than unfamiliar face identities in humans, there is no behavioral evidence for such effect in monkeys. This is not to say that monkeys, or other animal species, cannot recognize a few highly familiar individuals from their face, even on a still picture. In fact, several studies have shown that monkeys are able to do that, and even spontaneously associate these pictures to voice-identity information or affective responses (e.g., Sliwa, Duhamel, Pascalis, & Würth, 2011: 3 highly familiar individual faces; Landi & Freiwald, 2017: 3 highly familiar individual faces, both studies in rhesus monkeys; Pokorný & de Waal, 2009b: 8–9 highly familiar individuals in Capuchins). In the study of Micheletta et al. (2015) with crested macaques (4 highly familiar individual faces), although matching performance was not influenced by familiarity, the monkeys were differentially influenced by the dominance status of the individual for familiar and unfamiliar faces, indicating that they recognized the few familiar faces. However, monkeys' ability to recognize a few highly familiar individuals with well-known hierarchical relationships from their face alone does not imply reliance on a human-like expert system to readily extract the idiosyncratic configuration of numerous individual faces, and a dedicated neural circuitry for this expert individual face recognition function as in humans (see Section 4).

3.4. Conclusions: monkeys differ quantitatively and qualitatively from humans at individual face recognition behavior

To summarize this section, there is no evidence that macaque monkeys, or other monkey species, are naturally able to individuate various conspecifics based on their faces, let alone to come close to humans in terms of level of performance (i.e., level of expertise) at this function. There is no evidence either that monkeys rely on qualitatively similar cognitive processes as humans, showing no inversion or typical composite face effects, and exhibiting no advantage at matching pictures of familiar over unfamiliar individuals. In fact, across a number of

behavioural studies, there is evidence to the contrary: monkeys trained to individuate pictures of faces appear to rely merely on image-based cues (see Martin-Malivel, Mangini, Fagot, & Biederman, 2006 for direct evidence in the Guinea baboon, another Old World monkey). Hence, their performance vary considerably across trials (see Micheletta et al., 2015 for instance), generally drops when new images are introduced in a design, and is particularly poor when matching across changes in image format (i.e., invariance) is required. When transfer occurs, it is only for a few items and it could easily be accounted for by low-level cues that are preserved despite inversion (Bruce, 1982; Rosenfeld & Van Hoesen, 1979), scrambling or removal of internal features (e.g., experiment 2 in Parr et al., 2008). Monkey behavioural studies that do not rely on training and explicit IFR tasks but rather on visual habituation paradigms typically use identical images to compare distractors varying on many low-level cues but also and high-level cues non-identity cues such as eye gaze-direction (Fig. 2), showing some evidence of image discrimination at best, but not face discrimination based on identity signals.

In other studies, rhesus macaques did not respond preferentially to average faces (i.e., composites of different faces; Tomeo, Ungerleider, & Liu, 2017) nor were they able to match average faces (i.e., composites of multiple photographs taken of the same individual) more effectively to single instances (Taubert, Wardle, Flessert, Leopold, & Ungerleider, 2017). These latter studies indicate that averaging faces together does not yield the same behavioural advantage for monkeys as it does for humans. This might indicate a general resistance of monkeys' face processing system to process stimuli that fall into "uncanny valley". Alternatively, it might indicate a significant difference in how rhesus macaques encode morphological similarity among conspecific faces. Indeed this was the main conclusion of Parr, Taubert, Little, and Hancock (2012) who attempted to investigate perceptual distinctiveness among macaque monkeys faces.

Similarly to studies performed in human infants and children, it could be argued that the burden of proof should be systematically lowered for people working with monkeys in a comparative context because it is difficult to collect behavioural data from nonhuman subjects without severely changing the methodology used in studies of (adult) human behaviour. For instance, we might forgive a failure to replicate because, unlike human subjects, monkeys cannot be verbally instructed. We do not deny that verbal communication plays a large role in behavioural measures of human performance, and that comparing performance at explicit behavioral tasks – which reflect the outcome of many sensory, cognitive and motor processes – across species or human populations is challenging. Nevertheless, it is worth noting that members of an ape species, namely common chimpanzees, have often performed more comparably to humans at behavioural face individuation tasks (Parr, 2011; Parr, Siebert, and Taubert, 2011; Parr et al., 2012; Taubert, Aagten-Murphy, and Parr, 2012; Taubert, Qureshi et al., 2012; Taubert, Weldon, and Parr, 2017; Weldon, Taubert, Smith, and Parr, 2013; also Taubert and Parr, 2009 for a comparison between Old and New World monkeys; and Talbot, Mayo, Stoinski, and Brosnan (2015) for a study in orang-utans). These direct comparisons across nonhuman primate species indicate that it is not the lack of verbal instruction that leads to rhesus macaques systematically "failing" researcher expectations. Instead, these studies point to cognitive discontinuities across the primate order, perhaps driven by qualitative and quantitative differences in social demands.

