

ORIGINAL ARTICLE

Socio-cognitive, expertise-based and appearance-based accounts of the other-‘race’ effect in face perception: A label-based systematic review of neuroimaging results

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Abstract

Two competing theories explain the other-‘race’ effect (ORE) either by greater perceptual expertise to same-‘race’ (SR) faces or by social categorization of other-‘race’ (OR) faces at the expense of individuation. To assess expertise and categorization contributions to the ORE, a promising—yet overlooked—approach is comparing activations for different other-‘races’. We present a label-based systematic review of neuroimaging studies reporting increased activity in response to OR faces (African, Caucasian, or Asian) when compared with the SR of participants. Hypothetically, while common activations would reflect general aspects of OR perception, ‘race’-preferential ones would represent effects of ‘race’-specific visual appearance. We find that several studies report activation of occipito-temporal and midcingulate areas in response to faces across different other-‘races’, presumably due to high demand on the visual system and category processing. Another area reported in response to all OR faces, the caudate nucleus, suggests the involvement of socio-affective processes and behavioural regulation. Overall, our results support hybrid models—both expertise and social categorization contribute to the ORE, but they provide little evidence for reduced motivation to process OR faces. Additionally, we identify areas preferentially responding to specific OR faces, reflecting effects of visual appearance.

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KEYWORDS

atlas-based review, face perception, fMRI, label-based review, neuroimaging, other-race effect, own-race bias, perceptual expertise, racial bias, social categorization, systematic review, visual appearance

Practitioner points

- We performed a systematic, label-based review of neuroimaging findings on 27 studies. We identified both (1) brain regions that show increased responses to all other—'race' faces, and (2) brain regions that seem to respond preferentially to specific other—'race' faces.
- The regions responding to faces of all other—'races' suggest that these stimuli require visual effort and elicit categorical and socio-affective processing, in line with hybrid models of the other—'race' effect.
- The regions responding preferentially to faces of individual other—'races' suggest specific appearance and/or stereotype effects.

INTRODUCTION**The concept of 'race' and the other-'race' effect in face memory**

Despite its extensive use in public discourse and everyday language, the concept of 'race'¹ has been challenged as lacking scientific foundation (Jablonski & Chaplin, 2010; Kohn, 1995; Reich, 2018; Sinha et al., 2006) and genetic evidence in particular (Tishkoff & Kidd, 2004). As a result, 'race as a biological theory fails' (Anemone, 2015, p. 193). However, this does not mean that effects of the variation of human appearance on behaviour and cognition are negligible. Indeed, people automatically categorize others, often based on visual appearance (Macrae & Bodenhausen, 2000), and this profoundly shapes social behaviour (Cottom, 2009; Hourihan et al., 2013; Howard & Rothbart, 1980; McKone et al., 2021; Paladino & Castelli, 2008). One robust and well-known effect in visual face recognition is the so-called 'other-race effect' (ORE), which is defined as the difficulty to memorize and recognize faces of people who are perceived as belonging to a different 'race' (Bothwell et al., 1989; Malpass & Kravitz, 1969; Meissner & Brigham, 2001; Singh et al., 2021), accompanied by the sensation that other-'race' (OR) faces 'all look the same'. The ORE has been explained in several ways, spanning from hypotheses about physiognomic homogeneity in other-'races' (Chiroro & Valentine, 1995), to observers' racial attitudes (Meissner & Brigham, 2001). In general, these explanations fall into two broad groups of theories that can be framed as either perceptual or socio-cognitive (or hybrid, see [Discussion](#)).

Perceptual expertise theories frame differences between a given face and an observer's perceptual norm, or prototype, as crucial for the ORE (Caldara & Abdi, 2006; Valentine & Endo, 1992). According to influential representational models of multidimensional 'face space' (Valentine, 1991; Valentine et al., 2016), OR faces are remembered poorly because they strongly deviate from a mental prototype acquired through long term exposure to same-'race' (SR) faces (Goldstein & Chance, 1980). Crucially, although distance-to-norm makes SR faces more distinctive and recognizable, OR faces all deviate from the norm in the same direction, making their categorization easy (other 'race' classification advantage, ORCA) but their individual recognition difficult (Valentine, 1991; Zhao & Bentin, 2011). Conversely, *socio-cognitive theories* assume that categorization of a face into an 'outgroup' is crucial (Bernstein et al., 2007; Shriver et al., 2008)—the ORE could be a consequence of category-(mis)driven attention, reduced motivation, or both. In

¹The term 'race' is enclosed in quotation marks throughout this paper, following the reasoning given in the main text, and in line with the title of this Special Issue.

the first hypothesis, perceivers resort to categorical encoding at the cost of individuation of OR faces (Levin, 1996, 2000). Accordingly, one pays attention to category-diagnostic (e.g., 'white woman') rather than identity-diagnostic information (e.g., 'Angela Merkel') (Correll et al., 2017). Following the reduced motivation hypothesis, OR faces are processed more poorly than SR faces because they are perceived as part of an outgroup, thus eliciting intergroup biases (Hewstone et al., 2002), low motivation to remember them (Bernstein et al., 2007; Brebner et al., 2011), and reduced empathic and mentalizing responses (Molenberghs & Louis, 2018).

Thus, in perceptual expertise theories, OR faces are difficult to recognize because one's perceptual system is not calibrated on them. Instead, in socio-cognitive theories, they are recognized poorly because less cognitive resources are invested in them. In other words, in the first case people *can't* recognize OR faces as accurately as SR faces, in the second case they simply *don't* (Levin, 2000).

Functional neuroimaging of other-'race' face processing

Functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), which indirectly measure neuronal activity by contrasting changes in metabolic signals to different task conditions (Raichle, 2009), are widely used to investigate how 'race' is processed in the brain. Numerous studies compared brain activation when processing OR and SR faces, using multiple methods and paradigms (for reviews, see Amodio, 2014; Chekroud et al., 2014; Ito & Bartholow, 2009; Kubota et al., 2012; Mattan et al., 2018; Molenberghs & Louis, 2018; Natu & O'Toole, 2013). Fewer studies have specifically tried to pin down the neural signature of the ORE with fMRI by targeting recognition memory (Brown et al., 2017; Golarai et al., 2020; Golby et al., 2001; Liu et al., 2015), reporting variable evidence for or against the two theories described above. Neural measures of the ORE can be modulated by previous exposure and OR contact quality (Cao et al., 2015; Farmer et al., 2020; Hughes, Babbitt, et al., 2019; Walker et al., 2008, but see He et al., 2009), but also by racial prejudice (Beer et al., 2008; Brosch et al., 2013; Golarai et al., 2020; He et al., 2009). Thus, neural responses to OR faces and their link to these psychological variables seem potentially compatible with both perceptual expertise and socio-cognitive accounts. However, even after extensive research, it remains difficult to evaluate their respective contributions, as detailed below.

