Neuroscience and Biobehavioral Reviews 179 (2025) 106397

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Monkeys lack humanlike behavioral and neural inversion costs in face identity recognition

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ARTICLE INFO

Keywords:
Face identity recognition
Monkeys
Inversion
Adaptation
Fusiform gyrus

ABSTRACT

There is long-standing confusion in the scientific literature as to whether macaque monkeys show, like humans, a large decrease of performance for recognizing the identity of faces presented upside-down. Clarifying this issue is important because performance decrease for inverted faces is a hallmark of our species' expertise at face identity recognition (FIR), and the macaque monkey is widely considered as the reference animal model to clarify the neural mechanisms of this function. Here I report a theoretically-oriented critical review of behavioral and neural studies regularly cited as having tested the effect of inversion on FIR in macaque monkeys. I show that the confusion originates essentially from studies in macaques showing a mere behavioral or neural preference for upright over inverted faces independently of identity recognition, or confounding effects of stimulus inversion with training and stimulation constancy. Considering studies that properly tested the effect of inversion on FIR makes it clear that there is no behavioral or neural cost of such stimulus manipulation in macaques. This conclusion is congruent with a wide source of neurofunctional evidence indicating that the macaque monkey is not a valid animal model for human face identity recognition.

1. Introduction

Humans have an astonishing ability to discriminate, i.e., provide a differential response (to), conspecifics based on their faces alone, and to generalize this specific response across widely variable views of the same face identity. In neurotypical human adults, this *face identity recognition* (FIR) function which, as defined above, applies to both familiar and unfamiliar faces, is generally considered as being efficient, fast and automatic (Rossion, 2018). Nevertheless, due to the extremely large number of individual faces to differentiate (Jenkins et al., 2018), their high physical resemblance, as well as the considerable changes that can occur in viewing conditions for a given face identity, FIR is extremely challenging, thus requiring extensive experience during a long developmental period (Carey, 1992; Mondloch et al., 2002; Lawrence et al., 2008; Laurence and Mondloch, 2016; Hills and Lewis, 2018) and showing considerable interindividual variability in the normal adult population (Wilhelm et al., 2010; Wilmer et al., 2012). Understanding how the human brain achieves FIR, arguably its ultimate recognition function (Rossion, 2022), is generally considered as of primary importance in the (neuro)scientific community and has generated considerable interest and research for decades (Young and Ellis, 1989; Calder et al., 2011; Behrmann et al., 2016; Young and Bruce, 2024).

Here I review scientific evidence showing that rhesus macaques do not present with a key aspect of human FIR: the massive decrease of behavioral performance and identity-related neural activity when faces are presented upside-down (i.e., 180° rotated, or flipped along the horizontal axis). I consider that addressing this issue, which may appear perhaps limited in scope to the naïve reader, is in fact both important and timely, for several reasons. First, rhesus macaques (Macaca mulatta), a primate genus often called rhesus monkeys that are separated from our species by about 25–30 million years of evolution (Kay et al., 1997; Kaas, 2014), are widely considered as the best available animal model of human brain function, in particular of visual recognition (Passingham, 2009; DiCarlo et al., 2012). In fact, in the common parlance of neuroscientists, rhesus monkeys and other macaques are often referred to as simply 'monkeys' (Preuss, 2000). In face recognition research specifically, an influential line of research is based on the view that recording the activity of (face-selective) neuronal populations in the macaque brain will fully clarify – or has even already largely clarified according to some authors - the neural mechanisms of human face

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https://doi.org/10.1016/j.neubiorev.2025.106397
Received 21 July 2025; Received in revised form 16 September 2025; Accepted 2 October 2025
Available online 3 October 2025

(identity) recognition (Chang and Tsao, 2017; Hesse and Tsao, 2020; Freiwald, 2020; Kanwisher, 2025; for earlier studies see e.g., Rolls et al., 1984; Perrett et al., 1984; Leopold et al., 2006). This view seems to be widely accepted in the (neuro)scientific community (e.g., Leopold and Rhodes, 2010; Duchaine and Yovel, 2015; Barton, 2023; Kanwisher, 2025). Second, as developed below (Section 2), the drop of identity recognition performance for inverted faces in humans is not a trivial effect. It is particularly large and has been consistently observed for decades across a wide variety of stimuli and experimental paradigms, constituting arguably the most robust effect in human face (identity) recognition research, and one of the most robust in experimental psychology in general. Regardless of its theoretical account, the drop of performance for inverted faces is also clearly associated with human expertise at FIR, being significantly reduced or even absent in cases of prosopagnosia due to brain damage acquired at adulthood (Busigny and Rossion, 2010 for review). Thus, whether the best available animal model of human face recognition shows a humanlike effect of face inversion appears to be of utmost importance to assess the validity of this model. However, and this is the third reason why a critical review on this issue is timely and important, despite a number of studies and reviews, there is continuous confusion in the scientific community as to whether macaque monkeys present with such an effect, let alone a comparable effect to humans (Section 3). A comprehensive critical account of this issue may therefore be particularly welcome.

How does the present review differ from previous accounts (e.g., Parr, 2011; Rossion and Taubert, 2019), in particular a relatively recent meta-analysis on the topic (Griffin, 2020)? First, the present paper does not provide a meta-analysis, i.e., a statistical procedure with effects sizes based on aggregated data reported in a number of studies, and is therefore not limited to studies that provide sufficient data information. Instead, all relevant studies are identified, with key studies selected and critically analyzed. Second, for reasons detailed below (Section 2), the review focuses on the drop of FIR performance associated with inversion and is not concerned by whether this effect is larger for faces than other mono-oriented stimuli (the initial and typical definition of the 'face inversion effect' (FIE); Yin, 1969). Third, the review does not include all non-human primates (i.e., other monkeys, or apes) studies, being limited to face inversion effects tested in macaques (Section 3). This is not only due to the fact that the vast majority of behavioral face inversion studies in non-human primates have been performed in macaques, but also due to the privileged status of macaques in understanding the neural mechanisms of human FIR. Fourth, and importantly, the present review goes beyond an analysis of behavioral performance by also considering the effect of inversion on neural markers of face identity recognition (tested only in humans and macaques to my knowledge; Section 4). Finally, the theoretical implications of this in-depth critical analysis are drawn in the last Section (5).

2. The behavioral cost of inversion in human FIR

While the large drop of performance in human FIR for inverted (i.e., 180 degrees rotated or flipped around the vertical axis) pictures is generally attributed to Yin (1969), it was in fact noticed and even reported even before this author's landmark paper (Khöler, 1940; Hochberg and Galper, 1967). Technically, following Yin (1969), the 'inversion effect' refers to the larger cost of inversion for recognizing individual exemplars of faces than other mono-oriented objects (cars, planes, etc.). This often leads to confusion and endless debates about which types of stimuli provide adequate comparisons to faces, how they should or not be controlled for certain stimulus features, etc. As mentioned above, partly for this reason, but also in order to provide a more comprehensive and clearer theoretical account here, the present review is not restricted to studies that compare faces to other stimuli.

2.1. A large consistent effect

In humans, large costs of inversion have been found for (7) decades with a wide variety of face stimuli (i.e., familiar and (usually) unfamiliar faces, full or transformed photographs, schematic stimuli, same and other-race faces, etc.) and FIR tasks (i.e., simultaneous or delayed paired discrimination tasks, matching to sample with variable number of distractors, old/new decision tasks, familiarity decisions, etc.) (Fig. 1; e.g., Hochberg and Galper, 1967; Yin, 1969; Valentine, 1988; Barton et al., 2001; Freire et al., 2000; Le Grand et al., 2001; Mondloch et al., 2002; Barton et al., 2003; Riesenhuber et al., 2004; Megreya and Burton, 2006; Leder and Carbon, 2006; Goffaux and Rossion, 2007; Rhodes et al., 2007; Russell et al., 2007; Busigny and Rossion, 2010; Prete et al., 2015; Balas et al., 2019). It is important to acknowledge that picture-plane inversion is not a trivial stimulus manipulation, and that it significantly affects all types of face recognition functions in humans (e.g., emotional expression recognition, gender, age, etc.; McKelvie, 1995; White, 1999; Durand et al., 2007; Chatterjee and Nakayama, 2012). In fact, even the basic recognition of a sensory stimulus as a face is affected by inversion, in particular when the stimulus is degraded or ambiguous (e.g., Lewis and Edmonds, 2003; Liu-Shuang et al., 2015; pareidolia: e.g., Pavlova et al., 2020).

However, the effect of inversion is particularly large in all tasks that tap into FIR (even familiar/nonfamiliar or old-new decisions, for which a specific identity does not have to be explicitly identified). Quantifying the behavioral effect of inversion on FIR is difficult because depending on the task performed, the time constraints and the measured variables, it can be expressed in accuracy rates, sensitivity, and/or (correct) response times. However, large drops of accuracy rates and RT increases, on the order of 20 %, are typically observed (see studies cited above). For instance, in a recent study involving a simultaneous two-alternative forced-choice task with natural images of faces (task described in Volfart and Rossion, 2024; Fig. 1**A**), inversion reduced young adults' percent accuracy by 10–12 % for both unfamiliar and familiar (famous) faces, also increasing correct RTs by about 40–53 %.

2.2. Brief theoretical note

Contrary to previous reviews on the topic, I do not go deeply here into the theoretical reason(s) advanced for the significant drop of performance in human FIR for inverted faces. In a nutshell, in line with, and/or inspired by other authors, I think that this drop of performance is essentially due to *an inability to readily match an inverted sensory face input (coming from primary visual cortices) to a visual memory representation (in the association cortex) built from experience (with upright faces)*. This visual memory representation is *holistic,* i.e., a face is not stored in memory as a collection of independent parts (e.g., an eye, a mouth, a nose, …) but rather as a single unit, with both its parts and their specific configural relationships (i.e., the relative position and distances between the parts) being integral to the representation (Farah et al., 1995a; Rossion, 2008; Young et al., 1987; Yovel, 2009). In neurotypical human adults, this holistic visual memory representation of faces, distributed in specific regions of the human association cortex (e.g., the fusiform gyrus), is essential for efficient, fast and automatic FIR. Since an inverted low-level face input cannot readily match a holistic memory-based visual representation, it has to be analyzed part-by-part. This leads to a reduction of the perceptual field for inverted faces (Rossion, 2009). This particular loss, or severe disruption, of holistic/configural processing for inverted faces, was already proposed by the Gestalt psychologist

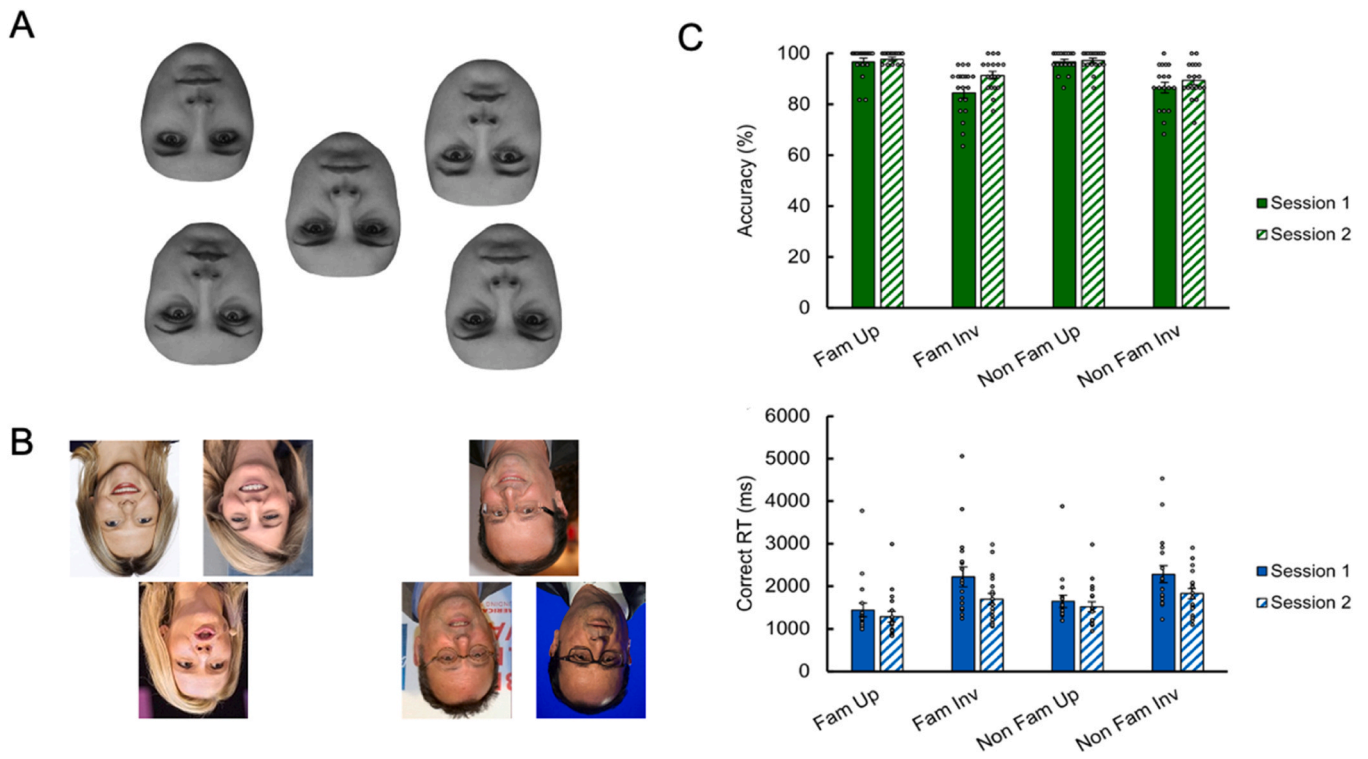

Fig. 1. Effect of stimulus inversion on human face identity recognition. **A.** Pictures of different unfamiliar faces, here devoid of external features, appear as being extremely similar perceptually when presented upside-down. Figure adapted from Rossion (2009), with permission. **B.** Illustration of a 2 alternative-forced choice (2AFC) face identity task with natural images of unfamiliar faces (left) or (right) celebrities (from Volfart and Rossion, 2024, with permission; Face photographs are licensed under Creative Commons, attribution left to right for each triplet: For license information, Sylvi Listhaug: https://flic.kr/p/DJAdYE (CC BY 2.0), Kommunesektorens organisasjon; Wikimedia Commons (CC BY 3.0), FrPMedia; Mélanie Joly: https://flic.kr/p/2nN386y (CC BY-SA 2.0), Richard Koek; François Hollande: Wikimedia Commons (CC BY 2.0), A. Bouirabdane; Wikimedia Commons (CC BY-SA 3.0), C. Truong-Ngoc; Jean Reno: https://flic.kr/p/7XYrq2 (CC BY 2.0), David Shankbone. **C.** Performance of a group (N = 18) of human adult participants in the task depicted in B, showing substantial decreases for inverted faces (unfamiliar or familiar), and RT increases (below) (Volfart and Rossion, 2024).

Wolfgang Khöler (1940), as well as by Yin (1969) based on verbal reports of his participants.[1] It is supported by numerous sources of evidence (e.g., Sergent, 1984; Young et al., 1987; Bartlett and Searcy, 1993; Rhodes et al., 1993; Tanaka and Farah, 1993; Hole, 1994; Farah et al., 1995a; Searcy and Bartlett, 1996; Tanaka, Sengco, 1997; Murray et al., 2000; Barton et al., 2001; 2003; Freire et al., 2000; Boutsen and Humphreys, 2003; Rossion and Boremanse, 2008; see Rossion, 2008; 2009 for reviews) including experiments with gaze-contingency providing direct evidence that the perceptual field of vision shrinks to parts for inverted faces (Van Belle et al., 2010, 2015; see also Poltoratski et al., 2021 for neural evidence).

It is fair to say that not every researcher in human face recognition is convinced about this theoretical account of the FIE (e.g., Civile et al., 2014; Murphy et al., 2020; Gerlach and Mogensen, 2024), which has admittedly suffered from lack of clarity and authors' agreement about the definition of configural/holistic processing, what constitutes a (face) part, etc. (Rhodes et al., 1993; Rossion, 2008, 2009; Yovel, 2009; Piepers and Robbins, 2012). It is certainly less controversial to claim that picture-plane inversion affects human FIR *qualitatively*, in the sense that different facial cues are affected differently by this manipulation (i.e., a difference of a difference, or interaction): internal and external face parts, different internal face parts, relative distances between these parts in the vertical and horizontal axes, surface or shape cues, etc. (e.g., Sergent, 1984; Searcy and Bartlett, 1996; Rhodes et al., 1993; Murray et al., 2000; Freire et al., 2000; Goffaux and Rossion, 2007; Sekunova and Barton, 2008; Jiang et al., 2009). While rare studies have reported quantitative effects of inversion (Riesenhuber et al., 2004; Sekuler et al., 2004; Murphy et al., 2020), they are a very small minority and they essentially reveal a lack of sensitivity of the methods used in the specific studies (i.e., their conclusion cannot be generalized).

2.3. A hallmark of expertise at FIR

In any event, the theoretical account of the effect of inversion on FIR is not very important for the present review. What is important is to emphasize the robustness of the negative effect of inversion (Section 2.1 above) and that this effect constitutes a hallmark of human (adult) expertise at identity recognition based on facial cues. Supporting this last statement, cases of visual agnosia following brain damage (in the association cortex), and even more specifically prosopagnosia, do not present with a cost of inversion in FIR tasks, even when these tasks are adjusted to allow these patients to perform well above chance level with upright faces (e.g., McNeil and Warrington, 1991; Farah et al., 1995b; Boutsen and Humphreys, 2002; Delvenne et al., 2004; for review: Busigny and Rossion, 2010). Importantly, it is not the case in people who have severe difficulties recognizing familiar face identities due to general episodic or semantic memory deficits, as in e.g., Alzheimer's disease or fronto-temporal semantic dementia or (Busigny et al., 2009; Lavallée et al., 2016). The cost of inversion also follows a relatively long developmental course, with some behavioral studies showing that it appears significantly only around 10 years of age and keeps increasing until adulthood (Schwarzer, 2000; Hills and Lewis, 2018; but see Cashon and

[1] '*They seemed to use two alternative strategies, either searching for some distinguishing feature or attempting to get a general impression of the whole picture. The first tended to be used for most of the materials; the second was used mostly for faces. None of the subjects, however, reported being able to use the second strategy when looking at the inverted face* (Yin, 1969, p.145).