4. Neural specializations

If macaques do not possess a human-like ability to individually recognize faces, why would they have a complex network of cortical face-selective areas as identified with fMRI (Tsao, Moeller, & Freiwald, 2008)? For a start, we note that the mere presence of face-selective regions, or face-selective populations of neurons, does not imply that they support an IFR function. For instance, a face-selective cortical

network as extended as in macaques has also been found in marmosets (Hung, Yen, Ciuchta, Papoti, & Bock, 2015), a new world species of monkeys with a smaller and more primitive brain than macaques (Fleagle, 1999), for which there is no evidence of behavioral IFR ability. Also, a face-selective area has been identified in the temporal cortex of dogs (Dilks et al., 2015), despite no evidence that dogs rely on faces to recognize other individual dogs. In the same vein, groups of face-selective neurons have been found in the temporal cortex of sheep (Kendrick & Baldwin, 1987), a species with no evidence of large interindividual morphological variability in the face, natural ability, and social requirement to individuate conspecifics¹.

4.1. The cortical face network in the monkey STS

Coming back to the macaque brain, their network of brain regions responding selectively to faces in fMRI is found along the superior temporal sulcus (STS), where face-selective-cells have systematically been recorded since the seminal study of Gross, et al. (1972). In some studies, up to six face-selective regions have been reported, in the posterior, middle and anterior sections of the STS, occupying space in the fundus, or the lower bank of the sulcus, close to its lateral tip (Fig. 4; Tsao et al., 2008). These regions have been named according to their localization within the STS, with e.g., the ML region being located in the Lower bank of the Middle section of the STS, while MF is located in the Fundus of the Middle STS (Fig. 4).

4.2. A lack of ventral cortical face network in the monkey brain

Importantly, unlike in the human brain, face-selective regions have not been found in the ventral occipito-temporal cortex of the monkey: even the most anterior face region, labelled AM, is found outside of the STS and located on the lateral surface of the anterior temporal lobe (Fig. 4). Note that this difference alone does not imply that there is no homologous relationship between human and monkey cortical face networks. For instance, while human primary visual cortex is essentially located medially around the calcarine sulcus, macaque's primary visual cortex, V1, extends much more laterally than human V1 (Schira, Tyler, & Rosa, 2012) and monkey's ventral visual stream is thought to run on the lateral occipito-temporal cortex surface. However, V1 is also relatively (i.e., compared to other visual areas and the entire brain) much larger in macaques than humans (10% of the total cortical surface vs. 3%, respectively; Van Essen, 2005). In contrast, the temporal lobe is much smaller and thinner in macaques than humans, even accounting for body size differences (Rilling & Seligman, 2002; Fig. 5). Beyond size, they are also major differences in gyrification between the brains of macaques and humans (Zilles, Palomero-Gallagher, & Amunts, 2013). In humans, the ventral occipito-temporal surface 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, the most important structure for IFR (Barton, 2008; Meadows, 1974; Rossion, 2014). In contrast, 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 (Fig. 5).

In addition to a ventral network of face-selective areas, the human brain also holds a network of face-selective regions along the STS (Duchaine & Yovel, 2015; Haxby et al., 2000; Fig. 4). This STS network in humans does not seem to contribute significantly to IFR (e.g., there are no known cases of prosopagnosia following selective STS damage in humans). Rather, STS face-selective regions appear to be involved the

coding of dynamic (i.e., rapidly changing) aspects of faces such as eye gaze direction, head orientation and facial expressions (Allison, Puce, & McCarthy, 2000; Bernstein & Yovel, 2015; Carlin, Calder, Kriegeskorte, Nili, & Rowe, 2011; Hoffman & Haxby, 2000; Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011; Pitcher, Duchaine, & Walsh, 2014; Winston, Henson, Fine-Goulden, & Dolan, 2004).

These anatomico-functional differences between species, together with the lack of human-like ability at IFR in macaque monkeys as reviewed in previous sections, raise the intriguing possibility that the ventral face-selective recognition system – which is found essentially all along the fusiform gyrus and adjacent sulci (Fig. 4) – emerged relatively recently in evolution, and may even be so extensively developed specifically in the human species or its closest cousins (see e.g., Parr & Heintz, 2009; Chance et al., 2013 for neural studies relevant to face processing in chimpanzees).

4.3. A ventral shift of the STS face-selective network in the monkey brain?

Despite these obvious differences between species in cortical organization of face-selective networks, some authors consider that the STS cortical face network in the monkey brain is divided into two parts: (1) a dorsal part, which would be homologous to the face-selective STS network in humans, and (2) a ventral part, which would correspond to the face-selective VOTC network in humans (Freiwald, Duchaine, & Yovel, 2016; Lafer-Sousa, Conway, & Kanwisher, 2016; Tsao et al., 2008; Weiner & Grill-Spector, 2015; Yovel & Freiwald, 2013; Fig. 4B). According to this view, the putative ventral part of the monkey STS system would have been pushed onto the ventral surface of the brain over the course of human evolution by the expansion of regions engaged in language and social cognition, in particular the temporal parietal junction (see fig. 9 in Lafer-Sousa et al., 2016 for instance). In monkeys, then, the more dorsal network would be involved in representing dynamic aspects of faces, such as facial expressions or eye gaze direction, and this putative “ventral” network would be involved in processing face identity (Fig. 4B; Fisher & Freiwald, 2015). Thus, these monkey STS regions are not only argued by some to constitute a precursor system in non-human primates of the human ventral cortical face network, but also to be homologous one-by-one to the face-selective regions found in the human brain (Tsao et al., 2008).