Different hypotheses, different methodological choices

As described by Natu and O'Toole (2013), neuroimaging studies tend to divide into those focusing on socio-cognitive aspects and those focusing on visual processing. This divide is expressed in the specific effects targeted—but also in methodological choices, such as experimental manipulations, or restriction of analyses to certain brain regions. For instance, researchers primarily concerned with socio-cognitive aspects tend to recruit participants of different 'races' (e.g., Cassidy & Krendl, 2016; Cunningham et al., 2004; Hehman et al., 2014; Norton et al., 2013; Phelps et al., 2000; Stolier & Freeman, 2017). Conversely, researchers interested in visual processing of OR faces tend to use racially homogeneous groups or to assess contact levels with one particular OR (e.g., Brosch et al., 2013; Cloutier et al., 2014; Feng et al., 2011; Kim et al., 2006; Natu & O'Toole, 2011; Ratner et al., 2013; but see Ng et al., 2006). Therefore, when evaluating these two groups of studies together, the effects of visual expertise and familiarity between them may not be easily comparable.

Similarly, different regions of interest (ROIs) are typically chosen *a priori* within the two lines of research based on theoretical assumptions about those regions. One striking example is the amygdala: Researchers focussing on the amygdala often assume that it responds to salient social stimuli (Hart et al., 2000), emotional relevance (Lieberman et al., 2005; Phelps et al., 2000; Sankar et al., 2018) or threatening/aversive stimuli (McCutcheon et al., 2018). As such, interpretations proposed in these cases tend to prioritize socio-affective over perceptual processes, e.g., social/emotional relevance (Hart et al., 2000; Phelps et al., 2000) or acquired associations (Lieberman et al., 2005), instead of, say, 'novelty'. In other studies of this kind, ROIs are based on socio-affective tasks, such as mentalizing (Cassidy

et al., 2021). Conversely, perception researchers tend to choose ROIs based on passive observation tasks (Hughes, Camp, et al., 2019), on effects of face > rest (Ratner et al., 2013), or on face localizers (Golby et al., 2001; Kim et al., 2019; Liu et al., 2015; Natu et al., 2011). When considering brain activation to OR faces as a proxy to understand the ORE, one should be mindful about these choices.

Studies targeting neural correlates of the ORE

An evaluation of neuroimaging studies against the main theoretical accounts of the ORE is challenging, even for studies which target neural correlates of the ORE explicitly. For example, Brown et al. (2017) asked participants to memorize SR and OR faces and recorded BOLD signals during a delayed recall task. They found that reduced engagement of parietal components of the cognitive control network predicted unsuccessful retrieval of OR faces, whereas increased connectivity of the dorsal attentional network with the fusiform gyrus (FG) predicted successful retrieval of SR faces. Liu et al. (2015) found a trade-off in neural responses: OR faces are harder to recognize and elicit more activity in regions encoding face identity (FFA, OFA), whereas SR faces are harder to categorize and engage different regions like the pSTS. Similarly, Feng et al. (2011) also report that categorizing SR (compared with OR) faces requires more neural engagement. Although the authors interpret their findings in terms of differential perceptual expertise, exposure for that OR was invariably reported absent. Together, while indicators of more superficial encoding of OR faces may be seen as favouring socio-cognitive mechanisms (Hugenberg et al., 2010; Levin, 2000), contributions of expertise remain open.

Other studies targeting neural effects of 'race' on face memory are consistent with this possibility. An early study investigating the ORE with fMRI (Golby et al., 2001) reported larger FFA responses to SR faces, and showed that both FFA and parahippocampal activity correlated with memory differences between OR and SR. According to the authors, these differences could be due to reduced perceptual expertise with OR faces. Several electrophysiological studies suggest that OR faces require more effortful perceptual processing. For instance, OR faces undergo increased configural processing, and elicits a *larger* early occipito-temporal N170 response in the event-related potential (Stahl et al., 2008; Wiese et al., 2012; Wiese & Schweinberger, 2018). Herzmann et al. (2018) observed that disrupted holistic processing of SR faces elicited effects comparable to those observed with OR faces during encoding, suggesting that OR faces are processed less holistically. Other studies highlight the difference of OR faces to one's perceptual norm, eliciting decreased P200 component, as distinctive SR faces do (Lucas et al., 2011; Stahl et al., 2008; Wuttke & Schweinberger, 2019). Together, these results may stress the importance of perceptual expertise for the ORE.

Finally, one fMRI study seems to support both hypotheses. Golarai et al. (2020) investigated the relationship between 'race' perception during an n-back task and a separate recognition task across different age groups. Their results indicate that the SR processing advantage increases with age, with increased activity in the FFA, higher recognition performance and stronger implicit associations as participants grow older. This indicates that 'social and perceptual experiences shape a protracted development of race effects in face processing' (Golarai et al., 2020, p. 17). Overall, neuroimaging evidence for expertise and social categorization accounts is in line with electrophysiological evidence for both (early) expertise and (later) social evaluation processes (Walker et al., 2008).

Findings within single studies can be difficult to interpret

Even at the level of individual studies, interpretations endorsed by the authors might still be challenged. For instance, Cao et al. (2015) report increased ACC activity for observed SR (compared with OR) faces which were undergoing painful stimulation. Lower pain empathy for OR faces might seem in line with socio-cognitive theories. Intriguingly, for OR faces, this neural empathic activation of the ACC also increased with the level of contact observers reported to this OR. This effect was related to mere everyday exposure, and not closeness of personal contact, which instead seems consistent with perceptual expertise theories. Conversely, another study reported reduced amygdala responses to OR faces in partic-

ipants with more OR exposure during childhood, when compared with participants with less exposure (Cloutier et al., 2014). Although the authors explain this effect in terms of perceptual expertise (p. 2002), childhood interracial contact reduced amygdala responses for familiar, but not for unfamiliar OR faces, which instead could suggest that factors beyond mere expertise for the OR category were present as well. Such factors could include ingroup biases (see above) or qualitatively different representations for familiar vs. unfamiliar faces (e.g., robust vs. image-based; Burton et al., 2011; Young & Burton, 2018).