Holt, 2015). While this is in line with a critical role of memory-based representations progressively built from experience in driving the inversion effect, the strongest argument in favor of the involvement of such visual memory representations is that upright and inverted faces do not differ in terms of the amount of sensory cues provided for identity recognition (that is, they contain the same amount of sensory 'information' to discriminate face identities). This shows that recognition - even for unfamiliar faces - does not depend only on sensory information given but on an interaction between this sensory information and *perceptual knowledge* (Gregory, 1997), here referred to as associative cortical memories.

3. Lack of behavioral inversion effect in macaque monkeys

Charles Bruce, a prominent neurophysiologist who led the first recording studies of face-selective neurons in the monkey temporal lobe (Bruce et al., 1981; Desimone et al., 1984) also reported the first, and arguably the most significant behavioral study of the effect of inversion on FIR in macaque monkeys (Bruce, 1982). In his study, 6 macaques performed a large number of trials on the same 4 tasks (2 simultaneous discriminations, 2 learning and transfer to the same faces differing in expression, size and lighting) with upright or inverted images of 16 unfamiliar monkey faces. The orientation and valence (positive or negative) associated with each the face identities were counterbalanced across stimuli and individual monkeys tested. While the monkeys were able to learn the task (i.e., the specific identities associated with positive reinforcements) and transfer their acquired knowledge, the results of the experiment were clear, both at the learning and transfer stages: there was no advantage for upright over inverted faces, not even a trend, on monkeys' recognition performance. The title of the paper is unequivocal: '*Face recognition by monkeys: absence of an inversion effect*' (Bruce, 1982).

Yet, decades after this landmark study, as mentioned above, the presence of an effect of inversion on FIR in macaque monkeys remains somewhat ambiguous in the literature, as mentioned by several authors throughout the years (e.g., Keating and Keating, (1993), p.138: *'laboratory studies of facial inversion effects in monkeys have produced such diverse results*'; Vermeire & Hamilton, 1998, p.1010: *'The existence of an inversion effect in monkeys has been controversial since Bruce first reported its absence';* Pascalis and Bachevalier, (1998), p.88: '*Research in monkeys (regarding the face inversion effect) has provided mixed results';* Pascalis et al., 1999*, p.10: 'Overall, while monkeys can discriminate their conspecifics from a face picture, the effect of stimulus inversion is still somewhat uncertain';* Weiss et al., (2001), p.192–193*: '…, we have summarized in* Table 1 *some of the studies that have tested for inversion effects in nonhuman primates … given the mixed evidence for an inversion effect, …'*. Such statements of 'mixed results', or even of similar effects in macaques as in humans, have been repeated over the years, often carelessly in my opinion, including in review papers (Leopold and Rhodes, (2010), p. 4: '*the effect of rotational inversion on face recognition in monkeys has been mixed*'; Dahl et al., (2013), p.2: '*The findings from studies testing chimpanzees (with inverted faces) … are more consistent than findings from monkey studies*'; Hesse and Tsao, (2020), p.696: '*in monkeys, the face inversion effect has been controversial, with some studies claiming that monkeys do show recognition differences between upright and inverted faces and others claiming that they do not'* (see also Parr et al., 1999; Guo et al., 2003; Gothard et al., 2004; Adachi et al., 2009; Dahl et al., 2010). The most recent review on the neural mechanisms of face recognition in non-human primates even stated that '*Humans and macaques both show better performance on upright faces than on inverted faces'* (Amita et al., 2024, p.2), as if there were comparable inversion effects in the two species indeed.

Unfortunately, these incorrect statements rest on superficial analyses of the paradigms and outcomes of the relevant studies, with 3 factors contributing to the confusion.

Table 1
A full list of published behavioral studies (n = 21) to date that have compared the processing of upright and inverted faces in macaque monkeys. Besides the studies of Parr and colleagues, which tested a rotation effect rather than an inversion effect (also Gothard et al., 2009), only 8 of these studies (in bold) truly tested a FIR task (Rosenfeld and Van Hoesen, 1979; Bruce, 1982; Overman and Doty, 1982; Swartz, 1983; Keating and Keating, 1993; Wright and Roberts, 1996; Vermeire & Hamilton, 1998). Among those, the only three studies that do not suffer from a methodological bias failed to report any cost of inversion in FIR (Bruce, 1982; Swartz, 1983; Weldon et al., 2013).* Infant monkeys; ** Split-brain monkeys.

Study	N	Stimuli & Task(s)	Outcome
Rosenfeld & Van Hoesen (1979)	4	Learning to discriminate 9 pairs of face identities upright (conspecific faces)	Fast transfer to inverted images of the same faces (Fig. 3), indicative of no inversion cost
Overman and Doty (1982)	6	Simultaneous 2 AFC match-to-sample task (human and conspecific faces)	9 % drop of performance for inverted faces (after biased training only with the same upright faces)
Bruce (1982)	6	– Simultaneous discriminations of identity (2) (conspecific faces) – Learning and transfer to same faces differing in expression, size, lighting (2) – conspecific faces	No inversion cost at learning and any of the tasks
Swartz (1983)	24*	Habituation task to discriminate different conspecific individuals or species of macaques	Significant discrimination between macaque species at upright but not inverted orientations Failure to discriminate within macaque species
Perrett et al. (1988)	2	– Face *vs.* nonface objects/ body parts discrimination – Face *vs.* jumbled face discrimination	– No inversion cost – Inversion cost
Dittrich (1990)	4	– - Discrimination of conspecifics' emotional expression (schematic faces)	No effect of inversion
Keating and Keating (1993)	4	Recognition of one learned human schematic face among others	Drop of discrimination when the same face appears upside-down (3 monkeys)
Tomonaga (1994)	5	Viewing duration to monkey faces (Rhesus and Japanese monkeys)	Reduced viewing duration to inverted faces Reduced difference in viewing duration between human and monkey faces with inversion
Wright and Roberts (1996)	3	Same/different simultaneous identity discrimination task	No inversion effect for monkey faces. Inversion effect for human faces. Extensive training on upright images before testing inversion
Vermeire and Hamilton (1998)	20**	– Discrimination of identity (conspecific faces) – Discrimination of facial expression (conspecific faces)	Drop of performance for inverted faces (after extensive (re)training only with the same upright faces); larger inversion cost for facial expression
Parr et al. (1999)	4	Sequential matching to sample identity task. In inverted trials, sample presented upright while two comparisons upside-down. Conspecific faces.	Performance decrease (rotation effect) – similar effect for faces of other species and pictures of cars

(*continued on next page*)

Table 1 (*continued*)

Study	N	Stimuli & Task(s)	Outcome
Guo et al., (2003)	2	Passive viewing on upright and inverted faces, eye movement recordings. Conspecific faces, human faces.	Longer viewing times and more fixations for upright than inverted faces
Gothard et al. (2004)	4	Eye movement fixations on pairs of conspecific faces – habituation paradigm (conspecific faces)	Novel images of faces explored longer regardless of orientation
Parr and Heintz (2008)	5	Sequential matching to sample identity task. In inverted trials, sample presented upright while two comparisons upside-down. Conspecific faces.	Performance decrease (rotation effect) – similar effect for other species' faces and pictures of houses
Parr et al. (2008)	8	Sequential matching to sample identity task. In inverted trials, sample presented upright while two comparison stimuli upside-down. Conspecific faces.	Performance decrease (rotation effect) – similar effect for all species faces, not significant for nonface stimuli
Adachi et al. (2009)	4	Habituation paradigm with the 'Thatcher' illusion. Conspecific faces.	More dishabituation to Thatcherized monkey faces upright than inverted or to intact faces
Dahl et al. (2009)	3	Gaze fixations to upright and inverted faces (humans & conspecifics)	Reduction of fixations on the eyes for both human and monkey faces presented upside-down
Gothard et al., (2009)	3	Eye movement fixations on pairs of faces – habituation paradigm (conspecific & human faces)	Familiarization to upright faces, test of discrimination to the same inverted faces (rotation effect). Inconclusive because no direct comparison to the same task with upright faces.
Dahl et al. (2010)	3	Habituation paradigm with 'Thatcher' illusion (human & conspecific faces)	More dishabituation to Thatcherized monkey faces upright than inverted
Parr (2011)	6	Sequential matching to sample identity task. In inverted trials, sample presented upright while two comparisons upside-down. Conspecific faces	Performance decrease (rotation effect) – similar effect for nonfaces (houses, shoes) and chimpanzee faces
Weldon et al., (2013)	6	Sequential matching to sample identity task, upright and inverted faces, 'Thatcherized' or not. Conspecifics' faces.	Better performance for Thatcherized than unaltered stimuli, but no effect of inversion for either type of stimuli

3.1. Biased training/familiarization

The first factor was in fact already correctly addressed by Bruce (1982) himself, who referred to a paper published just before his own study, apparently reporting an effect of face inversion on monkeys' performance (Overman and Doty, 1982). As noted by Bruce (1982, p.516), '*Face inversion was not balanced across the tasks in that study … monkeys were trained to match-to-sample human and monkey faces. Following two consecutive days of meeting a 90 % criterion and an additional day of training, all with the same set of upright faces, the monkeys were tested for one day with all stimuli inverted. Average performance declined from 91 % to 82 % correct but it is unknown whether a similar decline would occur if monkeys were first trained with inverted faces and then tested once with upright ones. Therefore, although the experiment shows that monkeys are affected by the orientation of the face stimuli, in the absence of a balanced design it does not demonstrate an intrinsic superiority for recognition of upright faces*'. In line with this criticism, in Bruce (1982)'s own study, the monkeys did have some difficulty generalizing for faces learnt upright to the same stimuli presented upside-down, which could have been interpreted as a face inversion effect. However, the monkeys had just as much difficulty generalizing in the opposite direction, i.e., faces that had been learnt in the inverted orientation and then tested upright.

This basic methodological bias, i.e., (extensively) training monkeys with (a specific set of) upright faces only then comparing performance for (the same set of) upright and inverted faces (Fig. 2), can be found in at least three other studies that claimed significant inversion effects in a face identity discrimination task in macaques (Keating and Keating, 1993; Wright and Roberts, 1996; also Vermeire & Hamilton, 1998, who in fact acknowledged the procedural asymmetries bias in their results section, p. 1006[2]).

Yet, all of these reports, in particular (Overman and Doty, 1982), keep being cited as provided supportive evidence for an effect of inversion on macaques' FIR performance (e.g., Gothard et al., 2004; Pokorny et al., 2011; Hesse and Tsao, 2020), contributing to the 'mixed results' view.

3.2. Orientation change effects

The second factor/bias is even clearer: a number of studies have reported significant drop of performance for inverted faces in two-alternative forced-choice tasks requiring discrimination between two conspecifics' faces (Parr, 2011; Parr et al., 1999, 2000, 2008; Parr and Heintz, 2008). In these tasks, a picture is presented to the monkeys during the initial encoding phase (the "sample") followed by a match-distractor stimulus pair. However, 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 appear at a constant orientation (Fig. 2**b**). As pointed before (Dahl et al., 2013; Rossion and Taubert, 2019; Griffin, 2020), this paradigm (which is never used in human studies) therefore measures a "face rotation effect" rather than a "face inversion effect". The same limitation applies to studies measuring such a face rotation effect in a habituation/novelty paradigm in rhesus monkeys (Gothard, et al., 2009, see Fig. 3 in that study). Contrary to what was done in these studies, fairly assessing the effect of inversion on monkey's FIR performance would have required *all* stimuli to be presented *either* upright *or* upside-down (as in Gothard et al., 2004, in which no effect of inversion on face identity discrimination was found)

Given the methodological bias, unsurprisingly, in these studies, "rotation effects" are found for all 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 and colleagues (2008) in fact concluded that rhesus monkeys lack human-like expertise at face identity recognition.

3.3. Identity-independent inversion sensitivity

The third source of confusion comes from studies showing that inversion of faces affects monkeys' performance and/or eye movements in tasks or measures that are unrelated to identity recognition. For

[2] *'This experiment precludes a definitive comparison of the number of errors made when learning to discriminate the upright and inverted faces. The monkeys originally learned the upright faces about four years earlier and since then had received extensive practice on these discriminations. Thus, the inverted discriminations were learned under quite different conditions than the original upright ones. Whereas the relearning of upright faces reported here immediately preceded the inverted learning, and thus was made under similar conditions, the errors for relearning upright faces are not directly comparable to learning them inverted because of the monkeys' extensive practice with upright faces and because the degree of transfer from performance with upright faces to performance with inverted faces is not independently known' (Vermeire & Hamilton, 1998, p.1006).*

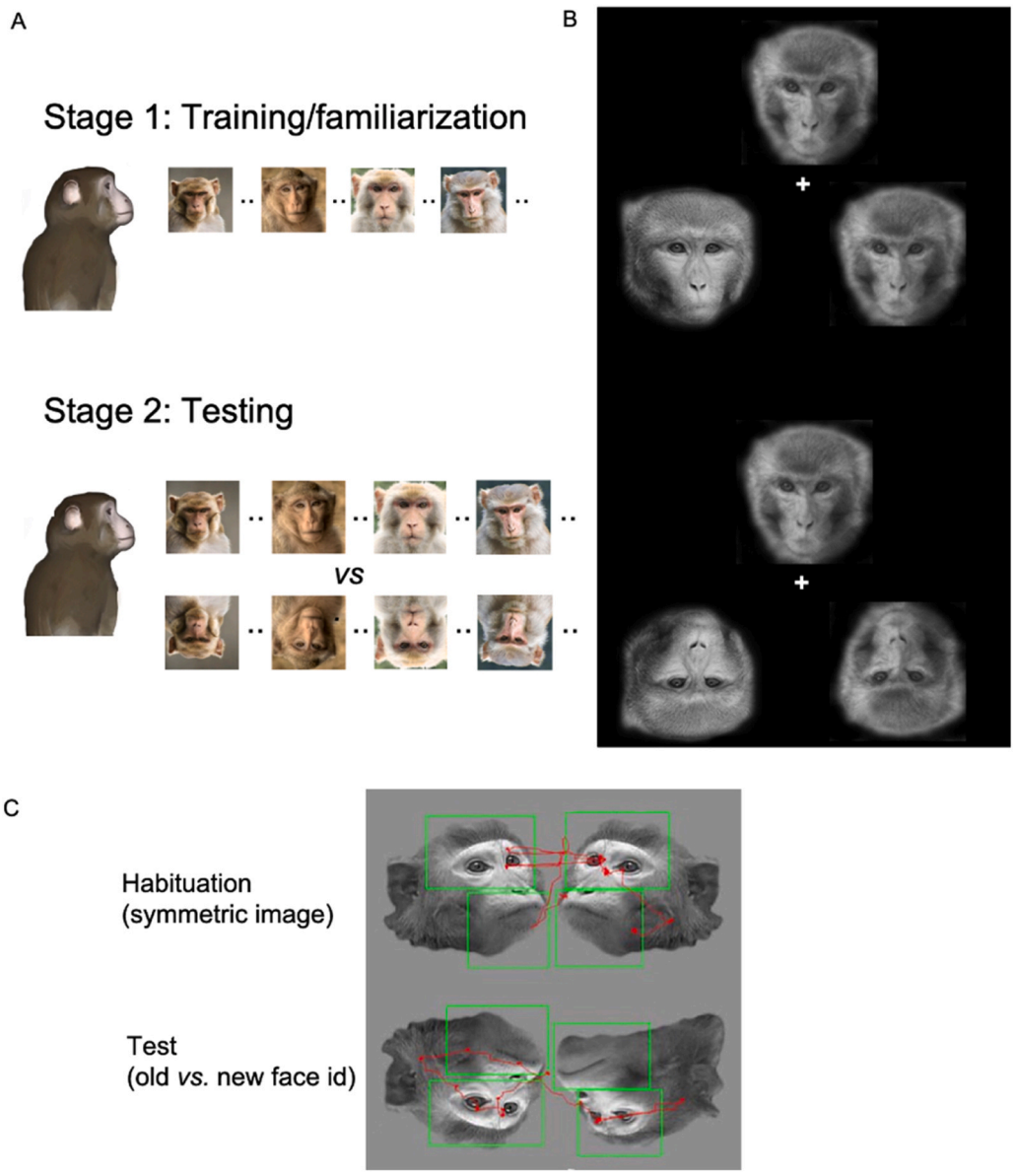

Fig. 2. Examples of methodological biases in measures of the effect of inversion in face identity recognition tested with macaque monkeys. **A**. Several studies train macaques extensively with a specific set of upright faces of conspecifics to learn or discriminate at the individual level, following by a test of the same images either at (trained) upright or (untrained) inverted orientations, confusing the effects of training with orientation (Overman and Doty, 1982; Keating and Keating, 1993; Vermeire & Hamilton, 1998; see also Gothard et al., 2009). Even when new images are introduced at testing, prior extensive training with upright faces only at a specific task can provide an unfair advantage for the upright orientation (Wright and Roberts, 1996). **B**. In the experiments of Parr and colleagues (Parr et al., 1999, 2000, 2008; Parr and Heintz, 2008), macaques usually have to match a face presented (slightly before) on top of the fixation cross to either one of two images presented below the cross (usually the exact same image to match is used, with different images used in some subtests; see Parr, 2011). Rather than presenting all stimuli upright vs. all stimuli inverted, the 'inverted' condition has the target on top at upright orientation, confusing an effect of inversion with an effect of orientation (see criticisms in Dahl et al., 2013; Rossion and Taubert, 2019). **C**. As in B, evidence of failed discrimination of a novel from an habituated monkey face identity (Gothard et al., 2009) suffers from a rotation confound, with the habituation images and test images shown at different orientations. This task is compared to a task in which all stimuli are presented at upright orientation, failing to properly measure an inversion effect in FIR (adapted with permission from Gothard et al., 2009).

instance, presenting pictures upside-down reduces monkeys' performance at (primate) species categorization (Swartz, 1983; see also Tomonaga, 1994), discrimination between a normal face and a face with jumbled features (Perrett et al., 1988), or facial expression recognition (Dittrich, 1990; see also Vermeire & Hamilton, 1998) (Table 1). These studies are undoubtedly interesting, showing that macaques clearly and spontaneously differentiate between upright and inverted images of conspecifics' faces, and present an advantage for upright stimuli in functions that are ecologically relevant for this species (e.g., recognizing a face stimulus as being a conspecific, its emotional expression, gender/attractiveness, gaze direction, health, kinship etc.). This is in line with macaque monkeys living predominately on the ground, like humans, and thus primarily being exposed to upright as compared to inverted faces.