Establishing neuroanatomical homologies between two species which shared a common ancestor 25 million years ago (Kumar & Hedges, 1998) and differ considerably in brain size and gyrification (Zilles et al., 2013) is of course extremely difficult, and one must remain very careful in making strong statements on this issue. However, the arguments advanced in favour of this homology between a “ventral” face-selective STS system in the monkey brain and the face-selective VOTC human network are certainly not compelling, for a number of reasons.

First, according to the authors favouring this inter-species homology, the number of posterior face-selective regions identified with fMRI would be the same across species, i.e., 6 in each hemisphere, and these regions would be organized according to the same processing hierarchy (Tsao et al., 2008; see Figs. 1 and 2 in that publication; Freiwald et al., 2016; Yovel & Freiwald, 2013). Under this view, the face-selective region known as ML in the monkey STS would correspond to the human mid-fusiform gyrus (“FFA”) for instance. However, the numbers do not add up because the region known as PL would then correspond to a face-selective region in the human inferior occipital gyrus (the “occipital face area”, OFA, Freiwald et al., 2016; Fig. 4) rather than to the human posterior STS, which would therefore not have any corresponding area in the monkey brain. Another example is that, in comparison to the single ML cluster in the monkey STS which would be part of the monkey “ventral” system, the human fusiform gyrus holds several sub-regions, for instance labelled FFA1 and FFA2 (or PFus and mFus) in a number of studies (Grill-Spector et al., 2017; Weiner & Grill-Spector, 2013; see Fig. 4A and C). In general then, the claim of one-to-

¹ Some studies have argued that sheep possess a human-like ability to recognize individual faces of conspecifics (e.g., Kendrick et al., 2001) or human faces (Knolle et al., 2017), but they suffer from the same kinds of limitations as raised in sections 1 and 2 about monkey studies.