Integrating theories through systematic, between-'races' approach

As reviewed above, comparing two lines of studies contrasting OR with SR faces is arduous for multiple reasons. Despite considerable progress in understanding the nature of the ORE in face perception, the heterogeneity of studies remains an important challenge. One possible way forward is to examine activity differences due to 'race' (OR > SR faces) in the whole brain, aggregating across studies. This would even out any methodological disparity and disregard interpretation idiosyncrasies (Müller et al., 2017). In this direction, Bagnis et al. (2020) performed an extensive neuroimaging meta-analysis on 'race' perception, considering studies with SR and OR stimuli (bodies, hands, complex scenes and faces). Their convergence analysis revealed one common region for SR and OR perception (the striatum), and several regions specific to either SR (left insula/inferior frontal gyrus and medial frontal gyrus) or OR perception (right FG, left middle occipital gyrus, right amygdala, left inferior parietal lobule and right insula). With respect to possible mechanisms behind the ORE, these findings leave open important questions. First, Bagnis et al. investigated the perception of OR individuals, not exclusively of their faces. Regarding the ORE in face processing, aggregating studies that compare OR and SR faces specifically would be more informative. Second, since the authors included both main effects and correlations with measures of racial prejudice, their convergence results might reflect a mix of pure 'race' perception and racial bias. Evaluating the respective contribution of perceptual and socio-cognitive processes to the ORE would benefit from a specific focus on the main effect of OR faces across studies.

Importantly, previous research generally neglected potential differences between different OR faces at the neural level, by including only one OR in each study. We regard this as a critical gap, since behavioural evidence for comparable OR effects (Singh et al., 2021) does not permit to conclude that the ORE involves the same neural mechanisms for all OR faces. Direct comparisons between neural responses to different ORs exist only occasionally (He et al., 2009; Losin et al., 2014; Reynolds Losin et al., 2012; Zhou et al., 2020), with inconsistent and incomplete findings (with the possible exception of Zhou et al., 2020).

In this label-based review, we present the first systematic comparison between brain responses to different OR faces across neuroimaging studies. Crucially, unlike the meta-analysis by Bagnis et al. (2020), our work specifically addresses the processing of OR *faces*, focusing on the main effect of OR > SR face perception in the available neuroimaging literature. For systematic comparison between ORs, we collected data about the perception of three OR subgroups—African, Caucasian² and Asian. Here, common activation regions across OR subgroups would represent general effects of OR face perception. The specific pattern of these common regions would then be suggestive of the degree to which the major theories of the ORE receive indirect support. Note that we do not investigate neural correlates of the ORE directly. Rather, we consider effects of perceiving OR faces as a proxy to understand which mechanisms may accompany the ORE, which is defined as a face memory effect.

Specifically, if OR faces require high visual effort due to low perceptual expertise, we would expect to find regions that respond to visual load, domain-specific visual expertise, or faces. These include occipito-temporal areas (Martens et al., 2018; Song & Jiang, 2006), especially the FG, as related to visual expertise and face processing (Duchaine & Yovel, 2015; Gauthier et al., 2000; Rossion et al., 2003; Xu, 2005). Instead, socio-cognitive theories predict that OR faces are categorized as outgroup members,

²Note that we use the term 'Caucasian' in this paper for ease of communication and cross-referencing with published work. We alert the reader to the fact that this term has a problematic history and its current use still can have adverse consequences, including in patient identification in medical care (e.g., Rambachan, 2018).

preventing individuation. Thus, regions commonly associated to categorical processing would be more supportive of the socio-cognitive account. Specifically, visual categories independently of shape similarities are represented in the lateral occipitotemporal cortices (Kaiser et al., 2016), and the ventral temporal cortex seems to discriminate visual categories (Jacques et al., 2016; Margalit et al., 2020; van den Hurk et al., 2017). Finally, regions responding preferentially to individual OR subgroups should inform us about the effects of ‘race’-specific *visual appearance* effects for that subgroup. Per default, and reflecting much of the existing OR research, we expected to find similar brain activations to OR faces across subgroups. However, because of idiosyncrasies in the appearance of each subgroup, we also considered the possibility of finding regions that would be predominantly responsive to each OR subgroup.

MATERIALS AND METHODS

Literature search and selection

We performed a systematic search of potentially eligible articles on several online public databases. We searched on Pubmed and Web of Science to retrieve peer-reviewed works, and on Google Scholar to locate potentially eligible grey literature works. We decided to inspect also unpublished data in order to minimize selection bias on our results (Jennings & Van Horn, 2012), as suggested by recent guidelines (Siddaway et al., 2019). Moreover, we consulted the reference section of a recently published neuroimaging meta-analysis (Bagnis et al., 2020). We also hand-searched the reference lists of some review articles that did not overlap with those examined in the meta-analysis by Bagnis et al. (Ito & Bartholow, 2009; Molenberghs & Louis, 2018). For database search, we used the search terms (*race OR racial bias OR own-race bias OR ethnicity OR other-race effect OR racial categorization*) AND (*fMRI OR functional MRI OR PET OR positron emission tomography imaging*)[TOPIC] on Web of Science (for analogous search queries in other databases, see Appendix S1). The literature search ended in January 2021. After an initial screening phase, we applied several selection criteria. These were in line with recent and widely accepted guidelines for neuroimaging meta-analyses (Müller, Cieslik, et al., 2018), as no official guidelines of such kind exist for label-based reviews. Articles and related data were included if:

- i. they were written in English;
- ii. they were empirical works. Review articles and meta-analyses were excluded;
- iii. they used fMRI or PET to record brain activity. connectivity results were also excluded, although we contacted some authors to ask for neuroimaging contrasts of interest (OR > SR) they could have potentially analysed;
- iv. they reported coordinates of significant activation in standard stereotaxic space, i.e., Montreal Neurological Institute (MNI) or Talairach and Tournoux (1988) (TAL);
- v. they included a sample of healthy adults. Although perceptual narrowing of face processing for different species begins during the first year of life (Pascalis et al., 2002), with evidence for an ORE emerging in early childhood within the first three years of life (Chien et al., 2018; Macchi Cassia et al., 2014; Pezdek et al., 2003; Suhrke et al., 2015), we decided to exclude children and adolescents up to 15 years, to preserve comparability of different brain data on the same template. In case of age-mixed samples, we conservatively decided to exclude the study. Authors of studies investigating patient samples were contacted to retrieve data from healthy controls; and
- vi. the analysis of neuroimaging data was based on the whole brain. We excluded studies reporting only region of interest analyses or applying a small-volume correction, to avoid bias towards regions typically analysed. Examples that were excluded on this criterion are Golby et al. (2001) and Hughes, Camp, et al. (2019).