While there is nothing wrong with these studies' results apparently, they are surprisingly regularly cited as evidence in favor of an inversion effect (on identity recognition) in macaque monkeys, contributing to the 'mixed' or 'controversial' results conclusions that currently prevail in the literature (Keating and Keating, 1993; Gothard et al., 2004; Leopold and Rhodes, 2010; Pokorny et al., 2011; Dahl et al., 2013; Hesse and

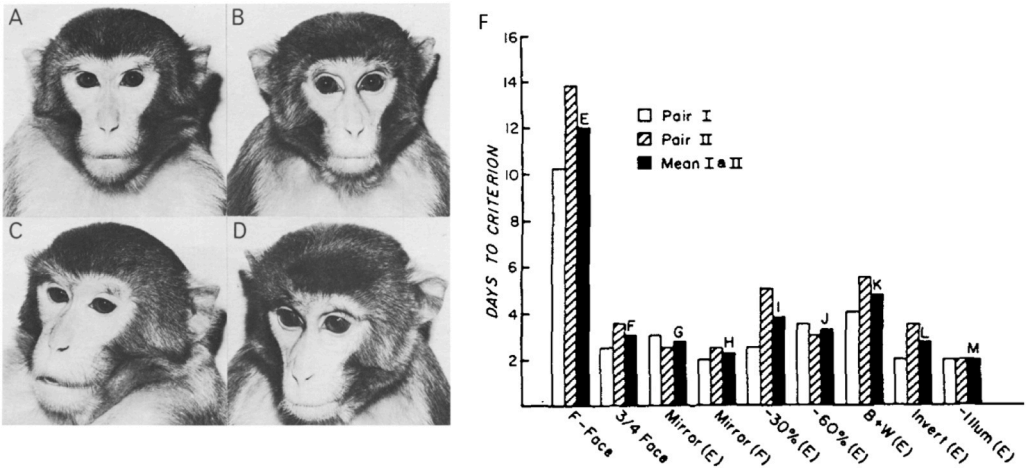

Fig. 3. Stimuli and results from the first behavioral study of FIR in macaque monkeys (adapted from Rosenfeld and Van Hoesen, 1979, with permission). Left, A and B: example images of a pair of monkeys presented at learning, with one of them reinforced positively, the other negatively. Original images were presented in full color mode. Below, C and D, the two monkeys presented at ¾ orientation (task F on the right). Note that beyond the face, the upper part of the body could also provide identity cues for discrimination. On the right (F), number of days to reach criterion (>90 % performance at choosing the positively reinforced monkey across 9 pairs) for various tasks (E to M). Pair I and Pair II refer to two pairs of monkeys tested. F-Face (task E) is the original learning task. Following learning, all other tasks are performed much faster, including discrimination of the upside-down faces (task L), which is faster to learn than the transfer to greyscale images (task K).

Tsao, 2020; Amita et al., 2024). In fact, even the mere preference for upright faces over inverted faces (Tomonaga, 1994; see also Tomonaga, 2018a; 2018b) or differences in eye movement exploration between upright and inverted faces (Guo et al., 2003; Adachi et al., 2009; Dahl et al., 2009; Dahl et al., 2010) are often considered and cited as evidence for 'inversion effects' on FIR in macaque monkeys, against Bruce (1982)' initial findings of a lack of effect (Dahl et al., 2013[3]; Amita et al., 2024). This is unfortunate because these findings have nothing to do with the issue at stake, which is whether the discrimination and matching (generalization) of facial *identity*, i.e., its recognition function, is affected by inversion in monkeys (as in humans).

3.4. Intermediate conclusions

Even if the number of animals tested is usually relatively small, many (i.e., 21 published to my knowledge) studies have compared the presentation of upright and inverted (usually conspecific) faces in rhesus monkeys (Table 1). All but four of these studies (Rosenfeld and Van Hoesen, 1979; Bruce, 1982; Dittrich, 1990; Weldon et al., 2013) reported that inversion of the face stimuli affected monkeys' performance (or eye movement exploration). Thus, once again, monkeys appear to readily perceive that (conspecific) faces are presented upside-down, and this manipulation affects their behavior. However, only 8 of these studies are directly relevant for the issue at stake, namely face *identity* recognition. Three of them (Overman and Doty, 1982; Vermeire & Hamilton, 1998; Wright and Roberts, 1996) presented a clear methodological bias favoring performance for upright faces, and the last one even failed to find an inversion effect for conspecific faces. A fourth study had the same flaw and only showed a trivial effect of a lack of discrimination for an inverted (human) face due to biased sampling of the upper and lower parts of stimuli (Keating and Keating, 1993). Importantly, the only studies that were performed with a counterbalanced design, i.e., no unfair advantage given to specific images of upright faces, showed no cost of inversion at all on FIR in 6 monkeys each (Bruce, 1982; Weldon et al., 2013). Finally, two studies deserve special mention. First, Swartz (1983) tested infant pigtail macaques' discrimination of 4 faces using an habituation paradigm. Although 75 % of the macaques failed to reach the habituation criterion of the study, the author reported longer fixation times to faces of different macaque species, this effect disappearing in a second experiment for stimuli upside-down. However, crucially, macaques showed no discrimination at all between a new picture of the habituation stimulus and a picture of another female of the same species as the habituation stimulus, i.e., no ability to individuate conspecifics (see Fig. 1 in Swartz, 1983). Second, the study of Rosenfeld and Van Hoesen (1979) deserves mention not only because it is the very first published study reporting 'successful' learning of (a few) conspecifics face identities in (4) monkeys, but also since it is sometimes cited in favor of an effect of inversion in macaque monkeys (Keating and Keating, 1993). In reality, this effect was not tested in that study, which simply evaluated generalization of learned upright full front colour faces to a series of transformations of the same face stimuli, including inversion (Fig. 3). If anything, generalization was better (i.e., performance criterion reached earlier) to faces presented upside-down than faces depth-rotated by 30° or simply presented without colour cues (Rosenfeld and Van Hoesen, 1979; Fig. 3). Such an outcome would never be found in humans and suggest indeed that stimulus inversion has virtually no effect on monkeys' FIR performance.

In short, the repeated claim that face inversion leads to 'mixed' or 'controversial' results across studies with macaque monkeys is incorrect and misleading. In reality, behavioral studies are generally consistent in showing a viewing preference for upright *vs.* inverted faces, sensitivity to first-order configuration of features (e.g., 'Thatcherized'[4]; faces), as well as better performance for upright faces. However, this superior performance is found only in tasks that are unrelated to face identity recognition, with no effect at all found in studies that properly tested this cognitive function. Note that for reasons advanced at the outset of the present review, the above analysis focuses on non-human primate studies performed on macaques only, which constitute the large majority of studies. However, the few experiments performed in other

[3] Dahl et al. (2013)'s claim that '*there is plenty of evidence from scientifically valid assessments in monkeys of various species that FIE exists in those species and FIE reflects configural processing of facial* features' (p.2) is supported by 7 studies as cited by the authors. Yet, only one of them, not performed in macaques, measured a face identity recognition effect.

[4] The 'Thatcher illusion' refers to faces in which the eyes and the mouth are locally flipped at 180°, causing a salient grotesque look. These changes are much less detectable when the whole face is presented upside-down, presumably because each part of a loss of holistic/configural face perception. The illusion was first demonstrated on a face picture of the former prime minister of England, Margaret Thatcher (Thompson, 1980).

monkeys (New World Monkeys) tested with upright and inverted faces are clearly unconvincing and suffer from the same methodological issues as studies performed in macaques (Phelps and Roberts, 1994; Weiss et al., 2001; Neiworth et al., 2007; Pokorny et al., 2011; Calcutt et al., 2017[5]). As for behavioral experiments performed in Chimpanzees, they tend to suggest the presence of an inversion effect in FIR in our closest primate relatives, although this effect is relatively weak (compared to humans) and inconsistent across studies (e.g., Tomonaga, 1999; Dahl et al., 2013; Kret and Tomonaga, 2016; Griffin, 2020).

4. The neural cost of face inversion

In line with the large behavioral effects of inversion in humans, neural measures of FIR are significantly affected by this simple stimulus manipulation.

4.1. Global electrophysiological inversion effects in humans

With electroencephalography (EEG), reliable measures of FIR have been provided by comparing neural signals evoked by a repeated face identity in comparison to a novel identity (since Barrett et al., 1988).

4.1.1. Time-domain measures: N170 and N250r

The N170 is the most consistent face-selective negative event-related potential (ERP), peaking over occipito-temporal sites at around 170 ms post-stimulus onset (Bentin et al., 1996; for reviews Rossion and Jacques, 2008; 2011). A significant reduction of N170 voltage amplitude to an immediately (i.e., without intervening stimuli) repeated face identity as compared to a different identity has been observed in numerous studies (Barrett et al., 1988; Schweinberger et al., 1995; Guillaume and Tiberghien, 2001; Itier and Taylor, 2002; Heisz et al., 2006; Jacques et al., 2007; Caharel et al., 2009a; Caharel et al., 2009b; Caharel et al., 2011; Vizioli et al., 2010; Caharel et al., 2015; Shen et al., 2017; Fig. 4). This effect depends on methodological parameters, with long duration of an adapting face, but brief and variable (i.e., jittered) delays between the first and the second (i.e., repeated) face stimulus being optimal to disclose clear N170 amplitude reduction to face identity repetition (Jacques et al., 2007; Caharel et al., 2009a; Caharel et al., 2009b; Caharel et al., 2011; Caharel et al., 2015; Fig. 4). It has also been observed most consistently for pictures of unfamiliar faces, being present but modulated in various ways by (long-term) face familiarity (Barrett et al., 1988; Jemel et al., 2003; Heisz and Shedden, 2009; Caharel et al., 2011). Nevertheless, the N170 amplitude reduction to a repeated face identity is usually larger in the right hemisphere, in line with the well-known advantage of this hemisphere in human FIR, and can be found across substantial changes in stimulus size (Jacques et al., 2007; Caharel et al., 2009a) and even head orientation (Caharel et al., 2009b; Caharel et al., 2011; Caharel et al., 2015).

Strikingly, but in line with the behavioral effects briefly reviewed above, this amplitude decrease of the N170 for repeated face identities is abolished by stimulus inversion (Heisz et al., 2006; Jacques et al., 2007; Fig. 4**)**. This finding is important since it rules out an interpretation of the repetition effect on the N170 as being due to low-level visual cues (e.g., mere repetition of basic sensory features, independently of visual knowledge). It is also impressive given that the N170 is, somewhat paradoxically, *increased* in amplitude to pictures of inverted faces (e.g., Rossion et al., 1999; 2000; Itier and Taylor, 2002; Itier and Taylor, 2004; Jemel et al.;, 2009; Sadeh and Yovel, 2010; Civile et al., 2018; Brunet, 2023; Yamada et al., 2025), thus potentially leaving even more room for a repetition (suppression) identity effect. Importantly, this latter basic increase of N170 amplitude (and latency) to clearly visible pictures of inverted faces, which remains largely unexplained (Rosburg et al., 2010; Brunet, 2023), or the reverse larger N170 to upright than inverted faces in poor conditions of stimulus visibility (e.g., George et al., 2005; Schneider et al., 2007), should not be taken as an effect of inversion on face *identity* recognition.

Effects of face identity repetition on the N170 are particularly important because the time-window during which this ERP component takes places (i.e., about 120/130–200 ms, ms) indexes the first reliable category-selective neural responses in humans (Bentin et al., 1996; Rossion and Jacques, 2008; see also Jeffreys, 1996). Nevertheless, the effect of face identity repetition is larger, more consistent post-200ms, in the form of an enhanced posterior negativity for repeated faces also already observed early on (Barrett et al., 1988) (Fig. 4). This N250r ('r' for repetition) emerges approximately 220 ms after stimulus onset, is also maximal at (right) occipito-temporal electrodes, and is accompanied by a positivity at frontocentral electrode sites (see Schweinberger and Neumann, 2016, for review). It is larger for repetitions of familiar than unfamiliar faces (e.g., Barrett et al., 1988; Schweinberger et al., 2002; Herzmann et al., 2004; Herzmann and Sommer, 2007) and is not only elicited by repetitions of physically identical unfamiliar face stimuli, but also when different pictures of the same individual are presented in succession (e.g., Bindemann et al., 2008; Zimmermann and Eimer, 2013; Wirth et al., 2015; Fisher et al., 2016; Wiese et al., 2019; Wiese et al., 2024). Importantly, the N250r is also substantially reduced by stimulus inversion (Itier and Taylor, 2004; Schweinberger et al., 2004; Jacques et al., 2007; Towler and Eimer, 2016; Fig. 4), providing another electrophysiological index of the effect of inversion on FIR.

4.1.2. Frequency-domain measures of fast periodic visual stimulation

While time-domain analyses of EEG data following relatively slow (temporally jittered) and isolated stimulation provide useful information regarding the time-course of FIR and its modulation by inversion, they generally lead to relatively low signal-to-noise ratio (SNR) measures, as well as substantial ambiguities in identification and quantification of ERP components/time-window of interest. An alternative approach is to present visual stimuli at a fixed rate, focusing on EEG activity recorded exactly at that (known) rate in the frequency domain (after Fourier transform; 'steady-state visual evoked potentials', SSVEPs; Regan, 1966). This 'frequency-tagging' approach provides substantial advantages in sensitivity and objectivity of identification and quantification of neural responses (Regan, 1989; Norcia et al., 2015). In the first applications of this approach to EEG measures of human face (identity) recognition, a large effect of inversion (i.e., amplitude reduction) was already observed (Rossion and Boremanse, 2011; Rossion et al., 2012). A significant reduction of the 1.2 Hz neural index of FIR over the occipito-temporal cortex has been also systematically reported in a subsequently developed and well-validated oddball-like paradigm in which different unfamiliar face identities periodically (i.e., every 5 faces) interrupt the repetition of the same face identity at a fixed 6 Hz rate (166 ms stimulus-onset asynchrony; Liu-Shuang et al., 2014; Retter et al., 2021; Hagen et al., 2024). With this paradigm, the effect of inversion on the neural face identity discrimination signal has been quantified to more than half of the neural signal, i.e., 53 %, in young neurotypical adults (as reviewed in Rossion et al., 2020; Fig. 5**A**).

[5] Of all these studies, three claimed to find a face inversion effect on an identity task in their monkey species. Phelps and Roberts (1994) tested one monkey in each of two experiments, with no effect of inversion for monkey faces, but an effect for human faces. Neiworth et al. (2007); Tamarins)'study had an order bias (upright always tested before inverted faces) and a face discrimination task that involved large head orientations changes for distractor faces (see Rossion and Taubert, 2019). A significant inversion effect for conspecific faces only was also reported by Pokorny et al. (2011) in Capuchins, but the animals were trained with upright conspecific faces only (and had been trained and tested only with these types of stimuli for years). Moreover, FIR performance at a trivial odd one out task was limited (70 %)(see Rossion and Taubert, 2019). Calcutt et al. (2017: Capuchins) did not test face identity recognition. Finally, Parron and Fagot (2008) showed sensitivity to detection of swapping the position of the eyes and mouth in baboons, without any effect for detecting local inversion of these features. No face identity task was involved in that study.