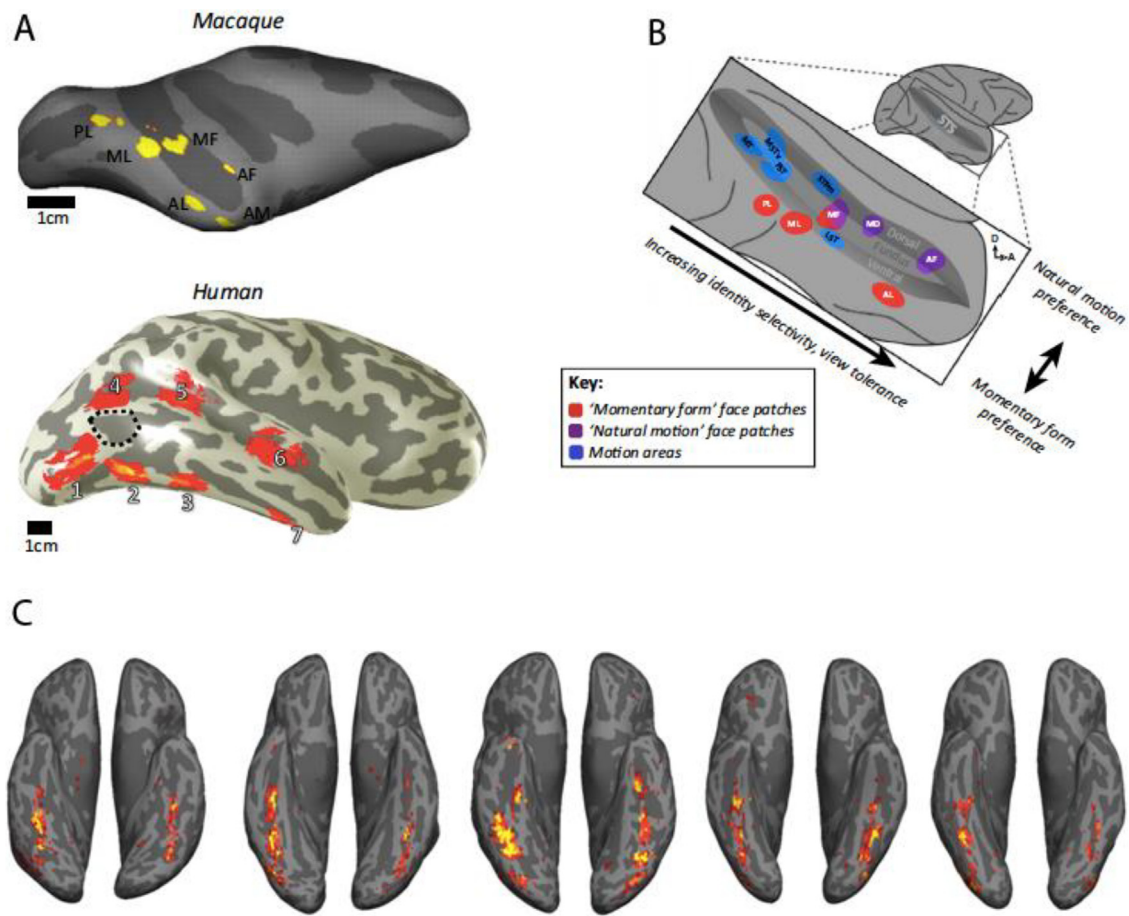


Fig. 4. A. Inflated segmented brains showing typical locations of face-selective regions in macaques (from Tsao et al., 2008) and humans (from Weiner & Grill-Spector, 2013). Up to six regions have been labelled in the macaque STS (as well as in marmosets; Hung et al., 2015), whereas humans have regions in both the STS (regions 4, 5 and 6 on the figure) and the VOTC (1, 2, 3, 7). Note that there is a gap in fMRI activation between the mid-fusiform gyrus (region 3) and the ventral anterior temporal lobe (region 7) due to magnetic susceptibility artifacts in fMRI (see Rossion et al., 2018). B. Proposal of a dissociation between dorsal and ventral face-selective systems in the monkey brain, with 3 regions (PL, ML, AL) proposed to belong to a ventral system involved in the coding of form (i.e., identity) (from Fisher & Freiwald, 2015). C. Ventral surface of individual human brains, showing the wide variability across five individuals in terms of the number and size of face-selective responses (data unsmoothed, obtained here with a highly sensitive and specific fMRI face localizer, see Gao et al., 2018). This ventral network of face-selective regions is absent in the monkey brain.

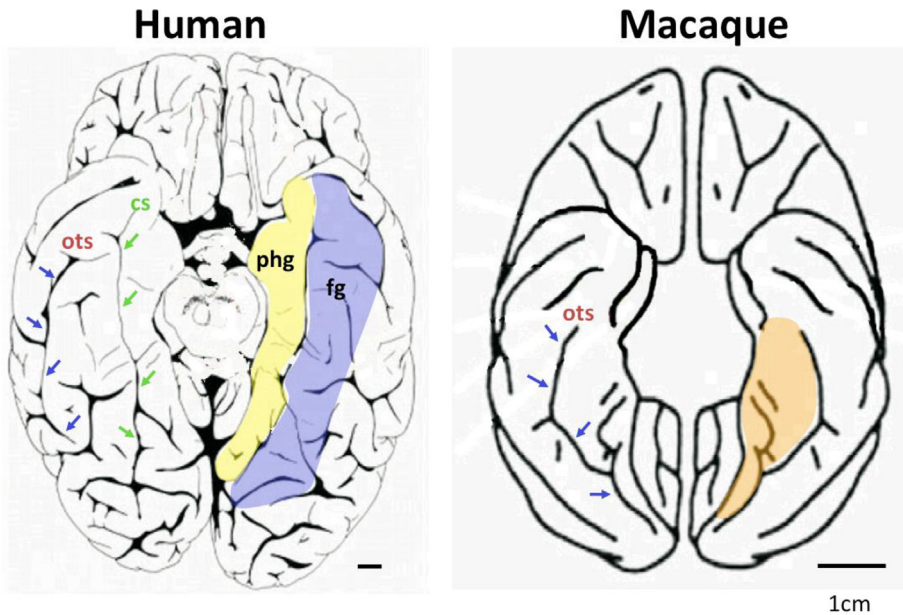


Fig. 5. The inferior surface of the brain in man and macaques, with the cerebellum removed. In the human brain, the occipito-temporal sulcus (ots) is labelled with blue (dark) arrows and the collateral sulcus (cs) with green (light) arrows. The human brain has two major gyri on its ventral surface while the macaque has only one (a minor sulcus, the mid-fusiform sulcus, separating the fusiform gyrus in its lateral and medial sections, has also been identified in the human brain, see Weiner et al., 2014). The fusiform gyrus (fg; blue area) lies between the ots and cs. The parahippocampal gyrus (phg; yellow region) lies medial to the cs. Based on anatomy, it is unclear whether the macaque gyrus best corresponds to the fg or phg, but contrary to humans, no face-selective activation is found in these regions of the monkey brain, while the monkey OTS and phg show selective responses to visual scenes, as the human phg and cs. The scale bar denotes 1 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

one homology is based on both a systematic overestimation of the number of independent face-selective regions in the monkey brain, which vary in reality between two and six (Bell, Hadj-Bouziane, Frihauf, Tootell, & Ungerleider, 2009; Nasr et al., 2011; Pinsk, DeSimone, Moore, Gross, & Kastner, 2005; Pinsk et al., 2009; Rajimehr, Young, & Tootell, 2009; Rajimehr et al., 2014; Tsao et al., 2003), together with an underestimation of the number of these regions in the human brain.