The following additional restrictions were applied:

- i. the visual stimuli were faces. We discarded studies using words, symbols, objects, and landscape images. Also, since we are concerned with the processing of 'racial' information from the face only, we excluded several studies with similar research questions using body parts, whole-body or half-length videos/photographs;
- ii. we included studies with a variety of tasks and paradigms, ranging from passive viewing to social categorization and trust games. A complete list of the paradigms included is available in Table S2;
- iii. importantly, we included activation foci if they resulted from a contrast between an other-'race' face, when compared with a SR face, e.g., Caucasian > African in African participants. The brain activity resulted from this contrast reflects the effect of observing an OR face of a specific 'race', when this is different than that of the participants. This means that we excluded contrasts between other-'race' faces and non-face stimuli, and activation foci of the opposite contrast, e.g., African > Caucasian in African participants. We excluded studies reporting no significant OR > SR effects, such as Feng et al. (2011), Idaka et al. (2008), Van Bavel et al. (2011), and Zhou et al. (2018), although these are considered in the Discussion. Authors of studies employing mixed-'race' samples were contacted to ask for unpublished data from separate sub-samples; and
- iv. we only included in the atlas-based analysis main effects obtained via subtraction contrasts. However, we also decided to include one study (Wei et al., 2014, Caucasian subgroup) which implemented an alternative analysis method. Since the outcome of their analysis can be in fact interpreted in a similar way to the other studies, we decided to include it (see Appendix S1).

In general, we contacted authors when criteria (i–x) were fulfilled, but data of interest were unavailable. This could be because the authors did not report whole brain analyses, included only interactions, correlations with other variables, or connectivity analyses, or because authors did not report different sub-samples (e.g., different 'races' or healthy controls) separately. For articles published 2005 or earlier, we did not contact the authors. We did not post any online advertisement to locate unpublished studies. If no response was obtained after three contact attempts or if the requested data remained unavailable, the articles were excluded.

Data extraction and coding

Potentially relevant information about the included studies has been extracted and organized in Table S1 and S2. We coded information about the article, sample description, task/stimuli and data analysis. The contrast name is not reported, as every study included examined the same (*other-'race'* > *own-'race'*), regardless of other variables. We then divided the activation foci in three subgroups, depending on which other-'race' effect they reflected, resulting in three separate groups of studies (African > own, Caucasian > own, Asian > own). Importantly, these different subgroups each contain data collected from participants of different 'races', each of whom perceiving the same other-'race' (Figure 1). We aggregated these data based on the assumption that the ORE is equally present in all these subgroups (for a recent meta-analysis on behavioural data supporting this assumption, see Singh et al., 2021).

Quantitative descriptive analyses

Since the number of studies was insufficient to perform a quantitative meta-analysis in two subgroups out of three (Eickhoff et al., 2016), we opted for a label-based (more specifically, atlas-based) approach (see Laird et al., 2005; Radua & Mataix-Cols, 2012 for an introduction to systematic reviews and meta-analyses of neuroimaging data; see also Appendix S1, p. 18). When compared with standard reviews that are based on authors' original labelling, atlas-based reviews reduce discrepancy between different labels due to authors' wording differences, promoting comparability of results (Laird et al., 2005). First, we converted all foci reported in MNI space to Talairach using the icbm2tal transform (Lancaster et al., 2007) in GingerALE 3.0.2 (brainmap.org; Eickhoff et al., 2009, 2012; Turkeltaub et al., 2012). Then, we submitted the

Data aggregation strategy: example of Caucasian subgroup

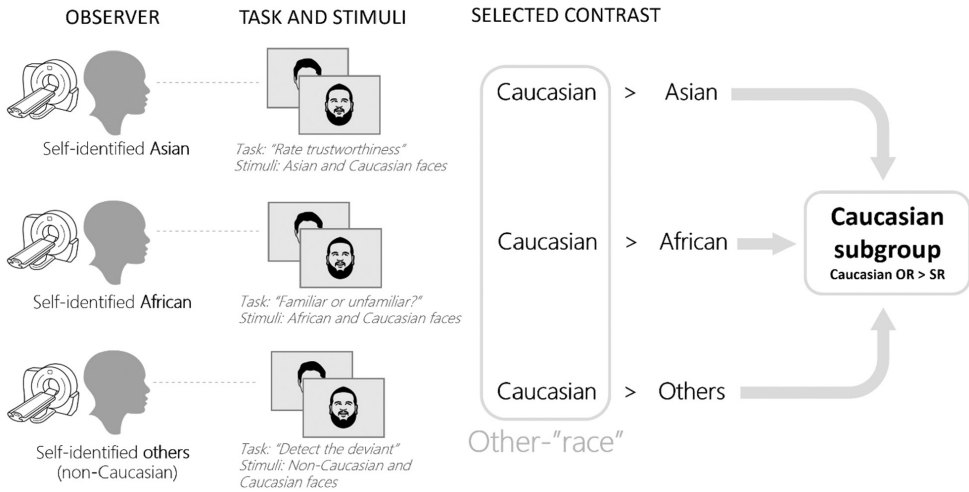


FIGURE 1 A schematic representation of our data aggregation procedure. We identified studies where participants who self-identified as a certain 'race' observed faces from their own and a different 'race'. Within the study, we selected the contrast(s) reflecting the main effect of perceiving the other-'race' against one's own, regardless of conditions and task instructions. We then aggregated the data from contrasts reflecting the same other-'race'. In sum, each OR subgroup contains data reflecting the effect of perceiving that 'race' in participants identifying with a different one.