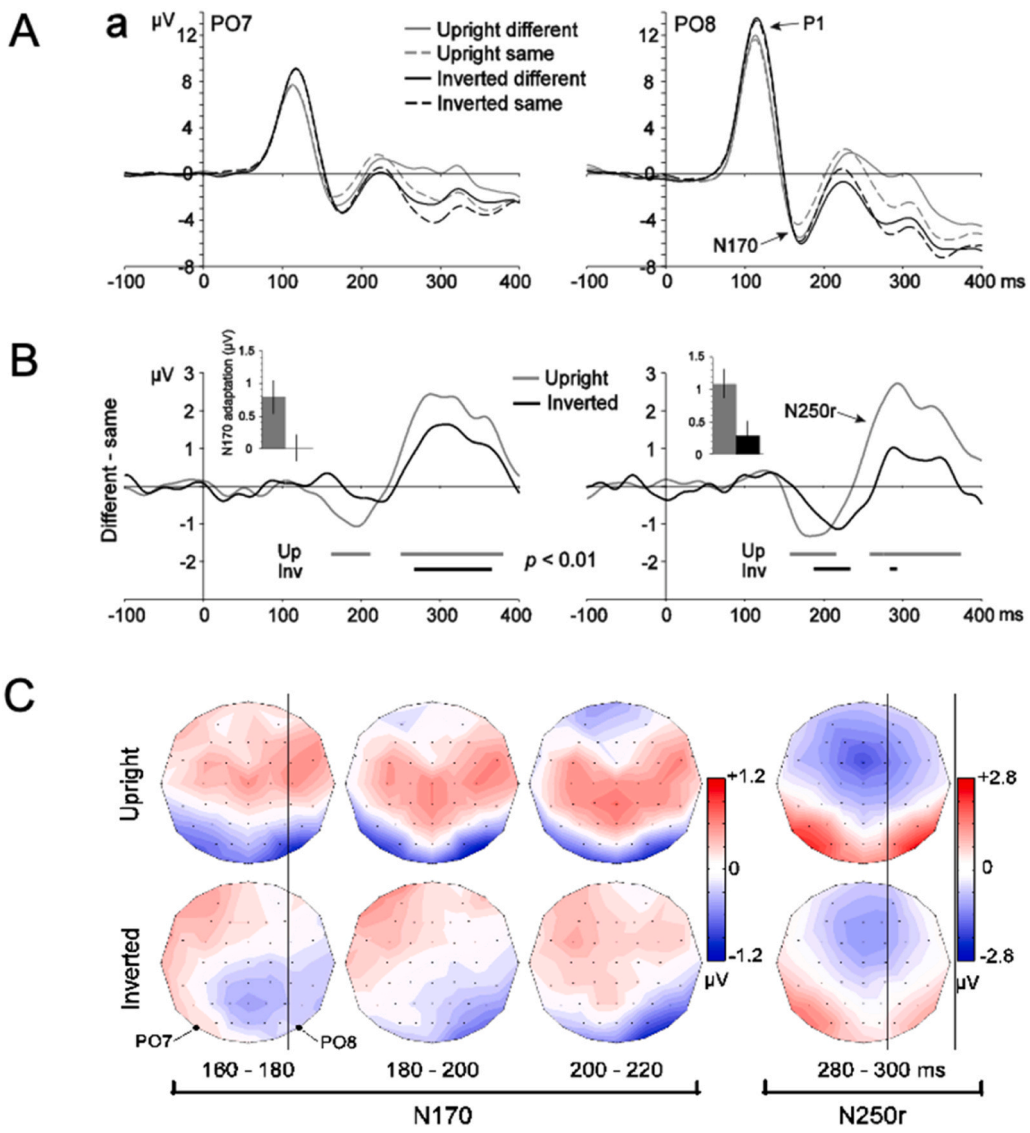

Fig. 4. Effect of stimulus inversion on face identity repetition effects as measured with human event-related potentials (from Jacques et al., 2007, with permission). **A**. Left (PO7 electrode) and right (PO8) waveforms following the presentation of an unfamiliar face identity preceded either by a different or the same face identity. The N170 occipito-temporal component is reduced in amplitude for a repeated face identity, but only for upright faces. **B.** Illustration of the differential waveforms (Different – Same) for upright and inverted faces, showing the larger and earlier difference for upright as compared to inverted faces. The amplitude of the face identity repetition effect is shown on the bar graphs, with a larger effect in the right hemisphere. The repetition effect is also expressed after 200 ms in the form of a N250r (for repetition effect), which is also much larger for upright than inverted faces. **C.** Scalp topographies of the difference between different and repeated (same) faces during the N170 and N250r time-windows. Note the clear occipito-temporal difference, larger in the RH, a marker of face identity recognition, which is delayed and smaller for inverted faces.

This observation implies that more than half of the neural FIR response in this paradigm cannot be attributed to objective physical differences between face stimuli. Critically, this does not mean that 47 % of neural FIR response, common to upright and inverted faces, is elicited by low-level visual cues (a common misinterpretation) because inverted faces are structured stimuli that also activate high-level visual regions of the human brain, including face-selective areas (Haxby et al., 1999) or non-face high-level visual brain regions (Rosenthal et al., 2017).

This reduction of neural signal to inverted images of faces is even considerably larger when measuring selective responses to natural images of familiar (famous) faces among unfamiliar faces (only 16–17 % of signal for inverted faces as compared to upright faces in Yan et al., 2020; Yan and Rossion, 2020). Compared to the typical size of inversion effects reported in human behavioral studies (Section 2), the neural effects are thus particularly large, potentially due to the fast presentation rate in these paradigms preventing detailed exploration of local features (i.e., single-glance recognition), but also because, as mentioned in Section 2, behavioral effects may be spread onto several variables.

4.2. *Human neuroimaging*

Functional magnetic resonance imaging (fMRI) studies have consistently shown that repeating the same face identity significantly decreases amplitude of the blood oxygen level dependent (BOLD) response as compared to the presentation of different faces in face-selective regions of the ventral occipito-temporal cortex (VOTC) (e.g., Gauthier et al., 2000; Grill-Spector and Malach, 2001; Eger et al., 2004; Schiltz et al., 2006; Gilaie-Dotan and Malach, 2007; Ewbank et al., 2013; Gentile and Rossion, 2014; Coggan et al., 2022; see Rossion, 2014 for review). Regardless of its neuronal basis (see Grill-Spector et al., 2006; Sawamura et al., 2006), this ‘adaptation’, or ‘repetition suppression’,

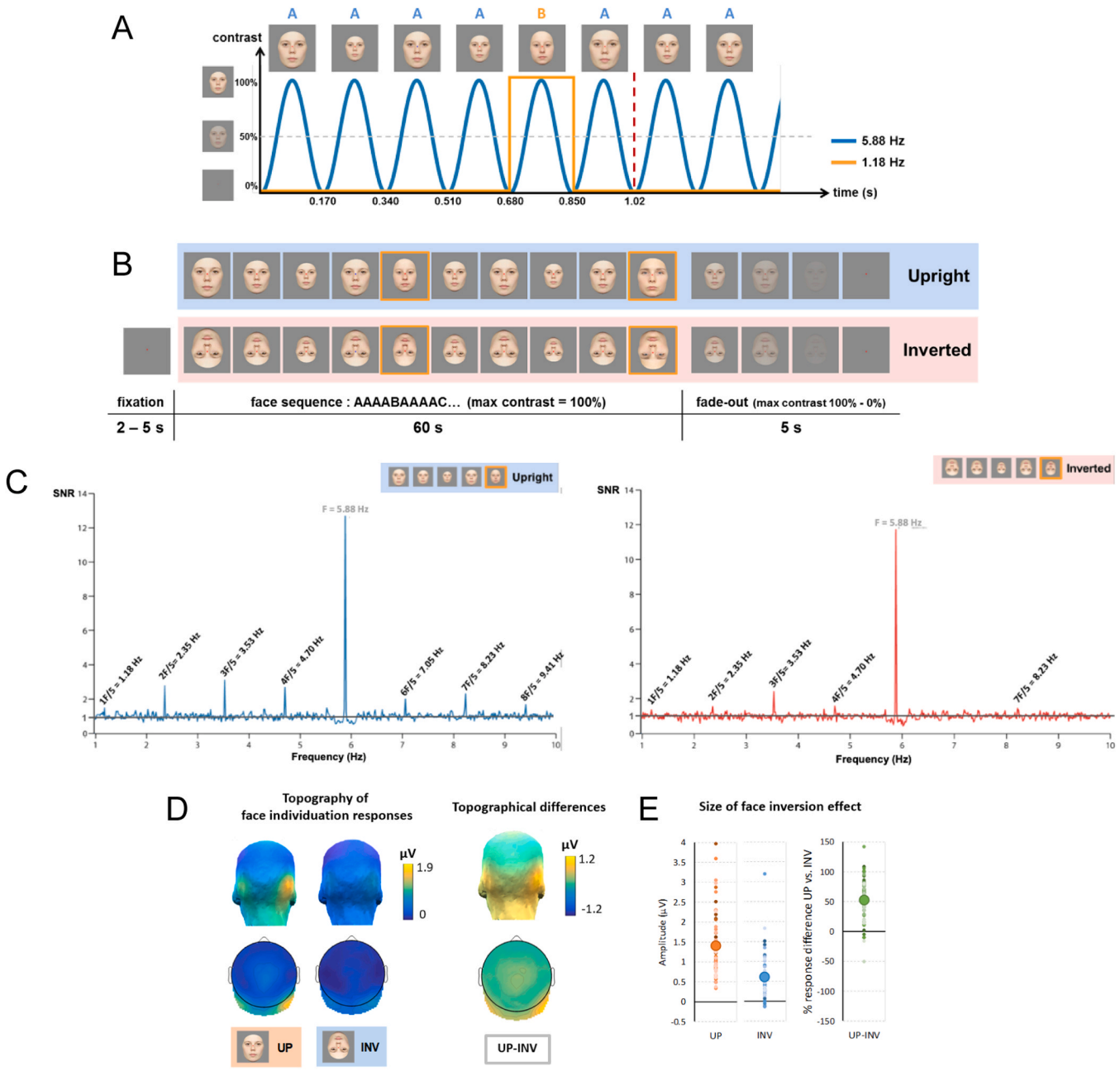

Fig. 5. Quantifying the neural face inversion effect with fast periodic visual stimulation in EEG**. A**. Face stimuli are typically presented through sinusoidal contrast modulation against a uniform grey background at a base frequency of 6 Hz or (as here) 5.88 Hz (170 ms SOA; Liu-Shuang et al., 2014). The base stimulus is one randomly selected face (A) repeating throughout the sequence. The oddball stimuli are different faces (B, C, D…) shown every 5th base face, or at a frequency of 5.88 Hz/5 = 1.18 Hz. A stimulation sequence is structured as follows: AAAABAAAACAAAADAA… Face size varies randomly between 74 % – 120 % in 2 % steps in order to control for low-level pixel-wise overlap differences between base and oddball stimuli. **B**. Trial structure of a sequence for upright and inverted face conditions: a fixation cross appears for 2 – 5 s (duration randomly jittered), followed by the periodic stimulation during 60 s. At the end of trial, the periodic stimulation fades out during 5 s by gradually decreasing the contrast modulation depth from 100 % (full contrast) to 0 % (background only). **C**. Frequency spectra showing the response to upright faces left) and inverted faces (right). While the response to the repeated face at 5.88 Hz is substantial in both conditions, discrimination of face identities as expressed at 1.18 Hz and harmonics (2.36 Hz, 3.53 Hz, etc.) is clear for upright faces but barely visible for inverted faces (A, B, C, from Liu-Shuang et al., 2014, with permission). **D**. The sum of baseline-corrected harmonics shows a much larger (unfamiliar) face identity recognition response for upright than inverted faces, focused over (right) occipito-temporal regions. **E**. The size of the neural face inversion effect as estimated from n = 53 human adults tested in this paradigm (D & E from Rossion et al., 2020, with permission).

effect demonstrates that the populations of neurons in these regions can tell apart the different face identities. The effect has been typically shown for pictures of unfamiliar faces (references above; see e.g., Weibert et al., 2016; Rogers et al., 2022 for evidence with familiar faces), supporting evidence from lesion studies (e.g., Barton et al., (2002); Bouvier and Engel, (2006); and direct intracranial electrical stimulation (Jonas and Rossion, 2021) of the role of these ventral face-selective regions (i.e., in the inferior occipital gyrus, IOG, 'occipital face area', OFA; middle fusiform gyrus, MidFG, 'fusiform face area', FFA) in human FIR.

Several fMRI studies have shown that picture-plane inversion decreases or even abolishes this face identity adaptation effect in the

bilateral face-selective VOTC (FFA, and OFA to a lesser extent; Yovel and Kanwisher, 2005; Mazard et al., 2006; Gilaie-Dotan et al., 2010; see also Schiltz and Rossion, 2006) (Fig. 6). This effect of inversion on face identity repetition is large and quite specific, being absent in face-selective regions of the superior temporal sulcus (STS) or in non-face selective regions (Lateral Occipital Cortex, LOC; Yovel and Kanwisher, 2005; Fig. 6).

4.3. Human intracerebral recordings

Finally, using the same frequency-tagging paradigm as described above, the effect of inversion on FIR has also been localized and quantified inside the human brain with intracerebral recordings performed with a large sample of epileptic patients (N = 69; Jacques et al., 2020). In that study, large decreases of the proportion of significant electrode contacts and amplitude in the VOTC (inferior occipital gyrus, lateral fusiform gyrus) for inverted faces were found, particularly in the right hemisphere (Fig. 7).

In summary, studies that have recorded neural signals reflecting FIR in humans with reliable stimulus repetition effects have reported large decreases of (differential) amplitude when the same stimuli are presented upside-down. These effects of inversion are found without explicit task, in spatial locations and time windows that are compatible with an early dominant role of the right ventral occipito-temporal cortex

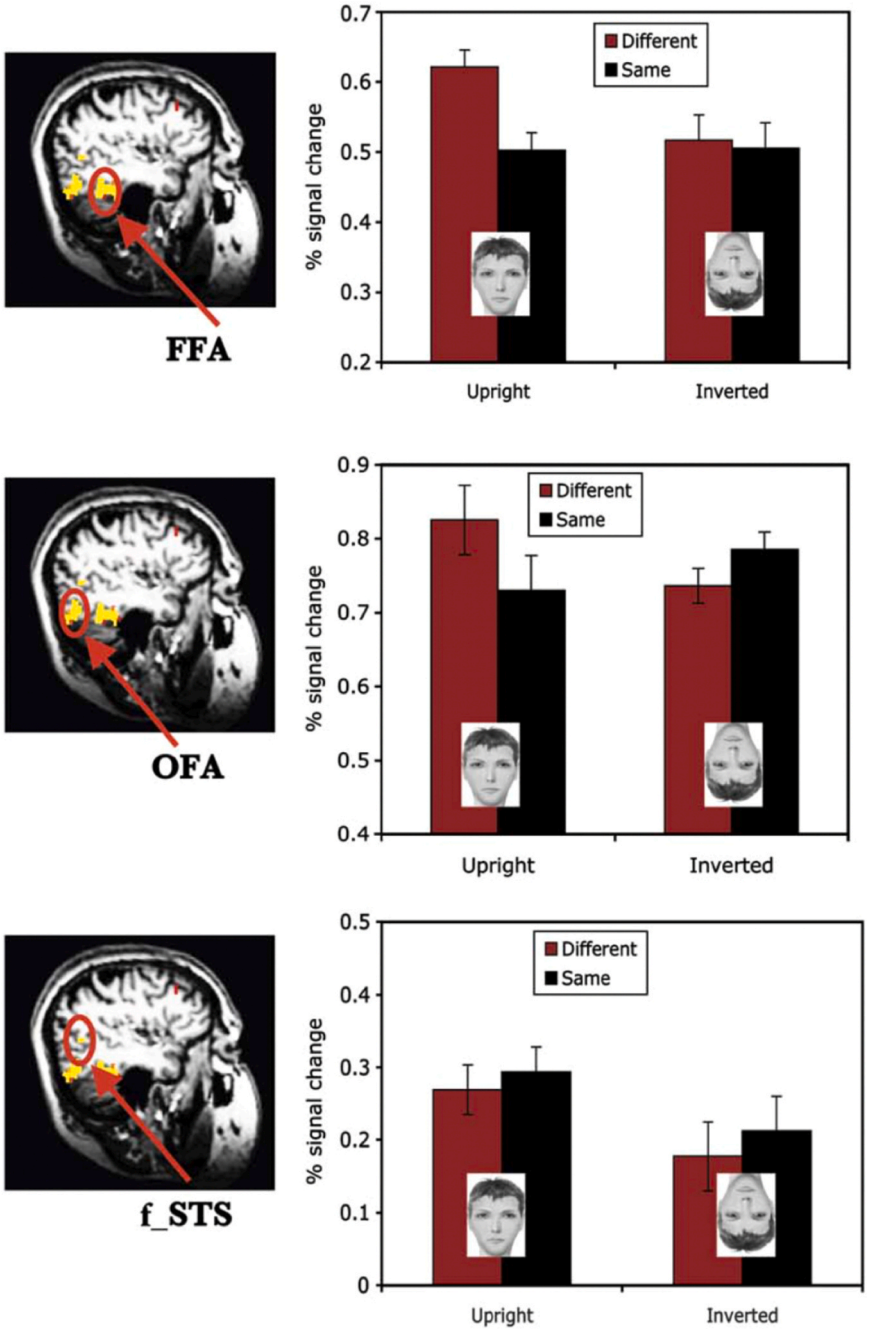

Fig. 6. The effect of inversion on face identity repetition in fMRI (from Yovel and Kanwisher, 2005, with permission). Both the fusiform face area (FFA) and occipital face area (OFA) showed reduced amplitude to repetition of the dame (unfamiliar) face identities, this effect being absent for the same images presented upside-down. The posterior portion of the STS, also a face-selective region, does not show a face identity repetition reduction (but an overall reduction for pictures of inverted faces, regardless of identity).