Indeed, in humans, in addition to several regions in the STS, up to 6 face-selective regions can be found in fMRI in the ventral occipito-temporal cortex alone in some individual human brains (Fig. 3C; Gao et al., 2018). Moreover, due to large magnetic susceptibility artifacts, the number of face-selective regions is typically underestimated in the ventral part of the human VOTC (Rossion, Jacques, & Jonas, 2018), with a “gap” between the typical location of the FFA in the lateral section of the mid-fusiform gyrus, and a face-selective region found in the ventral anterior temporal lobe (vATL; Fig. 3A and C). Supporting this claim of underestimation, recent intracerebral recordings in humans, which do not suffer from such artifacts, have disclosed up to 3 additional face-selective regions in between the midfusiform gyrus and the temporal pole, in the anterior fusiform gyrus, anterior collateral sulcus and occipito-temporal sulcus (Jonas et al., 2016; Rossion et al., 2018).

In short, since the number of face-selective regions remains unknown in both species, in particular varying largely across paradigms and individual human brains in fMRI paradigms (Rossion et al., 2012; Gao et al., 2018; Zhen et al., 2015; Fig. 4C), attempts to directly relate these functional regions one-by-one across species (Freiwald et al., 2016; Tsao et al., 2008; Yovel & Freiwald, 2013) and constrain human functional face processing models by monkey data (Duchaine & Yovel, 2015; Freiwald et al., 2016) in the absence of objective criteria appear premature and misleading.

Other arguments advanced to support the idea of homology between the face-selective VOTC regions in humans and a putative ventral STS face-selective system in monkeys are based on the positioning of the monkey network with respect to other functional regions. For example, whereas the STS face regions in humans are situated dorsally above MT, STS face regions in macaques (and marmosets) are ventral to the middle temporal area responding selectively to motion (MT/V5), potentially supporting the view of a ventral shift of these areas during evolution (Weiner & Grill-Spector, 2015). However, this ventral location with respect to MT in the monkey brain is valid for the *whole* network, not just the putative “ventral” section of this network. Similarly, based on the finding of neighbouring regions coding for places, color and faces, some authors (Lafer-Sousa et al., 2016) have also argued in favour of a ventral displacement “*en bloc*” of these networks during human evolution. However, this far-fetched story does not align with the fact that the so-called parahippocampal place area (PPA) lying next to the FFA in the human VOTC (Epstein & Kanwisher, 1998) is not found laterally but also ventrally in the monkey brain, at a similar location as in the human brain (Kornblith, Cheng, Ohayon, & Tsao, 2013). Hence, there is a large cortical space in the monkey brain between this region and the face-selective areas.

To summarize, at present, there is little objective evidence supporting a similarity in the gross topological structure into two parallel streams, a dorsal and a ventral face-selective network, in the two species. Rather, the most parsimonious account of current neuroimaging datasets is that *monkeys do not have a human-like ventral face-selective network*. In this context, it is worth reminding the reader of the origin of this putative functional dissociation between a ventral and dorsal STS network in the macaque brain. This view originates from the observation that neurons in the upper bank of the STS fire relatively more to variations of facial expressions, while neurons in the lower bank of the STS fire more for differences between individual faces (Hasselmo, Rolls, Baylis, & Nalwa, 1989). However, the claim made in that original study was based on a small number of neurons recorded, and has been openly

criticized on methodological grounds (Tiberghien, Baudouin, Guillaume, & Montoute, 2003). Moreover, face-selective patches have not been found in the upper bank of the STS in fMRI, but rather in the fundus, i.e., the regions labelled MF and AF (Fig. 4). Interestingly, both detailed anatomical connections determined by injected retrograde tracers (Grimaldi, Saleem, & Tsao, 2016) and electrical microstimulation combined with simultaneous fMRI (Moeller, Freiwald, & Tsao, 2008; Premereur, Taubert, Janssen, Vogels, & Vanduffel, 2016) show that the regions of the network are strongly and specifically connected to each other, arguing against a dorsal–ventral dissociation. As a matter of fact, ML and MF are often considered to form a single cluster in fMRI (Nasr et al., 2011; Rajimehr, Bilenko, Vanduffel, & Tootell, , Bilenko, Vanduffel, & Tootell, 2009; Rajimehr, 2014) but also in monkey physiology studies. For instance, studies measuring response properties of single neurons – in particular to decode face identity – conflate responses in ML and MF (e.g., Chang and Tsao, 2017), against any “ventral”–dorsal STS functional dissociation in the monkey brain (see also the recent study of Landi & Freiwald, 2017 in which, if anything, lower effects of familiarity with 3 individuals were found in the “ventral” face-selective regions of the network than in the “dorsal” regions, Fig. 3 of that study).