converted coordinates to the Talairach Daemon, using the 'search nearest grey matter' function to obtain automatic labels for each subgroup (Lancaster et al., 1997, 2000). Subsequently, we performed separate standard descriptive analyses on the subgroups. Similar to previous label-based reviews (Chan et al., 2009; Molenberghs et al., 2012; Phan et al., 2002), we counted the activation foci falling in each brain structure (Table S1), and then assessed the percentage of studies reporting activations in these regions (Figure 3 and Figure S1). Finally, we plotted the reported coordinates on a 3D brain template (Figure 4; Figures S2 and S3), to illustrate exact location of reported activity. Plots were generated using the Matlab-based version of BrainNet Viewer 1.7 (Xia et al., 2013) and the package *ggplot2* in R Studio (R Core Team, 2018). For completeness, we report the results of quantitative meta-analyses in Supporting Information (Table S3), where sufficient power (i.e., at least 17 independent experiments; Eickhoff et al., 2016) permitted, but refrain from interpreting such results.

RESULTS

Literature search and selection

The selection process is shown in Figure 2. Across all sources, we retrieved a total of 10,467 records. The first screening led to the exclusion of many articles published in unrelated fields (e.g., Sociology, Literature and Politics). At this stage, we also discarded several articles including the term 'race' with the meaning of 'competition'. Next, we inspected the abstract and the full-text of the remaining 127 articles, to verify their compliance to our criteria. Of these, 54 articles were discarded because they did not examine the phenomenon of interest. For instance, they experimentally modulated group affiliation with no reference to 'race'. Others were excluded because they did not include face stimuli, fMRI or PET measures, or adult healthy participants. If the contrasts of interest for us were not explicitly reported, we contacted the authors (57 articles). At the time of manuscript writing, unpublished data has been kindly provided for

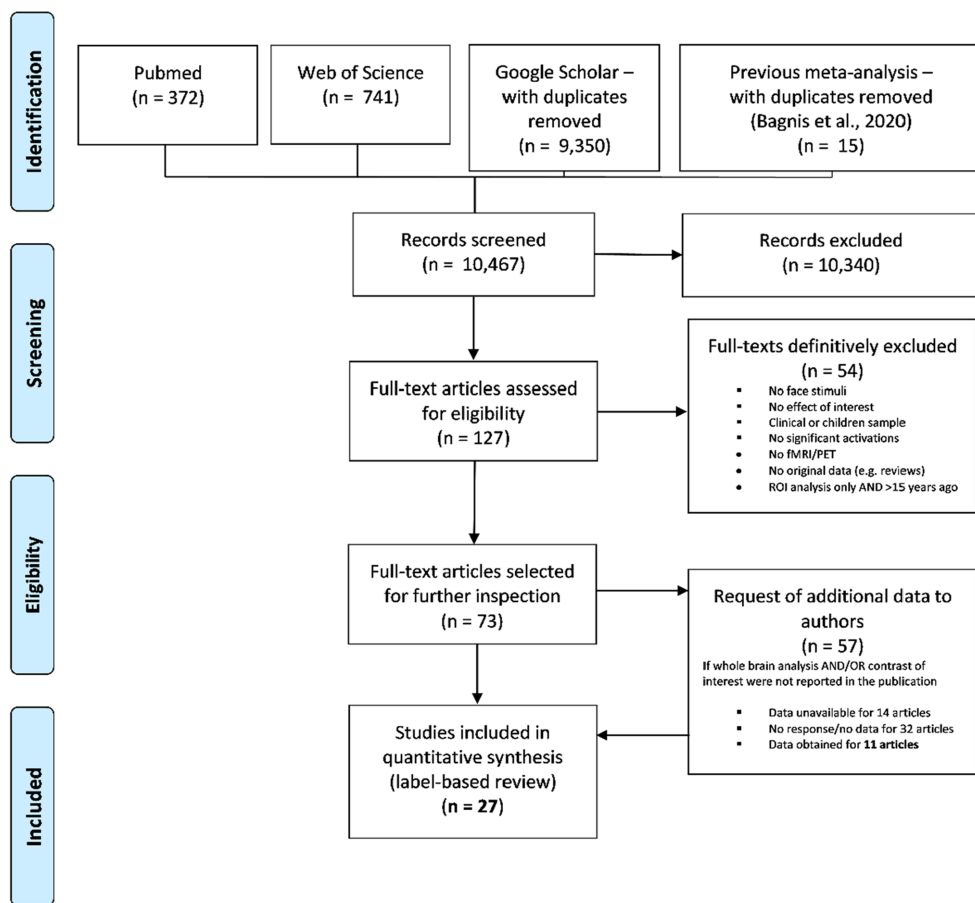


FIGURE 2 PRISMA flowchart illustrating the literature selection process.

11 articles (19.3% of the total requests sent), while for 14 articles data were unavailable (24.6%); for the remaining 56.1%, neither response nor data have been received. Finally, we included 27 articles.

The whole dataset is based on 704 participants (mean age = 25.2; 50.9% female), and 196 activation foci. All of the studies we included use fMRI. Of the included 27 studies, only 10 overlap with those included by Bagnis et al., 2020. As mentioned in the Introduction, this is due to our different research question and, consequently, to more stringent criteria. Importantly, the three subgroups greatly differed in terms of number of articles, participants and reported activation foci (African = 17 studies, Cauca-

TABLE 1 Description of the sample characteristics of the studies included in the present review

Subgroup	No of studies	No of participants	No of foci	Percentage of females (% studies available info)	Mean age (% studies available info)
African > own 'race'	17	439	115	38.7% (82.4%)	25.0 (82.4%)
Caucasian > own 'race'	10	204	63	36.7% (80.0%)	25.4 (80.0%)
Asian > own 'race'	4	136	18	67.1% (100%)	41.4 (75%)
Total	27	704	196	50.9% (92.6%)	25.2 (92.6%)

Note: Note that 75 participants are the same in the African and the Caucasian subgroup for one study (Cassidy et al., 2021), thus the total does not add up to the total number of studies.