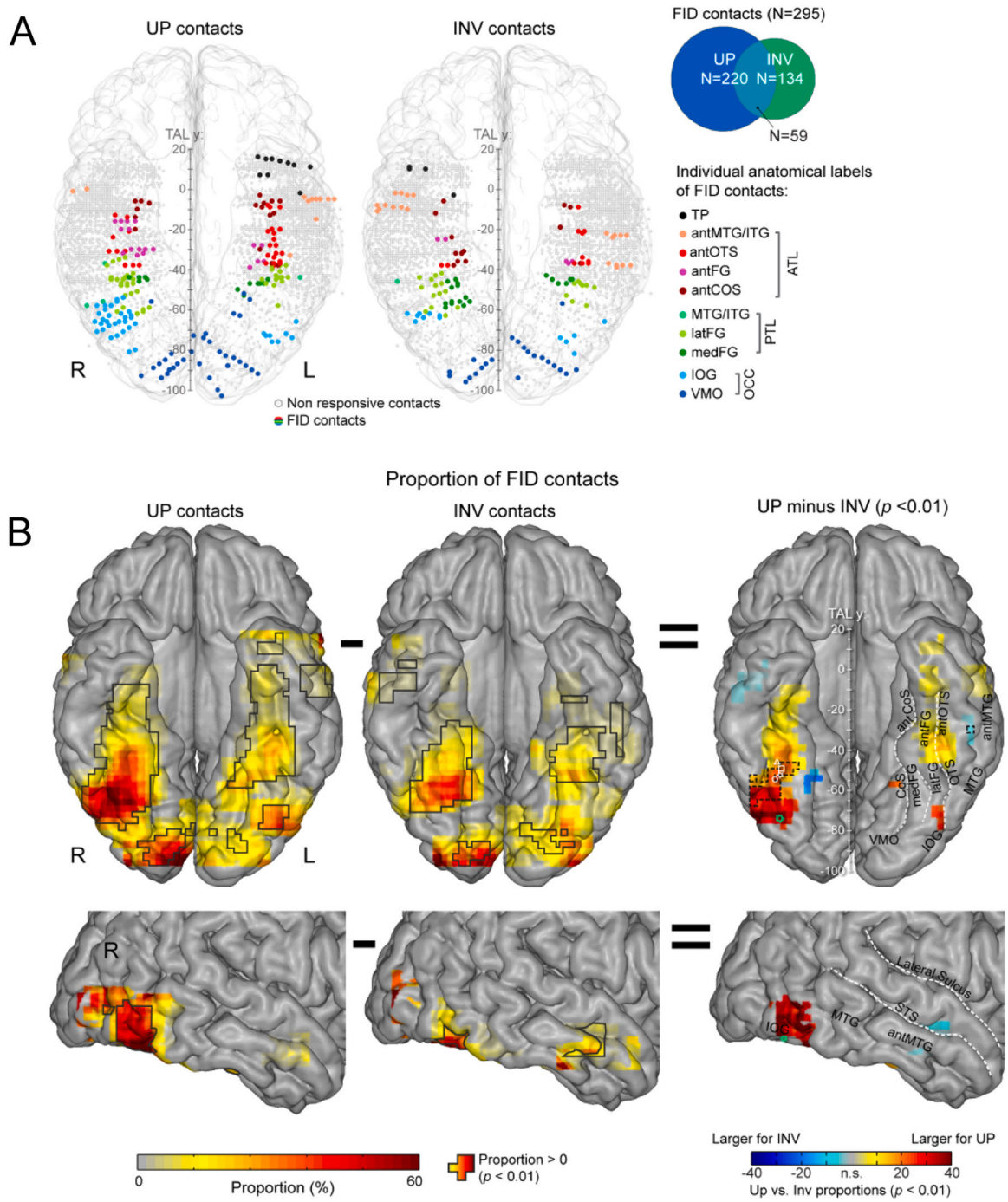

Fig. 7. Spatial distribution of the face inversion effect with intracerebral recordings (adapted from Jacques et al., 2020, with permission). **A**. Map of 3825 VOTC recording contacts across 69 individual brains displayed in the Talairach space using a transparent reconstructed cortical surface of the Colin27 brain (ventral view). Each circle represents a single recording contact. Color-filled circles correspond to contacts showing a significant face individuation (FID) response, at upright (UP) (left map, N = 220, see Venn diagram inset on the right) or inverted (INV) orientation (right map, N = 134). UP and INV contacts are color-coded according to their anatomical location in the original individual anatomy . White-filled circles correspond to contacts on which no significant FID responses was recorded. Values along the Y axis of the Talairach coordinate system (antero-posterior) are shown near the interhemispheric fissure. **B**. Ventral and right lateral maps of the local proportion of UP contacts (left) and INV contacts (middle) relative to number of recorded contacts, and statistical comparison between the local proportions of UP and INV contacts across the VOTC (right, only significant differences of proportions at $p < 0.01$ are displayed). For left and middle maps, black solid contours outline proportions significantly above zero at $p < 0.01$ panels. For the ventral map on the right, the dashed black contour lines show the location of the proportion difference between UP and INV contacts that are significantly ($p < 0.01$) larger in one hemisphere. This indicates that the higher proportion of UP compared to INV contacts in the IOG and latFG is significantly larger in the right hemisphere.

in human FIR.

4.4. Lack of neural inversion effect in macaque monkeys

A number of studies are regularly cited as showing inversion effects on neural activity to faces in monkeys (Perrett et al., 1988, 1998; Pineda

and Nava, 1993; Tsao et al., 2006; Bell et al., 2009; Freiwald et al., 2009; Pinsk et al., 2009; Taubert et al., 2018; Table 2). However, whether these studies show inversion effect on the recognition of *facial identity*, let alone comparable to humans quantitatively and qualitatively, is an entirely different story. The first study cited above reported that about 60 % of face-selective neurons in the monkey STS had delayed onset latencies for inverted faces (Perrett et al., 1988). Yet, as shown in previous reports, there was no reduction in response amplitude (Perrett et al., 1982, 1985; see also Perrett et al., 1998). The delayed response to inverted faces was confirmed by Tsao et al. (2006) in face-selective regions located in the middle portion of the STS (lateral bank and fundus; regions labelled ML and MF respectively), this time together with a substantial reduction (a factor of 2.2) of spiking activity. The substantial reduction in spike rate was later confirmed in ML as well as to a lesser extent in the anterior lateral face-selective STS, in a study controlling for selection biases of the neurons and showing position tolerance of the inversion effect (Taubert et al., 2015a; see also Taubert et al., 2018). Overall, these neurophysiological findings in monkeys are in line with the large reduction of activity for inverted faces in these middle STS as well as temporal anterior face-selective regions as found in fMRI (Bell et al., 2009; Pinsk et al., 2009 – note however, the inconsistency between the findings of these two studies in terms of location of the effects).

Table 2
List of studies that have compared neural responses to upright and inverted faces in the macaque brain. While inverted faces appear to reduce neural activity to faces in general, there is no evidence of a decreased sensitivity to differences between facial identities. This has been tested only in two studies (in bold). The first one (Sugase-Miyamoto et al., 2014) showed decrease discriminative power of spike trains for inverted faces, but with a sample bias similar to behavioral studies. The second one (Taubert et al., 2018) used an independent selection of face-selective neurons and showed no advantage of upright faces in terms of spike rate discriminative power between individual faces (despite reduced spiking activity overall).

Study	N	Neural measures	Outcome
Perrett et al. (1982)	3 (21 cells)	Single neurons (spikes)	Upright and inverted faces: no difference in response magnitude in STS (fundus) face-selective cells
Perrett et al. (1985)	3 (10 cells)	Single neurons (spikes)	Delayed onset time for inverted faces (60 % face-selective cells), no change of amplitude
Perrett et al. (1988)	3 (25 cells)	Single neurons (spikes)	Delayed onset time for inverted faces (60 % face-selective cells), no change of amplitude
Pineda and Nava (1993)	2	EEG (ERPs)	Disappearance of a cross-species priming effect at 400–800 ms for inverted monkey faces
Tsao et al. (2006) (Supp. Material)	2 (69 cells)	Single neurons (spikes)	Delayed onset time and large reduction of spiking rate for inverted faces (STS: fundus and lower bank)
Bell et al. (2009)	4	fMRI	Significant reduction of raw activity to inverted faces in 4/6 face-selective STS regions. Larger effects in anterior than posterior (ML/MF) regions
Freiwald et al. (2009)	3 (64 cells)	Single neurons (spikes)	Reduction and change of tuning to features of cartoon (human) faces, especially eyebrows, with inversion (STS: fundus and lower bank)
Pinsk et al. (2009) Expt.2	2–3	fMRI	Reduction of activity to inverted faces in STS face-selective regions, with larger effects in the fundus than lateral bank.
Sugase-Miyamoto et al., (2014)	2 (120 cells)	Single neurons (spikes)	Reduced spiking activity and discrimination power among individual faces to inverted faces (4 monkey faces, 3 human faces). Biased sampling.
Taubert et al., (2015a)	2 (179 cells)	Single neurons (spikes)	Reduced spiking activity to inverted faces in lateral STS face-selective areas (ML, AL)
Taubert et al., (2015b)	2 (211 cells)	Single neurons (spikes)	Interaction in face-selective middle STS (ML) between the global orientation of a face and the local orientation of its eyes
Taubert et al., (2018)	2 (57 cells)	Single neurons (spikes)	Reduced spiking activity of independently defined face-selective cells to inverted faces (ML) but equal discrimination power among individual faces

Some studies have also found a reduction of sensitivity to differences between face stimuli when images are presented upside-down, although without relating these measures to recognition (i.e., generalized discrimination) of identity. With EEG recordings, Pineda and Nava (1993) showed larger negative ERPs between 400 ms and 800 ms to monkey faces preceded by monkey faces than human faces, this effect disappearing for inverted stimuli. Back to single neuron recordings, Freiwald and colleagues (2009) reported that cells in the face-selective regions the middle STS (ML, MF) reduce their tuning to features of cartoon (human) faces, especially eyebrows, with inversion. In line with these observations, Taubert et al. (2015b) found differences in spike rate in the same region between an upright and inverted version of the same 'Thatcherized' faces.

Overall, it is clear that picture plane inversion of faces affects neural activity of face-selective populations of neurons in the monkey brain, particularly decreasing response amplitude and increasing latency. Decreased or altered sensitivity to stimulus manipulations with inversion has also been found in a handful of studies (Pineda and Nava, 1993; Freiwald et al., 2009; Taubert et al., 2015b). However, critically, there is no evidence of reduced sensitivity to the *coding of identity* within these populations of neurons. This is particularly surprising in light of the numerous monkey physiology studies that have investigated differences in spike rate of face-selective neurons between different facial identities, generally arguing that these differences provide a reliable code to recognize facial identities in sparse populations of neurons (Rolls, 1992; Young and Yamane, 1992; Leopold et al., 2006; Chang and Tsao, 2017). Presumably, if inversion decreased monkeys' FIR, shouldn't the discriminative power of spike rates be substantially reduced for inverted faces?

To my knowledge, only two studies directly addressed directly this question. In the first study, a decrease in discriminative power of spike trains was found when faces (monkeys and humans) were presented upside-down (Sugase-Miyamoto et al., 2014). The effects were very large, but found only for discrimination between 4 faces (monkeys or humans). Most importantly, neurons in that study were pre-selected based on their positive responses to the very same upright faces that served for the discriminative analysis. Hence, the study suffers from the same methodological issue (sometimes called 'double dipping') as many behavioral studies that used the same (upright) stimuli to train and then test the effect of inversion (Section 2; Fig. 2). Another limitation of that study is that the neurons were not drawn from face-selective regions in the monkey STS. In contrast, Taubert and colleagues (2018) defined neurons as face-selective in the ML region of two monkeys based on an independent face localizer experiment (Fig. 8). Activity of these neurons was then measured in response to novel images of upright and inverted (human) faces. In that study, different (12) faces elicited distinct patterns of activity across face-selective neurons that were reliable (i.e., predictable with a classifier) within a specific size and orientation condition (Fig. 8). Interestingly, a classifier trained with one orientation condition and tested on the other did not lead to performance above chance level, indicating that the spike rate pattern changed completely with picture-plane orientation of the faces. However, and despite the expected substantial reduction in the average response magnitude of face-selective neurons to inverted faces, the classifier performance was not superior for upright than inverted faces. In other words, despite

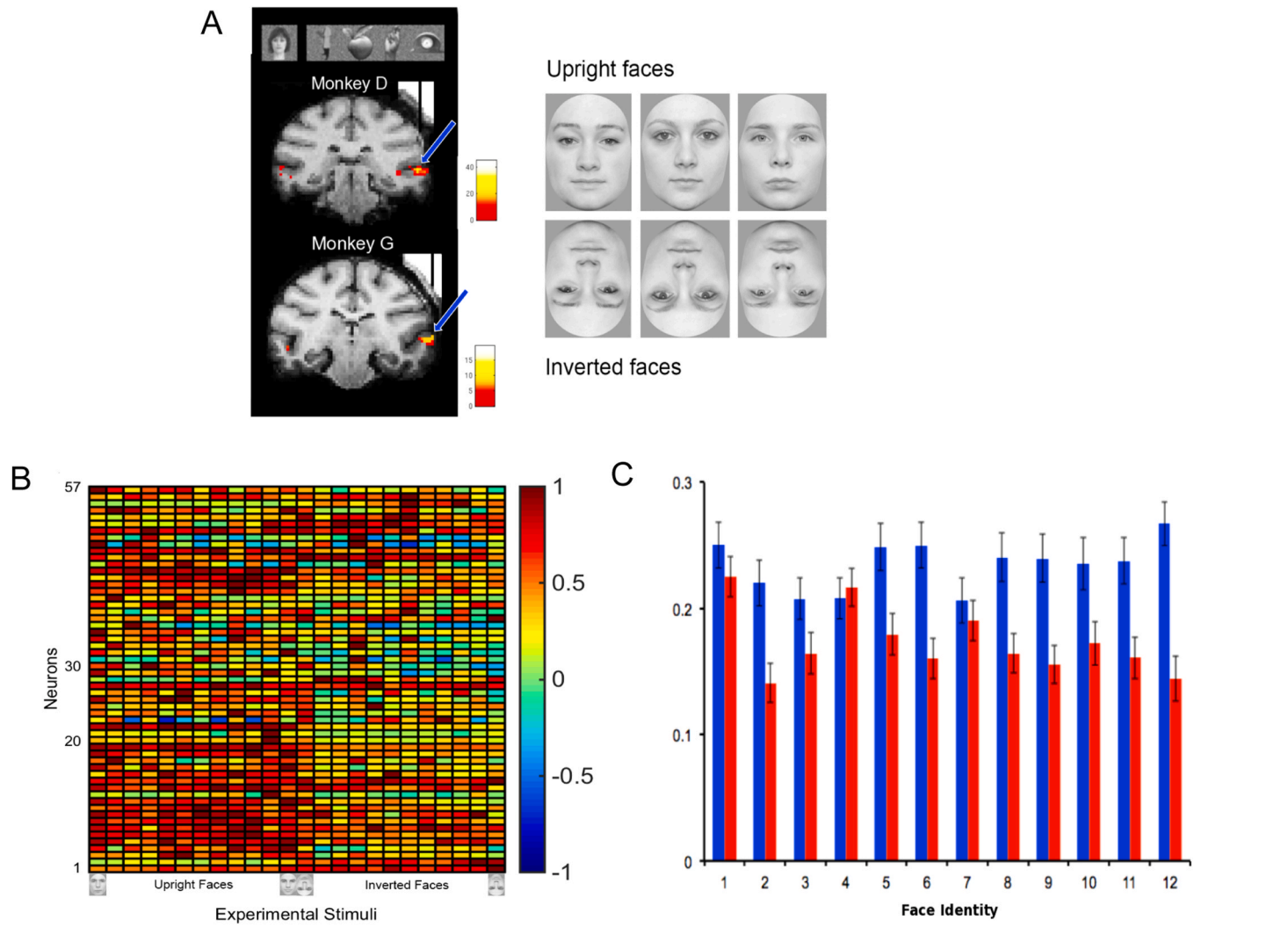

Fig. 8. Population-level larger response to upright than inverted faces, with equal variance in spike rate for various (human) face identities (adapted from Taubert et al., 2018, with permission). **A.** Face-selective region of the STS (ML) sampled in two monkeys presented with the same pictures of upright and inverted faces as illustrated on the right. **B**. Normalized responses of the 57 neurons for upright (left) and inverted (right) faces, showing an overall larger response to upright faces for a majority of neurons, and a substantial amount of variability of response across individual faces. **C**. This variability is also found in the averaged population response across 57 neurons for the different faces, also showing the lower response for all but one face identity (#4) with stimulus inversion. While this variability in spike rates is usually taken as reflecting a powerful code to distinguish different face identities, it was not larger for upright than inverted faces, i.e. no inversion effect in discriminative power between face identities.

having more room for variation, the different face identities were not discriminated better at upright than inverted orientation, i.e., a complete absence of neuronal inversion effect on FIR (Taubert et al., 2018; Fig. 8).

In conclusion, monkeys, generally like humans (except for N170 amplitude), show a reduction of (face-selective) neural activity in their temporal lobe to inverted pictures of faces (together with a delayed response) (Table 2). However, evidence for a reduction of sensitivity to *differences between face identities* with inversion as in humans, as reviewed in Section 3, has not been provided in macaque monkeys. Thus, the view that '*at the neural level, evidence is consistent that cells in face patches do show an inversion effect*' (Hesse and Tsao, 2020, p.696) is incorrect, at least when it comes to face identity recognition. Admittedly, part of the discrepancy could be due to the use of different recording methods and neural signals in the two species (i.e., EEG/fMRI in humans; single neuron activity in macaques). While single neuron recording in face-selective cortical regions of the human brain is particularly challenging and still in its infancy (e.g., Quian Quiroga et al., 2023), this issue could and should have been at least be investigated in macaque fMRI and EEG studies testing face identity repetition effects across upright and inverted orientations.

5. Lack of face inversion effect in macaques: theoretical implications

The published data extensively reviewed here indicates that, unlike humans, macaque monkeys do not suffer from any drop of performance, or reduced neural sensitivity, for recognizing the identity of conspecifics (or of humans) when they are presented upside-down. While there are much fewer studies performed in monkeys than in humans, and monkey studies generally involve a few subjects only (Table 1 **& 2**), the relatively large number of published studies, which span over 7 decades, seems to be sufficient to conclude that monkeys lack a face inversion effect, let alone a very large effect as found in our species. This conclusion is in line with relatively recent reviews that focused only on behavioral effects (Rossion and Taubert, 2019; Griffin, 2020), and dismisses the perpetually repeated claims that face inversion effects are present (e.g., Amita et al., 2024), or even 'controversial' or 'inconsistent' in monkeys (e.g., Keating and Keating, 1993; Pascalis and Bachevalier, 1998; Vermeire and Hamilton, 1998; Parr et al., 1999; Guo et al., 2003; Gothard et al.,

2004; Adachi et al., 2009; Dahl et al., 2010; Leopold and Rhodes, 2010; Pokorny et al., 2011; Dahl et al., 2013; Hesse and Tsao, 2020; Pascalis et al., 2021).