4.4. Right hemispheric specialization

Another important issue concerns hemispheric lateralization. In humans, cortical face-selective regions are typically larger in size or level of activation in the right as compared to the left hemisphere (e.g., Gao et al., 2018; Rossion et al., 2012; Sergent et al., 1992; Zhen et al., 2015; Fig. 4C). As mentioned at the beginning of the review, this right hemispheric lateralization in humans is critical for IFR: damage to or transient inactivation of the right but not the left VOTC leads to selective impairments at individual face recognition (e.g., Ambrus et al., 2017; Barton, 2008; Busigny, Graf, Mayer, & Rossion, 2010; Jonas et al., 2012; Jonas et al., 2015; Pitcher et al., 2007; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008; Sergent & Signoret, 1992). Although this right hemispheric specialization for faces is partly related to manual preference (Bukowski, Dricot, Hanseeuw, & Rossion, 2013), it is present already at a few months of age (de Heering & Rossion, 2015), preceding visual language specialization in the left VOTC (the Visual Word Form Area, VWFA, Cohen et al., 2002) during reading acquisition (Dehaene-Lambertz, Monzalvo, & Dehaene, 2018; Lochy et al., *in press*). Combined with the strictly bilateral cortical face network observed in monkey fMRI (e.g., Tsao et al., 2008), this suggests that this critical right lateralization of the face-selective VOTC may have developed at least partly independently of language lateralization, in order to support the required expertise level at IFR in the human species.

4.5. A cortical face network for dynamic social face cues

If monkeys are not experts at IFR, what could then be the function of their cortical face network? One account that considers both spatial localization and function of these regions is that the entire face-selective network in the monkey brain rather relates to functions supported by face-selective regions in the human STS (Fig. 4), i.e. the coding of dynamic (i.e., rapidly changing) aspects of faces such as eye gaze direction, head orientation and facial expressions (Allison et al., 2000; Bernstein & Yovel, 2015; Carlin et al., 2011; Hoffman & Haxby; Pitcher et al., 2011; Pitcher et al., 2014; Winston et al., 2004). In monkeys, the role of these regions at a systemic level of organization remains largely unknown, but must be related to monkey’s behavioural ecology in processing face signals. For instance, monkeys rely on faces to extract eye gaze direction and head orientation (Emery, Lorincz, Perrett, Oram, & Baker, 1997), as well as changes in facial expressions (Parr & Heintz, 2009) and their interactions (Goossens, Dekleva, Reader, Sterck, & Bolhuis, 2008), and it is likely that, as in humans, their STS cortical face

network supports these functions first and foremost (e.g., Perrett, Smith, Potter, Mistlin, & Head, 1985).

Supporting this view, removal of the entire macaque STS, including its lower bank, impairs the coding of eye gaze direction but has only little and unspecific effects on the animals' learned ability to discriminate pictures of individual faces (Heywood & Cowey, 1992). In other words, monkeys do not present with a condition similar to human prosopagnosia. Note that the functions of the monkey and human STS face-selective networks are certainly not analogous, and it is conceivable that the monkey brain – which has also considerably evolved from the common ancestor with humans 25 million years ago (Fleagle, 1999; Martin, 1990) – possesses a relatively more extensive STS network because this species may surpass humans in such face-related perceptual functions (e.g., coding for eye gaze direction without staring at an individual's face).

4.6. Summary

In summary, in line with their lack of human-like cognitive specializations, macaques appear devoid of a ventral (right lateralized) cortical face network, which is critical for IFR in the human species. Attempts to relate portions of the monkey STS cortical face network to the human ventral face network is not based on solid scientific arguments and may lead the scientific field in the wrong direction by searching for the cellular basis of individual face recognition in functional areas of the monkey brain (e.g., ML) that do not support this function in their natural environment.

In this context, it is unfortunate that despite the availability of monkey fMRI for more than 15 years, researchers have not tested functional homologies between monkey and human cortical regions at the system level of cortical organization, in particular using many individual faces and fMRI-adaptation, a technique which has been successfully used in humans to show sensitivity to individual faces in the VOTC (Davies-Thompson et al., 2009; Gauthier et al., 2000; Gentile & Rossion, 2014; Grill-Spector & Malach, 2001), in particular using holistic representations (Schiltz & Rossion, 2006; Schiltz, Dricot, Goebel, & Rossion, 2010). This absence of comparative functional relationships related to individuation of faces with fMRI, a technique available in the two species, is a major weakness in the search for functional homologies, which should rely on such comparisons (Passingham, 2009; Orban, Van Essen, & Vanduffel, 2004). In addition, robust and objective measures of rapid sensitivity to (unfamiliar) individual faces have been developed in human electroencephalography (EEG) research by using fast periodic visual stimulation (Rossion, 2014; Rossion & Boremanse, 2011). These measures of the function at a system level of organization are largely free of low-level image confounds, being robust to size variations (Dzhelyova & Rossion, 2014a,b). Moreover, they are largely and specifically reduced by inversion and contrast-reversal of images, as well as in patients with impaired IFR following brain damage (Liu-Shuang, Norcia, & Rossion, 2014; Liu-Shuang, Torfs, & Rossion, 2016) and intracerebral stimulation (Jonas et al., 2012; 2014; 2015). Since EEG recordings can be performed over the monkey brain (e.g., Peissig, Singer, Kawasaki, & Sheinberg, 2007), such paradigms could be readily applied to test for monkeys' high-level sensitivity to rapid invariant individuation of faces at a system level of organization, without having to train the animals in explicit behavioural tasks. Given the evidence reviewed above, we argue that these studies are unlikely to lead to robust and human comparable measures of sensitivity to individual faces in monkeys.