TABLE 2 Number of neuroimaging contrasts per task type, for each subgroup separately

	African > own (N = 17)	Caucasian > own (N = 10)	Asian > own (N = 4)	Total (N = 31)
Categorization	6	4	1	11
Observation	6	3	0	9
Rating	1	1	1	3
Memory	2	2	0	4
Mentalizing	2	0	2	4

sian = 10 studies, Asian = 4 studies; Table 1). Special caution is needed when interpreting the results from the Asian subgroup. First, at least five studies are recommended for label-based reviews (Lamsma et al., 2017). Second, samples include many more females than males, and participants are on average

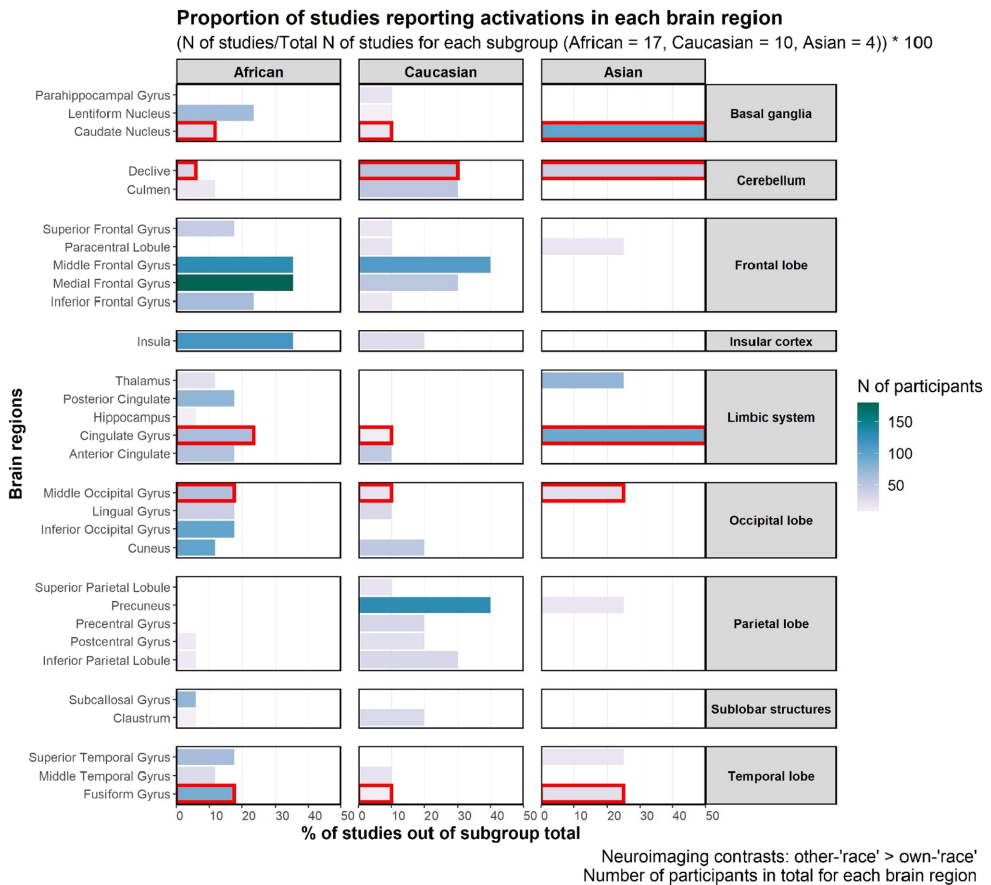


FIGURE 3 Overview of the percentages of studies reporting activation foci for each brain region, in the three subgroups separately. Y axis: brain region labels; X axis: percentage of studies out of the subtotal of each group (with 100% corresponding to 17, 10 and 4 articles for African, Caucasian and Asian, respectively). See Figure S1 for the percentages out of the 27 total studies and Figure S3 for the same plot including studies reporting non-significant findings in each respective subtotal. Colour intensity visually conveys the number of participants representing each brain region, and framed red bars indicate activations that were seen across all three subgroups. Results are grouped by brain macro-region to facilitate the comparison at this level. Only foci falling in defined grey-matter structures are shown. Note that the Asian subgroup contains four studies and can be considered as an outlier in terms of sample characteristics. Thus, the presented proportions in that case should be interpreted with caution.

Activations in response to faces of other-"races"