Admittedly, the present review focuses on studies performed on macaques, not only for consistency and because they constitute the vast majority of studies, but especially given the privileged status of this genus as an animal model of the human brain, in particular for face recognition (Desimone, 1991; DiCarlo et al., 2012; Freiwald, 2020; Hesse and Tsao, 2020; Kanwisher, 2025). Nevertheless, as noted above, rare studies performed in other monkeys (New World Monkeys) tested with upright and inverted faces are unconvincing and suffer from the same methodological issues as discussed in Section 3 (squirrel monkeys: Phelps and Roberts, 1994; Tamarins: Weiss et al., 2001; Neiworth et al., 2007; Capuchins: Pokorny et al., 2011; see footnote 5), supporting the view that monkeys *in general* do not show a cost of stimulus inversion in face identity recognition. An outstanding and obvious question then is why do monkeys fail to show a significant inversion effect in FIR when this effect is so prominent in our species? Here I want to briefly contrast two possibilities.

5.1. Are monkeys equally efficient at FIR for upright and inverted faces?

The first possibility is that monkeys recognize the identity of (conspecific) faces as humans do. Yet, unlike humans, they readily transfer this ability to faces presented upside-down. This is a highly unlikely, for a number of reasons. First, macaques do not have a prehensile tail, nor any specific adaptation for suspensory behaviour or arboreal locomotion such as brachiation. Like humans, they live predominately on the ground. Thus, there is no particular reason to believe that they are exposed nearly as often to inverted as upright faces. Second, and related to that, they *do* show clear differences, both at the behavioral and neural levels, between upright and inverted faces, often expressed in terms of preferences for upright faces (i.e., preferential selection, longer exploration times, larger neural responses; see the list of studies in Table 1 **& 2;** Fig. 8). Significant advantages in performance have also sometimes been found in monkeys for upright over inverted faces in tasks that are unrelated to face identity (e.g., Perrett et al., 1988; Vermeire & Hamilton, 1998). Third, as mentioned at the beginning of the present review, the cause of FIE in humans is largely thought to be a drop of holistic perception: while an upright face is processed as an integrated unit, an inverted face is processed in a (more) piecemeal fashion, feature-by-feature (Farah et al., 1995a; Rossion, 2008, 2009). Even if this latter view is not fully adopted in the scientific community (mainly due to what is thought to be a lack of direct evidence), humans undoubtedly show a number of behavioral effects with face stimuli, interpreted in terms of holistic processing/representation, that are reduced or absent when these stimuli are presented upside-down (Bartlett and Searcy, 1993; Barton et al., 2001, 2003; Farah et al., 1995a; Hole, 1994; Murray et al., 2000; Rhodes et al., 1993; Searcy and Bartlett, 1996; Sergent, 1984; Tanaka and Farah, 1993; Tanaka and Sengco, 1997; Young et al., 1987; Freire et al., 2000; Boutsen and Humphreys, 2003; Rossion and Boremanse, 2008). It is unclear at present that monkeys present with such effects, not only because the few studies that have addressed this issue have drawn negative conclusions or are inconsistent with each other (Adachi et al., 2009; Dahl et al., 2010; Weldon et al., 2013; Dahl et al., 2007; Taubert et al., 2012; see Rossion and Taubert, 2019), but also because monkeys' performance in face identity matching task appear to rely essentially on external features and/or features devoid of configural organization (Parr et al., 2008; Weldon et al., 2013). Finally, across the studies surveyed here and other studies, it seems pretty clear that monkeys are just not very good at identity recognition of conspecifics based on their faces in general, leading to the second possibility, as discussed below.

5.2. Monkeys lack human face identity recognition expertise supported by the ventral occipito-temporal cortex

The second possibility is indeed that monkeys are largely inefficient at FIR, in particular when compared to us humans. That is, unlike humans, monkeys would not present with a natural, or rather *naturally developed* (from experience), ability to rapidly individuate numerous conspecifics based on their faces only. Therefore, presenting faces upside-down in a given experimental setting does not change much or anything for monkeys: their performance at such tasks is limited anyway and based essentially on image-specific features that are useful only for a specific task and stimulus set. While the claim that monkeys lack a natural(ly developed) ability to efficiently recognize conspecifics based on their faces only may appear very strong, it is actually supported by a series of arguments (Parr et al., 2008; Parr, 2011; Rossion and Taubert, 2019): (1) the trivial picture discrimination or matching tasks that have been generally used to probe monkey's FIR ability (e.g., Swartz, 1983; Parr et al., 2008; Weldon et al., 2013; Moeller et al., 2017); (2) the relatively long training sessions usually required for monkeys to learn to explicitly discriminate pictures of conspecific faces for their identity (e.g., Rosenfeld and Van Hoesen, 1979; Parr et al., 1999; Parr et al., 2008; Weldon et al., 2013); (3) the limited performance level of monkeys at such tasks, sometimes barely above chance level (e.g., Parr et al., 2008; Weldon et al., 2013; Moeller et al., 2017); (4) the very small stimulus sets (e.g., Rosenfeld and Van Hoesen, 1979; Swartz, 1983; Dittrich, 1990; Keating and Keating, 1993; Vermeire & Hamilton, 1998; Vermeire et al., 1998; Adachi et al., 2009); (5) that are often repeated without or little generalization across variable views (Parr et al., 1999; Moeller et al., 2017); (6) the poorly controlled stimulus discriminations used with implicit measures in habituation/dishabituation paradigms (Guo et al., 2003; Gothard et al., 2004); (7) the overreliance on external features in face identity matching tasks (Parr et al., 2008; Weldon et al., 2013). Considered altogether, of these elements support the view that while monkeys are primates for which social interactions, in particular based on faces, are undoubtedly important (e.g., Emery et al., 1997; Deaner et al., 2005; Freiwald et al., 2016; Sliwa et al., 2011), they do not possess a naturally developed ability to efficiently recognize the *identity* of many conspecific faces, let alone an ability remotely comparable to humans (i.e., as a holistic snapshot).

This conclusion is in line with monkeys' relatively underdeveloped temporal lobe compared to humans (Bryant et al., 2019; Roumazeilles et al., 2020; Braunsdorf et al., 2021; Rilling and Seligman, 2002), in particular lacking critical (right-lateralized) ventral brain structures for FIR (Fig. 9**)**.

Specifically, monkeys lack a fusiform gyrus, a hominoid-specific structure (Weiner and Zilles, 2016; Bryant et al., 2019) that undoubtedly holds the most important populations of neurons supporting human FIR (Sergent et al., 1992; McCarthy et al., 1997; Kuskowski and Pardo, 1999; Barton et al., 2002; Keller et al., 2017; Jacques et al., 2020; Jonas and Rossion, 2021; Rossion et al., 2024). As a matter of fact, monkeys lack the whole ventral face-selective network of regions supporting FIR in our species (Rossion and Taubert, 2019; Rossion, 2022; Laurent et al., 2023; Fig. 9). While face-selective regions of the monkey superior temporal sulcus (STS) and/or anterior temporal lobe have been tentatively related to ventral face-selective regions supporting human FIR (and the inversion effect) (Tsao et al., 2006; Yovel and Freiwald, 2013; Fisher and Freiwald, 2015), this claim of homology is largely unsubstantiated at present and unlikely to be correct (Rossion and Taubert, 2019). Instead, both behavioral and neural evidence converge to suggest that monkeys do not possess the adequate ventral neural circuitry to support rapid recognition of a conspecific face based on holistic visual memory representation. Hence, their lack of a humanlike face inversion effect, which will therefore need to be clarified in terms of neuronal mechanisms in future single neuron level recordings performed directly in face-selective regions of the human brain.

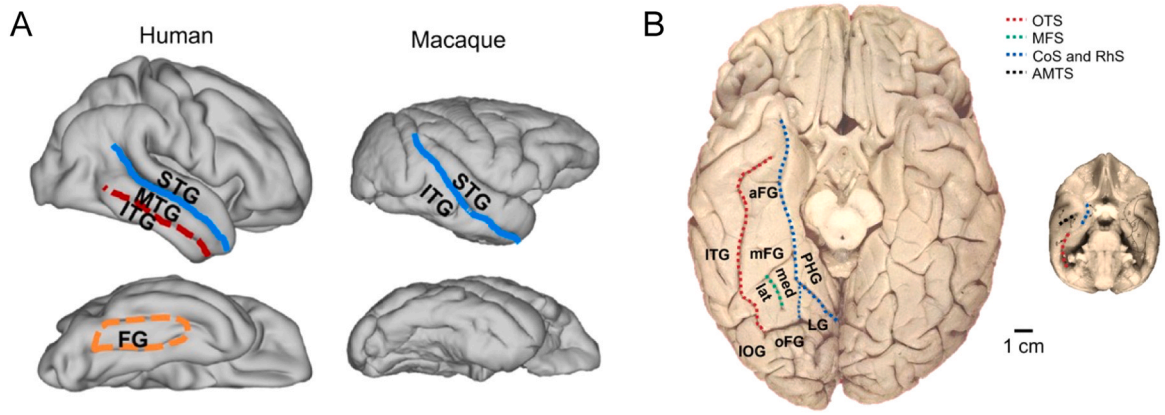

Fig. 9. Sulcal and gyral differences of the human and macaque temporal lobe. **A**. Above, lateral view of a human and macaque temporal lobe (not at respective sizes), showing the additional middle temporal gyrus (MTG) in humans, as defined by the inferior temporal sulcus (dotted line in red). One sulcus only, the STS (in blue) is visible in macaques. Below, ventral view of the temporal lobe to highlight the fusiform gyrus (FG) in humans, not present in the macaque brain. Brains not to scale. Adapted from Roumazeilles et al., (2020), with permission. **B**. Ventral views of a human and macaque brain, highlighting the fusiform gyrus defined by the occipito-temporal sulcus (OTS) and the collateral sulcus (Cos). The human fusiform gyrus is subdivided in occipital (oFG), middle (mFG) and anterior parts (aFG). The middle fusiform gyrus is additionally subdivided in lateral and medial parts by the midfusiform sulcus. AMTS, Antero-Medial sulcus; RhS: rhinal sulcus. Note the massive expansion of the ventral (occipito-)temporal cortex in humans as compared to macaques, who lack a fusiform gyrus.

Funding

This work was funded by an ERC Adg grant HUMANFACE 101055175 to BR.

Declaration of Competing Interest

The author has no conflict of interest to declare.

Acknowledgments

The author would like to thank two anonymous reviewers for their helpful comments on a previous version of this manuscript.

Data availability

No data was used for the research described in the article.

References

Adachi, I., Chou, D.P., Hampton, R.R., 2009. Thatcher effect in monkeys demonstrates conservation of face perception across primates. Curr. Biol. 19, 1270–1273.
Amita, H., Koyano, K.W., Kunimatsu, J., 2024. Neuronal mechanisms underlying face recognition in Non-human primates. Jpn. Psychol. Res. 66, 416–442.
Balas, B., Gable, J., Pearson, H., 2019. The effects of blur and inversion on the recognition of ambient face images. Perception 48, 58–71.
Barrett, S.E., Rugg, M.D., Perrett, D.I., 1988. Event-related potentials and the matching of familiar and unfamiliar faces. Neuropsychologia 26 (1), 105–117.
Bartlett, J.C., Searcy, J., 1993. Inversion and configuration of faces. Cogn. Psychol. 25, 281–316.
Barton, J.J., 2023. Face processing in the temporal lobe. In: Miceli, G., Bartolomeo, P., Navarro, V. (Eds.), The Temporal Lobe, 187. Handbook of Clinical Neurology.
Barton, J.J., Keenan, J.P., Bass, T., 2001. Discrimination of spatial relations and features in faces: effects of inversion and viewing duration. Br. J. Psychol. 92, 527–549.
Barton, J.J., Press, D.Z., Keenan, J.P., O'Connor, M., 2002. Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. Neurology 58, 71–78.
Barton, J.J., Deepak, S., Malik, N., 2003. Attending to faces: change detection, familiarization, and inversion effects. Perception 32, 15–28.
Behrmann, M., Scherf, K.S., Avidan, G., 2016. Neural mechanisms of face perception, their emergence over development, and their breakdown. Wiley Interdiscip. Rev. Cogn. Sci. 7, 247–263.
Bell, A.H., Hadj-Bouziane, F., Frihauf, J.B., Tootell, R.B., Ungerleider, L., 2009. Object representations in the temporal cortex of monkeys and humans as revealed by functional magnetic resonance imaging. J. Neurophysiol. 101, 688–700.
Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8, 551–565.
Bindemann, M., Burton, A.M., Leuthold, H., Schweinberger, S.R., 2008. Brain potential correlates of face recognition: geometric distortions and the N250r brain response to stimulus repetitions. Psychophysiology 45, 535–544.
Boutsen, L., Humphreys, G.W., 2002. Face context interferes with local part processing in a prosopagnosic patient. Neuropsychologia 40, 2305–2313.
Boutsen, L., Humphreys, G.W., 2003. The effect of inversion on the encoding of normal and "Thatcherized" faces. Q. J. Exp. Psychol. 56A, 955–975.
Bouvier, S.E., Engel, S.A., 2006. Behavioral deficits and cortical damage loci in cerebral achromatopsia. Cereb. cortex 16 (2), 183–191.
Braunsdorf, M., Blazquez Freches, G., Roumazeilles, L., Eichert, N., Schurz, M., Uithol, S., Bryant, K.L., Mars, R.B., 2021. Does the temporal cortex make us human? A review of structural and functional diversity of the primate temporal lobe. Neurosci. Biobehav. Rev. 131, 400–410.
Bruce, C., 1982. Face recognition by monkeys: absence of an inversion effect. Neuropsychologia 20, 515–521.
Bruce, C.J., Desimone, R., Gross, C.G., 1981. Visual propertics of ncurons in a polysensory arca in superior temporal sulcus of the macaque. J. Neurophysiol. 46, 369–384.
Brunet, N.M., 2023. Face processing and early event-related potentials: replications and novel findings. Front. Hum. Neurosci. 17, 1268972.
Bryant, K.L., Glasser, M.F., Li, L., Jae-Cheol Bae, J., Jacquez, N.J., Alarcón, L., Fields 3rd, A., Preuss, T.M., 2019. Organization of extrastriate and temporal cortex in chimpanzees compared to humans and macaques. Cortex 118, 223–243.
Busigny, T., Rossion, B., 2010. Acquired prosopagnosia abolishes the face inversion effect. Cortex 46, 965–981.
Busigny, T., Robaye, L., Dricot, L., Rossion, B., 2009. Right anterior temporal lobe atrophy and person-based semantic defect: a detailed case study. Neurocase 30, 1–24.
Caharel, S., d'Arripe, O., Ramon, M., Jacques, C., Rossion, B., 2009a. Early adaptation to unfamiliar faces across viewpoint changes in the right hemisphere: evidence from the N170 ERP component. Neuropsychologia 47, 639–643.
Caharel, S., Jacques, C., d'Arripe, O., Ramon, M., Rossion, B., 2011. Early electrophysiological correlates of adaptation to personally familiar and unfamiliar faces across viewpoint changes. Brain Res. 1387, 85–98.
Caharel, S., Collet, K., Rossion, B., 2015. The early visual encoding of a face (N170) is viewpoint-dependent: a parametric ERP-adaptation study. Biol. Psychol. 106, 18–27.
Caharel, S., Jiang, F., Blanz, V., Rossion, B., 2009b. Recognizing an individual face: 3D shape contributes earlier than 2D surface reflectance information. NeuroImage 47, 1809–1818.
Calcutt, S.E., Rubin, T.L., Pokorny, J.J., de Waal, F.B., 2017. Discrimination of emotional facial expressions by tufted capuchin monkeys (Sapajus apella). J. Comp. Psychol. 131, 40–49.
Calder, A.J., Rhodes, G., Haxby, J.V., Johnson, M.H. (Eds.), 2011. Oxford Handbook of Face Perception. Oxford University Press, pp. 149–176.
Carey, S., 1992. Becoming a face expert. Philos. Trans. R. Soc. Lond. B 335, 95–103.
Cashon, C.H., Holt, N.A., 2015. Developmental origins of the face inversion effect. Adv. Child Dev. Behav. 48, 117–150.
Chang, L., Tsao, D.Y., 2017. The code for facial identity in the primate brain. Cell 169, 1013–1028.
Chatterjee, G., Nakayama, K., 2012. Normal facial age and gender perception in developmental prosopagnosia. Cogn. Neuropsychol. 29 (5-6), 482–502.
Civile, C., McLaren, R.P., McLaren, I.P., 2014. The face inversion effect–parts and wholes: individual features and their configuration. Q. J. Exp. Psychol. (2006) 67 (4), 728–746.