5. Neuronal codes of facial identity in the monkey brain?

If macaques lack human expertise at individual face recognition and the ventral cortical face network necessary to support it, why then do face-selective neurons in the monkey brain respond differently to pictures of different individual faces of conspecifics (Baylis et al., 1985;

Perrett et al., 1984; Rolls, 1984; Rolls, 1992) or even of human faces (Chang & Tsao, 2017; Leopold et al., 2006; Tsao et al., 2006; Young & Yamane, 1992)? And why, from these different responses, seemingly intelligible neuronal codes of face “identity” can be derived? Clarifying these issues has implications for both our understanding of the neural basis of human IFR, and more generally for the interpretation of neural pattern decoding analyses, especially from populations of single neurons.

In our view, there are only a few criteria that must be met to derive a neuronal code based on single neurons' responses allowing discrimination of different images: (1) a significant *response* from the neurons sampled; (2) *variability* of this response, i.e., spike rates, across the elements sampled, i.e., the individual neurons here; (3) some degree of *consistency* or *reliability*, such that presenting the same face image twice elicits a pattern of response across the population of neurons that is more similar than for two different images. Criterion 1 is easy to meet: in the monkey retina, lateral geniculate nucleus (LGN) or primary visual cortex, cells fire in response to various images of faces, and it can be assumed that a large fraction of neurons in higher-order areas of the monkey visual cortex also fire to various images. In fact, visually responsive neurons do not even have to be defined as face-selective to derive a population code (e.g., Young & Yamane, 1992).

This second criterion is also easy to meet: even in the primary visual cortex of the monkey brain, different cells will respond differently to different images, such as those presented in these studies, which vary substantially in local contrast and in simple variation positions of the hairline for instance, where there is maximal contrast (see e.g., Fig. 1 in Young & Yamane, 1992; Figs. 1 and 3 in Chang & Tsao, 2017; and also the widely variable images used in the studies of Rolls, 1984; Baylis et al., 1985). The fact that face-responsive or face-selective IT neurons vary in their responses may also be due to their sensitivity to local contrast information. However, in the absence of stringent tests for invariance, successful decoding of differences in combinations of features, even across whole face images, is not evidence of a coding of face identity, since it could merely be due to a summation of low-level image statistics picked up on the whole images.

This leads to the third criterion for successful decoding: consistency of response for repeated trials, or reliability. What is needed for reliability? If images fall exactly in the same position on the retina from trial to trial, and between physically similar images, consistency, and thus successful decoding, could probably be achieved already at that level, certainly in the primary visual cortex. Hence, it is not impossible that a successful code of “face identity” – perhaps of a different nature – could be obtained by sampling V1 populations of neurons in the monkey brain. However, given the small receptive fields of V1 neurons, this code would not resist substantial changes of stimulus size (a simple manipulation which is nevertheless untested in these studies). In contrast, neurons in higher visual areas of the monkey brain such as IT have larger receptive fields, so that face-selective neurons in these regions are better positioned to pick up image statistics across the entire stimulus and to show some degree of reliability of responses across repeated presentations of the same faces (i.e., prediction).

Hence, a simple combination of sensitivity to visual stimuli, variability in responses across the population sampled, and neurons with a large receptive field, could suffice to derive an intelligible “code” for a finite set of images (Young & Yamane, 1992), show some degree of invariance for manipulation preserving low-level visual cues (i.e., rigid head rotation rather than changes in lighting direction for instance) and even generate new images based on this code (Chang & Tsao, 2017). Given that these neurons are located in face-selective areas, they may even be causally related to an artificial face discrimination task learned by the monkeys with such humanoid stimuli (Moeller, Crapse, Chang, & Tsao, 2017). However, the critical question is whether such an image-based code tells us anything about the neural mechanisms of IFR in the human species. Given the lack of comparable human expertise, as well as cognitive and neural specializations for individual face recognition in

monkeys, we believe that the answer to this question has to be negative, and the nature of the codes that are derived in such studies are only valid for a specific image set in a population of neurons which does not carry a human-like IFR function.

6. Conclusions

The elements reviewed here all point to a rejection of the macaque model for understanding the neural basis of human individual face recognition (IFR). Contrary to humans, macaques and other monkeys show little ability to recognize individual conspecifics from their face, there is no evidence that they rely on qualitatively similar representations as humans (e.g., fine-grained holistic representations of faces allowing to individuate at a glance) and macaques do not present with a (right lateralized) ventral occipito-temporal face-selective network.

Rather, through specific extensive experience during development with diagnostic signals in the environment (i.e., high interindividual morphological variability of the face) and social constraints (i.e., large groups and requirements to quickly individuate conspecifics based on the face only), it is the human species which reaches a high level of expertise at IFR, afforded by the large expansion, and functional lateralization, of the ventral section of its temporal lobe. Whether this high level of expertise is specific to humans or can be found to some extent in some other higher primates such as chimpanzees largely remains an open question, due to difficulties in carrying behavioural and neural investigations in this species (e.g., Chance et al., 2013; Parr & Heintz, 2009; Taubert, Wardle, et al., 2017).