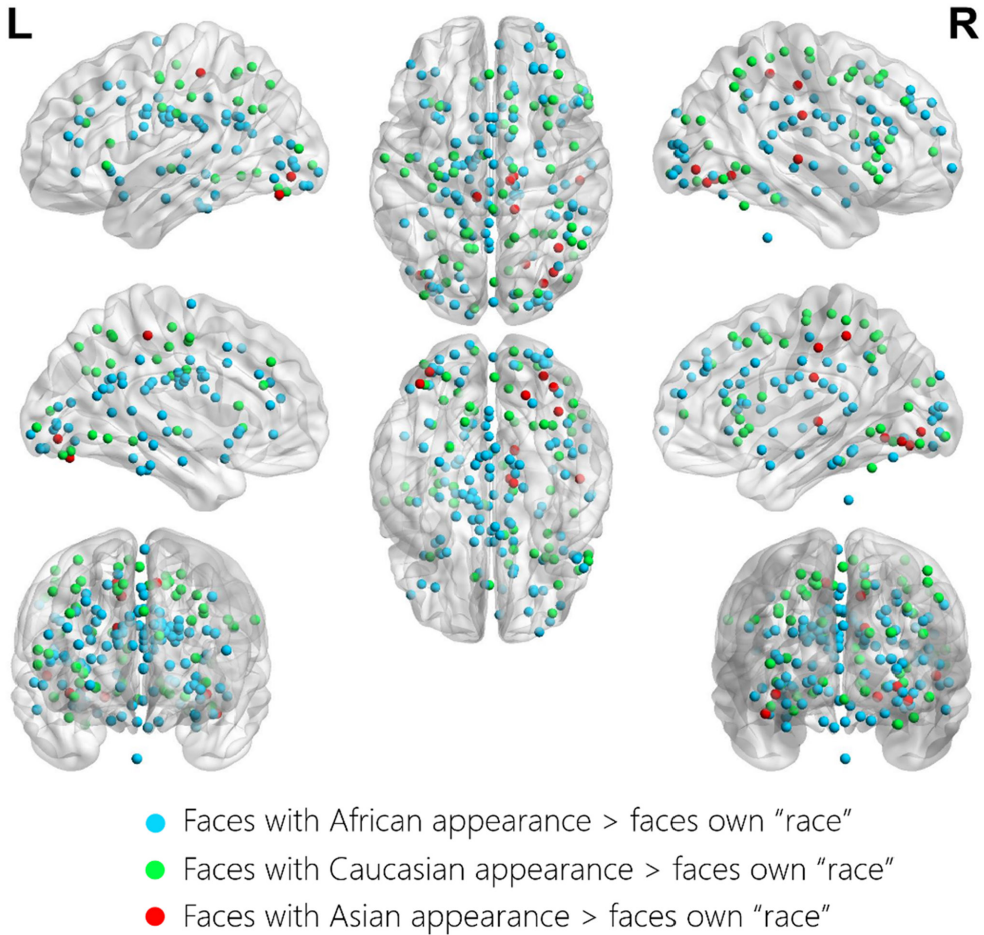


FIGURE 4 Activation foci from the original studies or the authors' data plotted on a 3D brain mesh. Different colours represent different OR subgroups (African OR in blue, Caucasian OR in green, and Asian OR in red). Foci falling outside the cerebrum are also shown (cerebellum and brain stem). See Appendix S1 for a similar figure which visually incorporates the proportions of studies reporting activations in each region (Figure S2). Also see Appendix S1 for a version of this figure with colour-blind friendly colour scales (Figure S3).

older than in the other two subgroups (Table 1). Therefore, besides evaluating the regions in common to all three subgroups, we focus on the Caucasian and African subgroup to assess preferential activations.

Tasks and paradigms in the three subgroups

The tasks used in the original articles varied in complexity and cognitive processes involved (Table 2, more details on Table S2). The most represented paradigms are categorization tasks (of gender, perceived race, or group affiliation) and observation (often combined with a minimal task to ensure attentional engagement). Other tasks included: (i) rating of face similarity and social traits; (ii) memory tasks (n-back tasks, active individuation, familiarity rating or recollection); (iii) mentalizing, empathizing or games involving inferences about others' mental states. Despite the numerical differences between subgroups, the relative frequency of task types seems comparable across the two larger subgroups. The Asian subgroup

is a possible outlier, as it contains more mentalizing tasks, and neither observation nor memory tasks. Task proportions are similar in the two larger subgroups ($\chi^2_{Afr-Cauc}$ (4, $N = 27$) = 1.4, $p = .849$), and all the groups together (χ^2_{all} (8, $N = 32$) = 9.3, $p = .317$), where N = number of contrasts per subgroup (Table S2).

Atlas-based review

Overview of the three subgroups

The proportions of studies reporting activation foci in different brain regions for the three subgroups is plotted in Figure 3, while the distribution of foci across the brain is illustrated in Figure 4. We examined both which regions are reported in all three subgroups and which regions respond preferentially to one OR face type (Table S4). Overall, our results show substantial spatial heterogeneity, with foci falling in a number of different and distant brain regions (also see non-significant ALE results, Table S3). Most studies on African OR faces report activity in frontal regions, such as the middle frontal gyrus (MFG), medial frontal gyrus (MedFG) and inferior frontal gyrus (IFG); other regions include the insulae, the mid-cingulate cortex (MCC), the caudate nucleus, and the middle occipital gyrus (MOG). Caucasian OR faces mostly activate the left precuneus, the MFG and some portions of the cerebellum. Lastly, activity in response to Asian OR faces is mostly reported in the caudate nucleus and the MCC, and to a lesser extent in the thalamus. We show the raw count of foci in the Supporting Information (Table S1).

Brain regions reported across all the three subgroups

Some regions are reported across all the three subgroups: the caudate nucleus (especially in the left hemisphere), the cerebellar declive, the posterior and midcingulate cortex, the MOG and the fusiform gyrus (FG). Notably, none of these common regions are supported by a uniformly high proportion of studies across all subgroups. For instance, all three subgroups report foci in cingulate gyrus, but only one of the 10 studies for the Caucasian subgroup found increased activation there. Also, discussed above, we consider the Asian subgroup as both low-powered and potentially different from the others in terms of task and sample characteristics. The inclusion of studies reporting non-significant findings does not alter this pattern (cf. Figure S3). When only considering the African and Caucasian subgroups, we find greater overlap in the labels (18/31 correspond), albeit again in different proportions (Figure 3 and Figure S1). The regions reported by most studies in both subgroups are the MFG, MedFG, and the anterior insulae.

Differences in brain regions reported between subgroups

Activity in response to African and Caucasian OR faces is predominantly located in several cortical regions, especially involving the frontal lobe. African OR faces seem to preferentially elicit activity in the MFG and the MedFG, but also in paralimbic regions such as the insula. Conversely, activation foci in response to Caucasian OR faces are mostly located in the precuneus and, to a lesser extent, the MFG. As for the Asian subgroup, we refrain from describing any preferential activity pattern due to the low number of studies which render these data exploratory at best.

DISCUSSION

Overview

We performed a systematic, label-based review of published studies reporting (or providing us with) brain responses to OR faces across a variety of experimental paradigms. While previous coordinate-based meta-analyses focused on social structure (Shkurko, 2013) or 'race' in general (Bagnis et al., 2020), our work examines the processing of different 'race' faces with the aim of better understanding the ORE in face recognition. Our design includes the same effects across a variety of paradigms, irrespective of the specific aim of the individual studies, and our results thus reflect main effects of *perceiving* an OR face. Accordingly, any influence of specific task instructions on the present results should be minimal. In the following discussion, we first consider the pattern of observed locations of responses common across the OR subgroups (African, Caucasian, Asian) as informative about the mechanisms underlying the ORE, independent of the type of OR face perceived. Second, a novel observation is the presence of 'race'-preferential brain responses. We hypothesized that these would potentially represent effects of visual appearance.