Civile, C., Elchlepp, H., McLaren, R., Galang, C.M., Lavric, A., McLaren, I., 2018. The effect of scrambling upright and inverted faces on the N170. Q. J. Exp. Psychol. (2006) 71 (11), 2464–2476.
Coggan, D.D., Watson, D.M., Wang, A., Brownbridge, R., Ellis, C., Jones, K., Kilroy, C., Andrews, T.J., 2022. The representation of shape and texture in category-selective regions of ventral-temporal cortex. Eur. J. Neurosci. 56 (3), 4107–4120.
Dahl, C.D., Logothetis, N.K., Hoffman, K.L., 2007. Individuation and holistic processing of faces in rhesus monkeys. Proc. R. Soc. Lond. B 274, 2069–2076.
Dahl, C.D., Logothetis, N.K., Bülthoff, H.H., Wallraven, C., 2010. The Thatcher illusion in humans and monkeys. Proceedings. Biological sciences 277, 2973–2981.
Dahl, C.D., Rasch, M.J., Tomonaga, M., Adachi, I., 2013. The face inversion effect in non-human primates revisited - an investigation in chimpanzees (Pan troglodytes). Sci. Rep. 3, 2504.
Deaner, R.O., Khera, A.V., Platt, M.L., 2005. Monkeys pay per view: adaptive valuation of social images by rhesus macaques. Curr. Biol. 15, 543–548.
Delvenne, J.-F., Seron, X., Coyette, F., Rossion, B., 2004. Evidence for perceptual deficits in associative visual (prosop)agnosia: a single-case study. Neuropsychologia 42, 597–612.
Desimone, R., 1991. Face-selective cells in the temporal cortex of monkeys. J. Cogn. Neurosci. 3, 1–8.
Desimone, R., Albright, T.D., Gross, C.G., Bruce, C., 1984. Stimulus-selective properties of inferior temporal neurons in the macaque. J. Neurosci. 4, 2051–2062.
DiCarlo, J.J., Zoccolan, D., Rust, N.C., 2012. How does the brain solve visual object recognition? Neuron 73, 415–434.
Dittrich, W., 1990. Representation of faces in longtailed macaques (Macaca fascicularis). Ethology 85, 265–278.
Duchaine, B., Yovel, G., 2015. A revised neural framework for face processing. Annu. Rev. Vis. Sci. 1, 293–416.
Duchaine, Freiwald, W., Yovel, G, B., 2016. Face processing systems: from neurons to Real-World social perception. Annu Rev. Neurosci. 39, 325–346.
Durand, K., Gallay, M., Seigneuric, A., Robichon, F., Baudouin, J.Y., 2007. The development of facial emotion recognition: the role of configural information. J. Exp. Child Psychol. 97, 14–27.
Eger, E., Henson, R.N., Driver, J., Dolan, R.J., 2004. BOLD repetition decreases in object-responsive ventral visual areas depend on spatial attention. J. Neurophysiol. 92 (2), 1241–1247.
Emery, N.J., Lorincz, E.N., Perrett, D.I., Oram, M.W., Baker, C.I., 1997. Gaze following and joint attention in rhesus monkeys (Macaca mulatta). J. Comp. Psychol. 111, 286–293.
Ewbank, M.P., Henson, R.N., Rowe, J.B., Stoyanova, R.S., Calder, A.J., 2013. Different neural mechanisms within occipitotemporal cortex underlie repetition suppression across same and different-size faces. Cereb. cortex 23, 1073–1084.
Farah, M.J., Tanaka, J.W., Drain, H.M., 1995a. What causes the face inversion effect? J. Exp. Psychol. Hum. Percept. Perform. 21, 628–634.
Farah, M.J., Wilson, K.D., Drain, H.M., Tanaka, J.R., 1995b. The inverted face inversion effect in prosopagnosia: evidence for mandatory, face-specific perceptual mechanisms. Vis. Res. 35, 2089–2093.
Fisher, C., Freiwald, W.A., 2015. Contrasting specializations for facial motion within the macaque face- processing system. Curr. Biol. 25, 261–266.
Fisher, K., Towler, J., Eimer, M., 2016. Facial identity and facial expression are initially integrated at visual perceptual stages of face processing. Neuropsychologia 80, 115–125.
Freire, A., Lee, K., Symons, L.A., 2000. The face-inversion effect as a deficit in the encoding of configural information: direct evidence. Perception 29, 159–170.
Freiwald, W.A., 2020. Social interaction networks in the primate brain. Curr. Opin. Neurobiol. 65, 49–58.
Freiwald, W.A., Tsao, D.Y., Livingstone, M.S., 2009. A face feature space in the macaque temporal lobe. Nat. Neurosci. 12, 1187–1196.
Gauthier, I., Tarr, M.J., Moylan, J., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. The fusiform "face area" is part of a network that processes faces at the individual level. J. Cogn. Neurosci. 12, 495–504.
Gentile, F., Rossion, B., 2014. Temporal frequency tuning of cortical face-sensitive areas for individual face perception. Neuroimage 90, 256–265.
George, N., Jemel, B., Fiori, N., Chaby, L., Renault, B., 2005. Electrophysiological correlates of facial decision: insights from upright and upside-down Mooney-face perception. brain Res. Cogn. brain Res. 24, 663–673.
Gerlach, C., Mogensen, E., 2024. The face inversion effect does not provide a pure measure of holistic face processing. Behav. Res. 56, 330–341.
Gilaie-Dotan, S., Malach, R., 2007. Sub-exemplar shape tuning in human face-related areas. Cereb. cortex 17, 325–338.
Gilaie-Dotan, S., Gelbard-Sagiv, H., Malach, R., 2010. Perceptual shape sensitivity to upright and inverted faces is reflected in neuronal adaptation. NeuroImage 50 (2), 383–395.
Goffaux, V., Rossion, B., 2007. Face inversion disproportionately impairs the perception of vertical but not horizontal relations between features. J. Exp. Psychol. Hum. Percept. Perform. 33, 995–1002.
Gothard, K.M., Erickson, C.A., Amaral, D.G., 2004. How do rhesus monkeys (*macaca mulatto*) scan faces in a visual paired comparison task? Anim. Cogn. 7, 25–36.
Gothard, K.M., Brooks, K.N., Peterson, M.A., 2009. Multiple perceptual mechanisms of face recognition in macaque monkeys. Anim. Cogn. 12, 155–167.
Gregory, R.L., 1997. Knowledge in perception and illusion. *philosophical transactions of the royal society of london. series b*. Biol. Sci. 352 (1358), 1121–1127.
Griffin, J.W., 2020. Quantifying the face inversion effect in nonhuman primates: a phylogenetic meta-analysis. Anim. Cogn. 23, 237–249.
Grill-Spector, K., Malach, R., 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol. 107 (1-3), 293–321.
Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn. Sci. 10, 14–23.
Guillaume, F., Tiberghien, G., 2001. An event-related potential study of contextual modifications in a face recognition task. Neuroreport 12, 1209–1216.
Guo, K., Robertson, R.G., Mahmoodi, S., Tadmor, Y., Young, M.P., 2003. How do monkeys view faces? A study of eye movements. Exp. Brain Res 150, 363–374.
Hagen, S., Laguesse, R., Rossion, B., 2024. Extensive visual training in adulthood reduces an implicit neural marker of the face inversion effect. Brain Sci. 14, 146.
Haxby, J.V., Ungerleider, L.G., Clark, V.P., Schouten, J.L., Hoffman, E.A., Martin, A., 1999. The effect of face inversion on activity in human neural systems for face and object perception. Neuron 22, 189–199.
Heisz, J.J., Shedden, J.M., 2009. Semantic learning modifies perceptual face processing. J. Cogn. Neurosci. 21, 1127–1134.
Heisz, J.J., Watter, S., Shedden, J.M., 2006. Progressive N170 habituation to unattended repeated faces. Vis. Res. 46, 47–56.
Herzmann, G., Sommer, W., 2007. Memory-related ERP components for experimentally learned faces and names: characteristics and parallel-test reliabilities. Psychophysiology 44, 262–276.
Herzmann, G., Schweinberger, S.R., Sommer, W., Jentzsch, I., 2004. What's special about personally familiar faces? A multimodal approach. Psychophysiology 41, 688–701.
Hesse, J.K., Tsao, D.Y., 2020. The macaque face patch system: a turtle's underbelly for the brain. Nat. Rev. Neurosci. 21, 695–716.
Hills, P.J., Lewis, M.B., 2018. The development of face expertise: evidence for a qualitative change in processing. Cogn. Dev. 48, 1–18.
Hochberg, J., Galper, R.R., 1967. Recognition of faces: an explanatory study. Psychol. Sci. 9, 619–620.
Hole, G.J., 1994. Configurational factors in the perception of unfamiliar faces. Perception 23, 65–74.
Itier, R.J., Taylor, M.J., 2002. Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. NeuroImage 15, 353–372.
Itier, R.J., Taylor, M.J., 2004. Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. NeuroImage 21, 1518–1532.
Jacques, C., d'Arripe, O., Rossion, B., 2007. The time course of the face inversion effect during individual face discrimination. J. Vis. 7, 1–9.
Jacques, C., Rossion, B., Volfart, A., Brissart, H., Colnat-Coulbois, S., Maillard, L., Jonas, J., 2020. The neural basis of rapid unfamiliar face individuation with human intracerebral recordings. NeuroImage, 117174.
Jeffreys, D.A., 1996. Evoked potential studies of face and object processing. Vis. Cogn. 3, 1–38.
Jemel, B., Pisani, M., Calabria, M., Crommelinck, M., Bruyer, R., 2003. Is the N170 for faces cognitively penetrable? Evidence from repetition priming of mooney faces of familiar and unfamiliar persons. brain Res. Cogn. brain Res. 17 (2), 431–446.
Jemel, B., Coutya, J., Langer, C., Roy, S., 2009. From upright to upside-down presentation: a spatio-temporal ERP study of the parametric effect of rotation on face and house processing. BMC Neurosci. 10, 100.
Jenkins, R., Dowsett, A.J., Burton, A.M., 2018. How many faces do people know? Proc. Biol. Sci. 285 (1888), 20181319.
Jiang, F., Dricot, L., Blanz, V., Goebel, R., Rossion, B., 2009. Neural correlates of shape and surface reflectance information in individual faces. Neuroscience 163, 1078–1091.
Jonas, J., Rossion, B., 2021. Intracerebral electrical stimulation to understand the neural basis of human face identity recognition. Eur. J. Neurosci. 54, 4197–4211.
Kaas, J., 2014. The evolution of the visual system in primates. N. Vis. Neurosci. 2.
Kanwisher, N., 2025. Animal models of the human brain: successes, limitations, and alternatives. Curr. Opin. Neurobiol. 90, 102969.
Kay, R.F., Ross, C., Williams, B.A., 1997. Anthropoid origins. Science 275, 797–804.
Keating, C.F., Keating, E.G., 1993. Monkeys and mug shots: cues used … face recognition in the rhesus monkey. Neuropsychologia 17, 503–509.
Keller, C.J., Davidesco, I., Megevand, P., Lado, F.A., Malach, R., Mehta, A.D., 2017. Tuning face perception with electrical stimulation of the fusiform gyrus. Hum. brain Mapp. 38, 2830–2842.
Khöler, W., 1940. Dynamics in psychology. Livelight, New York.
Kret, M.E., Tomonaga, M., 2016. Getting to the bottom of face processing. Species-specific inversion effects for faces and behinds in humans and chimpanzees (Pan troglodytes). PloS One 11 (11), e0165357.
Kuskowski, M.A., Pardo, J.V., 1999. The role of the fusiform gyrus in successful encoding of face stimuli. NeuroImage 9, 599–610.
Laurence, S., Mondloch, C.J., 2016. That's my teacher! children's ability to recognize personally familiar and unfamiliar faces improves with age. J. Exp. Child Psychol. 143, 123–138.
Laurent, M.A., Audurier, P., De Castro, V., Gao, X., Durand, J.B., Jonas, J., Rossion, B., Cottereau, B.R., 2023. Towards an optimization of functional localizers in non-human primate neuroimaging with (fMRI) frequency-tagging. NeuroImage 270, 119959.
Lavallée, M.M., Gandini, D., Rouleau, I., Vallet, G.T., Joannette, M., Kergoat, M.-J., Busigny, T., Rossion, B., Joubert, S., 2016. A qualitative impairment in face perception in alzheimer's disease: evidence from a reduced face inversion effect. J. Alzheimer's. Dis. 51, 1225–1236.
Lawrence, K., Bernstein, D., Pearson, R., Mandy, W., Campbell, R., Skuse, D., 2008. Changing abilities in recognition of unfamiliar face photographs through childhood and adolescence: performance on a test of non-verbal immediate memory (Warrington RMF) from 6 to 16 years. J. Neuropsychol. 2, 27–45.
Le Grand, R., Mondloch, C.J., Maurer, D., Brent, H.P., 2001. Neuroperception. Early visual experience and face processing. Nature 410, 890.