Understanding the neural basis of human IFR undoubtedly requires recordings (and disruption) at multiple levels of brain organization, from single neurons to large systems, with a high spatial and temporal resolution. Currently, single neuron recordings in humans are extremely rare (e.g., Quiroga, Reddy, Kreiman, Koch, & Fried, 2005; Rey et al., 2015), and limited by ethical and technical factors. In principle, the basic work of decoding the activity of populations of cortical cells would first have to be pioneered on macaques or other animal species. However, if the targeted animal species such as the macaque is not an adequate animal model of the function at stake, the outcome of this research can be severely misleading. For instance, searching for one-to-one homologies between face-selective regions belonging to different brain networks in the two species (Tsao et al., 2008; Yovel & Freiwald, 2013) when these respective networks do not carry the same function, and constraining human models of face recognition at the system level by monkey physiology data (e.g., Freiwald et al., 2016; Tovée & Tovée, 1993; Duchaine & Yovel, 2015) may lead the field in unwanted directions. Moreover, monkey physiologists tend to assume that macaques and all primates share the same level of expertise at IFR, pretty much regardless of the stimuli tested. Hence, monkeys are often presented with pictures of human faces, avatars, or even 2D schematic faces (e.g., Freiwald & Tsao, 2010), as if this species had any expertise at individualizing these faces, or could be trained in the laboratory to do so in a comparable way to human's natural expertise with faces of their own species (and often faces of their own ethnical origin, Malpass & Kravitz, 1969; see Rossion & Michel, 2011 for review). Yet, if anything, behavioral data collected without training in monkeys shows even poorer discrimination of individual human faces than monkey faces in monkeys (Pascalis & Bachevalier, 1998; Sugita, 2008).

At this stage, rather than focusing on understanding the neural basis of a function that is not human-like in monkeys, we suggest that the field devotes more effort to objectively define and operationalize human adult performance at IFR, and clarify why this level of performance deserves to be referred to as an *expert* level (Carey, 1992; Rossion, 2018; Tanaka, 2001; Young & Burton, 2018). That is, typical human adults are not only “able” to discriminate two different images of unfamiliar faces or match strictly identical images of the same face above chance level, something that not only monkeys but many animal species can be taught of with operant conditioning (even with human

faces for which there is no reason to expect any expertise; e.g. in bees and fish, see Dyer et al., 2005; Newport et al., 2016, respectively). Human expertise at IFR, supported by a large and specific network of brain regions, goes well beyond that, allowing us to recognize a large number of individual faces against variable distractors, automatically and extremely rapidly, and with a high degree of invariance to changes in e.g., size, head orientation, lighting conditions or emotional expression. Again, while some authors argue that this level of expertise is only reached for familiar(ized) faces (Young & Burton, 2018), it remains that these individual faces become familiar rapidly and automatically in typical human adults. Moreover, typical human adult performance at matching pictures of *unfamiliar* faces goes well beyond what can be achieved by other animal species (or patients with prosopagnosia, infants and young children for that matter), and in comparison can therefore truly be referred to as an “expert” performance. This brings back the question asked in the title of this review (i.e., *what can we learn about human individual face recognition from experimental studies in monkeys?*): experimental studies performed in monkeys certainly help us realizing that typical human adults possess indeed a high level of expertise at recognizing not only familiar but also of unfamiliar individuals from their faces. Further progress in the field of human face recognition and its neural basis depends at least as much on the development of proper diagnostic measures of this function, with adequate stimuli, as on single neuron recordings in the human species.

Finally, even if rhesus macaques do not have the same cognitive mechanisms for extracting identity from facial structure as humans, it does not imply that faces are not important visual stimuli to rhesus monkeys. There are numerous reports of face processing abilities in various monkey species, outside of IFR, that link directly to human behavior. For example a recent report has suggested that rhesus monkeys can detect illusory faces when they emerge by happenstance in otherwise inanimate objects (Taubert, Wardle, et al., 2017), much like humans do. Monkeys are sensitive to changes in conspecifics' expressions (Goossens et al., 2008; Parr & Heintz, 2009) and different monkey expressions elicit different patterns of activity from the brain at the system level (Hadj-Bouziane, Bell, Knusten, Ungerleider, & Tootell, 2008; Liu et al., 2015). Mate selection demands sensitivity to various social signals including gender (Afraz, Boyden, & DiCarlo, 2015) and dominance (Deaner et al., 2005). Indeed, we do not question the notion that monkeys might need to quickly determine the identity of a familiar conspecific (e.g., the dominant monkey of the small group), and would benefit from a specialized sensory system to support it – instead we posit that these abilities need not be based on facial structure simply because that is the case with humans. And even if faces were the primary source of identity information in rhesus macaques – there is no evidence to suggest that cognitive and neural mechanisms are continuous across all primates. We call for the careful mapping of behaviour across the primate order to better understand where cognitive continuities may exist. This will hopefully lead to stronger links between brain activity and behaviour.

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