Leder, H., Carbon, C.C., 2006. Face-specific configural processing of relational information. Br. J. Psychol. 97 (Pt 1), 19–29. *London, England:* 1953.
Leopold, D.A., Rhodes, G., 2010. A comparative view of face perception. J. Comp. Psychol. 124, 233–251.
Leopold, D.A., Bondar, I.V., Giese, M.A., 2006. Norm-based face encoding by single neurons in monkey infero-temporal cortex. Nature 442, 572–575.
Lewis, M.B., Edmonds, A.J., 2003. Face detection: mapping human performance. Perception 32 (8), 903–920.
Liu-Shuang, J., Norcia, A.M., Rossion, B., 2014. An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. Neuropsychologia 52, 57–72.
Liu-Shuang, J., Ales, J., Rossion, B., Norcia, A.M., 2015. Separable effects of inversion and contrast-reversal on face detection thresholds and response functions: a sweep VEP study. J. Vis. 15 (2), 11.
Mazard, A., Schiltz, C., Rossion, B., 2006. Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex. Neuropsychologia 44, 912–922.
McCarthy, G., Puce, A., Gore, J.C., Allison, T., 1997. Face-specific processing in the human fusiform gyrus. J. Cogn. Neurosci. 9, 605–610.
McKelvie, S.J., 1995. Encoding operations and recognition memory for faces. Can. J. Exp. Psychol. 49, 437–459.
McNeil, J.E., Warrington, E.K., 1991. Prosopagnosia: a reclassification. Q. J. Exp. Psychol. A Hum. Exp. Psychol. 43, 267–287.
Megreya, A.M., Burton, A.M., 2006. Unfamiliar faces are not faces: evidence from a matching task. Mem. Cogn. 34, 865–876.
Moeller, S., Crapse, T., Chang, L., Tsao, D.Y., 2017. The effect of face patch microstimulation on perception of faces and objects. Nat. Neurosci. 20, 743–754.
Mondloch, C.J., Le Grand, R., Maurer, D., 2002. Configural face processing develops more slowly than featural face processing. Perception 31, 553–566.
Murphy, J., Gray, K.L.H., Cook, R., 2020. Inverted faces benefit from whole-face processing. Cognition 194, 104105.
Murray, J.E., Yong, E., Rhodes, G., 2000. Revisiting the perception of upside-down faces. Psychol. Sci. 11 (6), 492–496.
Neiworth, J.J., Hassett, J.M., Sylvester, C.J., 2007. Face processing in humans and new world monkeys: the influence of experiential and ecological factors. Anim. Cogn. 10, 125–134.
Norcia, A.M., Appelbaum, G., Ales, J., Cottereau, B., Rossion, B., 2015. The Steady-State visual evoked potential in vision research: a review. J. Vis. 15 (6), 1–46, 4.
Overman, W.H., Doty, R.W., 1982. Hemispheric specialization displayed by man but not macaques for analysis of faces. Neuropsychologia 20, 113–128.
Parr, L.A., 2011. The evolution of face processing in primates. Philos. T R. Soc. B 366, 1764–1777.
Parr, L.A., Heintz, M., 2008. Discrimination of faces and houses by rhesus monkeys: the role of stimulus expertise and rotation angle. Anim. Cogn. 11, 467–474.
Parr, L.A., Winslow, J.T., Hopkins, W.D., 1999. Is the inversion effect in rhesus monkeys face-specific? Anim. Cogn. 2, 123–129.
Parr, L.A., Winslow, J.T., Hopkins, W.D., deWaal, F.B.M., 2000. Recognizing facial cues: individual recognition in chimpanzees (*pan troglodytes*) and rhesus monkeys (*macaca mulatta*). J. Comp. Psychol. 114, 47–60.
Parr, L.A., Heintz, M., Pradhan, G., 2008. Rhesus monkeys (*macaca mulatta*) lack expertise in face processing. J. Comp. Psychol. 122, 390–402.
Parron, C., Fagot, J., 2008. Baboons (Papio papio) spontaneously process the first-order but not second-order configural properties of faces. Am. J. Primatol. 70, 415–422.
Pascalis, O., Bachevalier, J., 1998. Face recognition in primates: a cross-species study. Behav. Process. 43, 87–96.
Pascalis, O., Damon, F., Guo, K., Méary, D., 2021. It takes one to know one: do human and nonhuman primates share similar face processing? Comp. Cogn. Common. Divers. 55–66.
Passingham, R., 2009. How good is the macaque monkey model of the human brain? Curr. Opin. Neurobiol. 19, 6–11.
Pavlova, M.A., Romagnano, V., Fallgatter, A.J., Sokolov, A.N., 2020. Face pareidolia in the brain: impact of gender and orientation. PloS One 15 (12), e0244516.
Perrett, D.I., Rolls, E.T., Caan, W., 1982. Visual neurones responsive to faces in the monkey temporal cortex. Exp. Brain Res. 47, 329–342.
Perrett, D.I., Smith, P.A., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., Jeeves, M. A., 1984. Neurones responsive to faces in the temporal cortex: studies of functional organization, sensitivity to identity and relation to perception. Hum. Neurobiol. 3, 197–208.
Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., et al., 1985. Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc. R. Soc. B 223, 293–317.
Perrett, D.I., Mistlin, A.J., Chitty, A.J., Smith, P.A.J., Potter, D.D., Broennimann, R., Harries, M.H., 1988. Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction timc studics. Behav. Brain Res. 29, 245–258.
Perrett, D.I., Oram, M.W., Ashbridge, E., 1998. Evidence accumulation in cell populations responsive to faces: an account of generalisation of recognition without mental transformations. Cognition 67 (1-2), 111–145.
Phelps, M.T., Roberts, W.A., 1994. Memory for pictures of upright and inverted primate faces in humans (Homo sapiens), squirrel monkeys (Saimiri sciureus), and pigeons (Columba livia). J. Comp. Psychol. 108, 114–125.
Piepers, D.W., Robbins, R.A., 2012. A review and clarification of the terms "holistic," "configural," and "relational" in the face perception literature. Front. Psychol. 3, 559.
Pineda, J.A., Nava, C., 1993. Event-related potentials in macaque monkey during passive and attentional processing of faces in a priming paradigm. Behav. brain Res. 53, 177–187.
Pinsk, M.A., Arcaro, M., Weiner, K.S., Kalkus, J.F., Inati, S.J., Gross, C.G., Kastner, S., 2009. Neural representations of faces and body parts in macaque and human cortex: a comparative fMRI study. J. Neurophysiol. 101, 2581–2600.
Pokorny, J.J., Webb, C.E., de Waal, F.B., 2011. An inversion effect modified by expertise in capuchin monkeys. Anim. Cogn. 14, 839–846.
Poltoratski, S., Kay, K., Finzi, D., Grill-Spector, K., 2021. Holistic face recognition is an emergent phenomenon of spatial processing in face-selective regions. Nat. Commun. 12, 4745.
Prete, G., Marzoli, D., Tommasi, L., 2015. Upright or inverted, entire or exploded: right-hemispheric superiority in face recognition withstands multiple spatial manipulations. PeerJ 3, e1456.
Preuss, T.M., 2000. Taking the measure of diversity: comparative alternatives to the model-animal paradigm in cortical neuroscience. Brain Behav. Evol. 55, 287–299.
Quian Quiroga, R., Boscaglia, M., Jonas, J., Rey, H.G., Yan, X., Maillard, L., Colnat-Coulbois, S., Koessler, L., Rossion, B., 2023. Single neuron responses underlying face recognition in the human midfusiform face-selective cortex. Nat. Commun. 14, 5661.
Regan, D., 1966. Some characteristics of average Steady-State and transient responses evoked by modulated light. Electro Clin. Neurophysiol. 20, 238–248.
Regan, D., 1989. London: chapman and hall; New York. Evoked Potentials in Psychology, Sensory Physiology and Clinical Medicine, 3rd edition. Wiley, p. 328.
Retter, T.L., Jiang, F., Webster, M., Michel, C., Schiltz, C., Rossion, B., 2021. Varying stimulus duration reveals consistent neural activity and behavior for human face individuation. Neuroscience 472, 138–156.
Rhodes, G., Brake, S., Atkinson, A.P., 1993. What's lost in inverted faces? Cognition 47, 25–57.
Rhodes, G., Hayward, W.G., Winkler, C., 2007. Expert face coding: configural and component coding of own-race and other-race faces. Psychon. Bull. Rev. 13, 499–505.
Riesenhuber, M., Jarudi, I., Gilad, S., Sinha, P., 2004. Face processing in humans is compatible with a simple shape-based model of vision. Proc. Biol. Sci. 271 (6), S448–S450.
Rilling, J.K., Seligman, R.A., 2002. A quantitative morphometric comparative analysis of the primate temporal lobe. J. Hum. Evol. 42, 505–533.
Rogers, D., Baseler, H., Young, A.W., Jenkins, R., Andrews, T.J., 2022. The roles of shape and texture in the recognition of familiar faces. Vis. Res. 194, 108013.
Rolls, E.T., 1984. Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. Hum. Neurobiol. 3, 209–222.
Rolls, E.T., 1992. Neurophysiological mechanisms underlying face processing within and beyond the temporal cortical area. Philos. Trans. R. Soc. Lond. B335 11–21.
Rosenfeld, S.A., Van Hoesen, G.W., 1979. Face recognition in the rhesus monkey. Neuropsychologia 17, 503–509.
Rosenthal, G., Sporns, O., Avidan, G., 2017. Stimulus dependent dynamic reorganization of the human face processing network. Cereb. cortex 27, 4823–4834.
Rossion, B., 2008. Picture-plane inversion leads to qualitative changes of face perception. Acta Psychol. 128, 274–289.
Rossion, B., 2009. Distinguishing the cause and consequence of face inversion: the perceptual field hypothesis. Acta Psychol. 132, 300–312.
Rossion, B., 2014. Understanding face perception by means of human electrophysiology. Trends Cogn. Sci. 18, 310–318.
Rossion, B., 2018. Humans are visual experts at unfamiliar face recognition. Trends Cogn. Sci. 22, 471–472.
Rossion, B., 2022. Twenty years of investigation with the case of prosopagnosia PS to understand human face identity recognition. Part II: neural basis. Neuropsychologia 173, 108279.
Rossion, B., Boremanse, A., 2008. Nonlinear relationship between holistic processing of individual faces and picture-plane rotation: evidence from the face composite illusion. J. Vis. 8, 1–13.
Rossion, B., Boremanse, A., 2011. Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. J. Vis. 11 (2), 1–21, 16.
Rossion, B., Jacques, C., 2008. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. NeuroImage 39, 1959–1979.
Rossion, B., Jacques, C., 2011. The N170: understanding the time-course of face perception in the human brain. In: Luck, S., Kappenman., E. (Eds.), The Oxford Handbook of ERP Components. Oxford University Press, pp. 115–142.
Rossion, B., Taubert, J., 2019. What can we learn about human individual face recognition from experimental studies in monkeys? Vis. Res. 157, 142–158.
Rossion, B., Delvenne, J.-F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., Guerit, J.-M., 1999. Spatio-temporal brain localization of the face inversion effect. Biol. Psychol. 50, 173–189.
Rossion, B., Gauthier, I., Tarr, M.J., Despland, P.A., Bruyer, R., Linotte, S., Crommelinck, M., 2000. The N170 occipito-temporal component is enhanced and delayed to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. Neuroreport 11, 69–74.
Rossion, B., Prieto, E., Boremanse, A., Kuefner, D., Van Belle, G., 2012. A steady-state visual evoked potential approach to individual face perception: effect of face inversion, contrast-reversal, and temporal dynamics. NeuroImage 63, 1585–1600.
Rossion, B., Retter, T.L., Liu-Shuang, J., 2020. Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. Eur. J. Neurosci. 52, 4283–4344.
Rossion, B., Jacques, C., Jonas, J., 2024. The anterior fusiform gyrus: the ghost in the cortical face machine. Neurosci. Biobehav. Rev. 158, 105535.
Roumazeilles, L., Eichert, N., Bryant, K.L., Folloni, D., Sallet, J., Vijayakumar, S., Foxley, S., Tendler, B.C., Jbabdi, S., Reveley, C., Verhagen, L., Dershowitz, L.B., Guthrie, M., Flach, E., Miller, K.L., Mars, R.B., 2020. Longitudinal connections and

the organization of the temporal cortex in macaques, great apes, and humans. PLoS Biol. 18 (7), e3000810.
Russell, R., Biederman, I., Nederhouser, M., Sinha, P., 2007. The utility of surface reflectance for the recognition of upright and inverted faces. Vis. Res. 47, 157–165.
Sadeh, B., Yovel, G., 2010. Why is the N170 enhanced for inverted faces? An ERP competition experiment. NeuroImage 53 (2), 782–789.
Sawamura, H., Orban, G.A., Vogels, R., 2006. Selectivity of neuronal adaptation does not match response selectivity: a single-cell study of the FMRI adaptation paradigm. Neuron 49, 307–318.
Schiltz, C., Rossion, B., 2006. Faces are represented holistically in the human occipito-temporal cortex. NeuroImage 32, 1385–1394.
Schiltz, C., Sorger, B., Caldara, R., Ahmed, F., Mayer, E., Goebel, R., Rossion, B., 2006. Impaired face discrimination in acquired prosopagnosia is associated with abnormal response to individual faces in the right middle fusiform gyrus. Cereb. Cortex 16, 574–586.
Schneider, B.L., DeLong, J.E., Busey, T.A., 2007. Added noise affects the neural correlates of upright and inverted faces differently. J. Vis. 7 (4), 4.
Schwarzer, G., 2000. Development of face processing: the effect of face inversion. Child Dev. 71, 391–401.
Schweinberger, S., Pfutze, E.M., Sommer, W., 1995. Repetition priming and associative priming of face recognition: evidence from Event-Related potentials. J. Exp. Psychol. Learn. Mem. Cogn. 21, 722–736.
Schweinberger, S.R., Neumann, M.F., 2016. Repetition effects in human ERPs to faces. Cortex a J. devoted Study Nerv. Syst. Behav. 80, 141–153.
Schweinberger, S.R., Pickering, E.C., Burton, A.M., Kaufmann, J.M., 2002. Human brain potential correlates of repetition priming in face and name recognition. Neuropsychologia 40 (12), 2057–2073.
Schweinberger, S.R., Huddy, V., Burton, A.M., 2004. N250r: a face-selective brain response to stimulus repetitions. Neuroreport 15 (9), 1501–1505.
Searcy, J.H., Bartlett, J.C., 1996. Inversion and processing of component and spatial-relational information in faces. J. Exp. Psychol. Hum. Percept. Perform. 22, 904–915.
Sekuler, A.B., Gaspar, C.M., Gold, J.M., Bennett, P.J., 2004. Inversion leads to quantitative, not qualitative, changes in face processing. Curr. Biol. 14, 391–396.
Sekunova, A., Barton, J.J., 2008. The effects of face inversion on the perception of long-range and local spatial relations in eye and mouth configuration. J. Exp. Psychol. Hum. Percept. Perform. 34, 1129–1135.
Sergent, J., 1984. An investigation into component and configural processes underlying face perception. Br. J. Psychol. 75, 221–242.
Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing. A positron emission tomography study. Brain 115 (Pt 1), 15–36.
Shen, C., Stasch, J., Velenosi, L., Madipakkam, A.R., Edemann-Callesen, H., Neuhaus, A. H., 2017. Face identity is encoded in the duration of N170 adaptation. Cortex 86, 55–63.
Sliwa, J., Duhamel, J.R., Pascalis, O., Wirth, S., 2011. Spontaneous voice-face identity matching by rhesus monkeys for familiar conspecifics and humans. Proc. Natl. Acad. Sci. USA 108, 1735–1740.
Sugase-Miyamoto, Y., Matsumoto, N., Ohyama, K., Kawano, K., 2014. Face inversion decreased information about facial identity and expression in face-responsive neurons in macaque area TE. J. Neurosci. 34, 12457–12469.
Swartz, K.B., 1983. Species discrimination in infant pigtail macaques with pictorial stimuli. Dev. Psychobiol. 16, 219–231.
Tanaka, J.W., Farah, M.J., 1993. Parts and wholes in face recognition. Q. J. Exp. Psychol. 46A, 225–245.
Tanaka, J.W., Sengco, J.A., 1997. Features and their configuration in face recognition. Mem. Cogn. 25, 583–592.
Taubert, J., Qureshi, A.A., Parr, L.A., 2012. The composite face effect in chimpanzees (*pan troglodytes*) and rhesus monkeys (*macada mulatta*). J. Comp. Psychol. 126, 339–346.
Taubert, J., Van Belle, G., Vanduffel, W., Rossion, B., Vogels, R., 2015a. The effect of face inversion for neurons inside and outside fMRI-defined face-selective cortical regions. J. Neurophysiol. 113, 1644–1655.
Taubert, J., Van Belle, G., Vanduffel, W., Rossion, B., Vogels, R., 2015b. Neural correlate of the thatcher face illusion in a monkey face-selective patch. J. Neurosci. 35, 9872–9878.
Taubert, J., Van Belle, G., Vogels, R., Rossion, B., 2018. The impact of stimulus size and orientation on individual face coding in monkey face-selective cortex. Sci. Rep. 8 (1), 10339. https://doi.org/10.1038/s41598-018-28144-z.
Thompson, P., 1980. Margaret thatcher: a new illusion. Perception 9, 483–484.
Tomonaga, M., 1994. How laboratory-raised Japanese monkeys (*macada fuscata*) perceive rotated photographs of monkeys: evidence for an inversion effect. Primates 35, 155–165.
Tomonaga, M., 1999. Inversion effect in perception of human faces in a chimpanzee (Pan troglodytes). Primates 40, 417–438.
Tomonaga, M., 2018b. Familiarity and Face-Inversion effect in Japanese macaques (Macaca fuscata) during the preferential looking task. bioRxiv, 267716.
Tomonaga, M., 2018a. Inverted face with upright body: further evidence for face inversion effect in Japanese macaques (Macaca fuscata). BIORXIV, 266676. https://doi.org/10.1101/266676.
Towler, J., Eimer, M., 2016. Electrophysiological evidence for parts and wholes in visual face memory. Cortex 83, 246–258.
Tsao, D.Y., Freiwald, W.A., Tootell, R.B., Livingstone, M.S., 2006. A cortical region consisting entirely of face-selective cells. Science 311, 670–674.
Valentine, T., 1988. Upside-down faces: a review of the effect of inversion upon face recognition. Br. J. Psychol. 79, 471–491.
Van Belle, G., de Graef, P., Verfaillie, K., Busigny, T., Rossion, B., 2010. Whole not hole: expert face recognition requires holistic perception. Neuropsychologia 48, 2609–2620.
Van Belle, G., Lefevre, P., Rossion, B., 2015. Face inversion and acquired prosopagnosia reduce the size of the perceptual field of view. Cognition 136, 403–408.
Vermeire, B.A., Hamilton, C.R., 1998. Inversion effect for faces in split-brain monkeys. Neuropsychology 36, 1003–1014.
Vermeire, B.A., Hamilton, C.R., Erdmann, A.L., 1998. Right-hemispheric superiority in split-brain monkeys for learning and remembering facial discriminations. Behav. Neurosci. 112, 1048–1061.
Vizioli, L., Rousselet, G.A., Caldara, R., 2010. Neural repetition suppression to identity is abolished by other-race faces. Proc. Natl. Acad. Sci. USA 107, 20081–20086.
Volfart, A., Rossion, B., 2024. The neuropsychological evaluation of face identity recognition. Neuropsychologia 198, 10886.
Weibert, K., Harris, R.J., Mitchell, A., Byrne, H., Young, A.W., Andrews, T.J., 2016. An image-invariant neural response to familiar faces in the human medial temporal lobe. Cortex 84, 34–42.
Weiner, K.S., Zilles, K., 2016. The anatomical and functional specialization of the fusiform gyrus. Neuropsychologia 83, 48–62.
Weiss, D.J., Kralik, J.D., Hauser, M.D., 2001. Face processing in cotton-top tamarins (Saguinus oedipus). Anim. Cogn. 3, 191–205.
Weldon, K.B., Taubert, J., Smith, C.L., Parr, L.A., 2013. How the thatcher illusion reveals evolutionary differences in the face processing of primates. Anim. Cogn. 16, 691–700.
White, M., 1999. Representation of facial expressions of emotion. Am. J. Psychol. 112, 371–381.
Wiese, H., Ingram, B.T., Elley, M.L., Tüttenberg, S.C., Burton, A.M., Young, A.W., 2019. Later but not early stages of familiar face recognition depend strongly on attentional resources: evidence from event-related brain potentials. Cortex 120, 147–158.
Wiese, H., Popova, T., Lidborg, L.H., Burton, A.M., 2024. The temporal dynamics of familiar face recognition: Event-related brain potentials reveal the efficient activation of facial identity representations. Int. J. Psychophysiol. 204, 112423.
Wilhelm, O., Herzmann, G., Kunina, O., Danthiir, V., Schacht, A., Sommer, W., 2010. Individual differences in perceiving and recognizing faces-One element of social cognition. J. Personal. Soc. Psychol. 99, 530–548.
Wilmer, J.B., Germine, L., Chabris, C.F., Chatterjee, G., Gerbasi, M., Nakayama, K., 2012. Capturing specific abilities as a window into human individuality: the example of face recognition. Cogn. Neuropsychol. 29, 360–392.
Wirth, B.E., Fisher, K., Towler, J., Eimer, M., 2015. Facial misidentifications arise from the erroneous activation of visual face memory. Neuropsychologia 77, 387–399.
Wright, A.A., Roberts, W.A., 1996. Monkey and human face perception: inversion effects for human faces but not for monkey faces or scenes. J. Cogn. Neurosci. 8, 278–290.
Yamada, E., Takeda, A., Nakazono, H., Tanaka, M., Ogata, K., Tobimatsu, S., 2025. How the brain differentiates human and monkey faces: neuromagnetic evidence from spatiotemporal dynamics. Neuroscience 565, 80–90.
Yan, X., Rossion, B., 2020. A robust neural familiar face recognition response in a dynamic (periodic) stream of unfamiliar faces. Cortex 132, 281–295.
Yan, X., Zimmermann, F., Rossion, B., 2020. An implicit neural familiar face identity recognition response across widely variable natural views in the human brain. Cogn. Neurosci. 21, 1–14.
Yin, R.K., 1969. Looking at upside-down faces. J. Exp. Psychol. 81, 141–145.
Young, A., Bruce, V., 2024. Face Perception, Second Edition. Routledge, Abingdon, UK, p. 462.
Young, A.W., Ellis, H.D., 1989. Handbook of research on face processing. PO Box 103, 1000AC. Elsevier Science Publishers, Amsterdam.
Young, A.W., Hellawell, D., Hay, D.C., 1987. Configural information in face perception. Perception 16, 747–759.
Young, M.P., Yamane, S., 1992. Sparse population coding of faces in the inferotemporal cortex. Science 29, 1327–1331.
Yovel, G., 2009. The shape of facial features and the spacing among them generate similar inversion effects: a reply to rossion (2008). Acta Psychol. 132, 293–299.
Yovel, G., Freiwald, W.A., 2013. Face recognition systems in monkey and human: are they the same thing? *f1000*. Prime Rep. 5, 10.
Yovel, G., Kanwisher, N., 2005. The neural basis of the behavioral face-inversion effect. Curr. Biol. 15, 2256–2262.
Zimmermann, F.G., Eimer, M., 2013. Face learning and the emergence of view-independent face recognition: an event-related brain potential study. Neuropsychologia 51, 1320–1329.