To put our results into perspective, we observe that several studies that analyzed the OR > SR contrast reported no significant effects (e.g., Feng et al., 2011; Iidaka et al., 2008; Van Bavel et al., 2011; Zhou et al., 2018) and others report decreased brain responses to OR faces (e.g., Golby et al., 2001; Hughes, Babbitt, et al., 2019; Wheeler & Fiske, 2005). Moreover, some studies among those included in our review report results for the opposite contrast, i.e., SR > OR (Cloutier et al., 2014; Cunningham et al., 2004; Kim et al., 2006; Lee et al., 2008; Mattan et al., 2018; Wang et al., 2015). Especially the role of FG in OR perception is complex: while some studies report larger volume of adaptation effects (and therefore less response) to SR compared with OR faces (Hughes, Camp, et al., 2019; Hughes, Babbitt, et al., 2019), others report greater activation in the FFA for SR faces (Golby et al., 2001; Kim et al., 2006; Krosch & Amodio, 2019). Indeed, the recruitment of the FG varies as a function of the individuation effort of participants (Kim et al., 2019). The results by Bagnis et al. (2020) also suggest that FG responses could be lateralized, with the right FG responding to OR faces (cf. figure 2 in Bagnis et al., 2020). However, they also suggest that the FG responds more to OR than to SR and not the opposite direction, which strengthens our interpretations.

Another consideration is that, overall, we observe wide spatial heterogeneity among the reported neural responses across studies, with several regions for which only few studies report activation. The overall activation pattern considering the three OR together does not strongly resemble any well-known large-scale network (cf. Figure 4). This heterogeneity can be due analytic flexibility, specificities of investigated samples, or experimental variation (Müller et al., 2017). We prioritized the similarity between contrasts across studies, but allowed for different tasks while checking that the distribution of tasks was similar between OR subgroups. Thus, the comparison between OR subgroups should be relatively unaffected by task differences. Within subgroups and overall, however, we cannot exclude that some regions could be driven by task specificities, and this may be why these are reported in some specific studies only. In fact, results of activation-based approaches tend to be heavily task-dependent, in the face of the similarity of stimuli across studies (Müller, Cieslik, et al., 2018; Müller, Höhner, et al., 2018). Note that, while we detect no convergence, Bagnis et al. (2020), with a bigger sample which also included non-face stimuli, did. However, this does not imply that there are no neural differences between OR and SR, or that these have no importance.

Regions reported in all OR subgroups

One central finding is that a several regions are found in all three OR subgroups (the MOG, the FG, the declive, the left caudate nucleus, and the MCC), although none of these are uniformly reported by a high proportion of studies across all subgroups and do not converge in any specific region.

Both the FG and the MOG are face-responsive. The FG is a well-known hub in face processing (Haxby et al., 2000; Müller, Cieslik, et al., 2018; Müller, Höhner, et al., 2018), is thought to encode invariant features of faces (Schweinberger & Neumann, 2016) like identity, gender, or ‘race’, and is sensitive to face repetition (Kovács et al., 2013; Summerfield et al., 2008). Both the FG and the MOG respond to cognitive and visual effort in a face perception task (Aben et al., 2020). Furthermore, several studies report responses in the MCC (especially its more posterior portion), which increase with cognitive load when forming visual percepts (Deary et al., 2004), and with image vividness (Fulford et al., 2018). Thus, the FG, MOG and potentially MCC activations might reflect effortful structural encoding when perceiving OR faces, consistent with perceptual expertise theories. Indeed, the ORE may act already at the level of visual working memory (Stelter & Degner, 2018) and to depend on the type of visual stimulation. For instance, static cropped face stimuli elicit stronger ORE than naturalistic movies (Zhao et al., 2014). This supports the idea that the ORE might be caused by an increased visual effort, presumably acting during the encoding of OR faces (Hayward et al., 2013; Walker & Tanaka, 2003).

However, some of the same regions seem to support category processing as well. In fact, MOG activation is also found when perceiving other categories of stimuli, such as bodies (Hummel et al., 2013; van de Riet et al., 2009) and symbols (Barquero et al., 2014; Gates & Yoon, 2005), while the posterior MCC shows increased activity when categorizing > individuating faces (Mason & Macrae, 2004). More evidence about category processing exists for the ventral-temporal cortex, which includes the FG. This region can discriminate not only between object categories (even in congenitally blind individuals, see van den Hurk et al., 2017) but also within categories. In fact, the FG also supports exemplar discrimination (Davidesco et al., 2014; Zachariou et al., 2018) and, importantly, can differentiate between faces of different ‘races’ (Brosch et al., 2013; Stolier & Freeman, 2017). Furthermore patients with right occipital brain damage show impairments in categorization tasks of visual objects (Perez et al., 2013). Therefore, involvement of MOG and FG might also indicate some form of categorical encoding of such faces.

In line with the idea that processes other than visual effort are involved when perceiving OR faces, our results also point to involvement of socio-affective processing and memory. The left caudate for example, is part of the reward system, and is thought to play a major role in the behavioural regulation in social contexts (Graff-Radford et al., 2017; Mason et al., 2009; Wardle et al., 2013) as well as goal-driven behaviour (Cox & Witten, 2019; Haber, 2016; Herrero et al., 2002), more specifically the selection of appropriate behavioural schemata (Grahn et al., 2008). Strikingly, a patient with a focal left caudate lesion also showed impairments both in empathy and theory of mind (Kemp et al., 2013), and a meta-analysis of neural responses to emotional faces reports this region too (Fusar-Poli, Placentino, Carletti, Allen, et al., 2009; Fusar-Poli, Placentino, Carletti, Landi, et al., 2009).

Foci in the cingulate cortex, in turn, might to some extent also support socio-affective processing. However, it must be acknowledged that this is a large region with structurally and functionally different regions (Vogt, 2019), with anterior parts primarily associated to emotion, middle parts to decision making and response selection, and posterior parts to self-referential processing (Vogt, 2019). More specifically, the posterior cingulate cortex (PCC) is commonly known as a hub of the default-mode network (DMN) (Buckner et al., 2008; Buckner & DiNicola, 2019) and has been shown to contribute to autobiographical memory, mentalizing (Schurz et al., 2014; Spreng & Mar, 2012), memory of personally familiar faces and objects (Sugiura et al., 2005) as well as self-relatedness of others (Finlayson-Short et al., 2020). Moreover, its activity increases with memory efforts, as suggested by increased connectivity with the hippocampus (Beckmann, Johansen-Berg, & Rushworth, 2009). Interestingly, different parts of the cingulate gyrus preferentially respond to different OR faces (cf. Figure 4): foci in left posterior and in right anterior portions are reported for African OR faces, left posterior/middle portions for Caucasian OR faces, and middle portions for Asian OR faces. The activation profiles to different OR faces in the cingulate gyrus therefore further indicate that each OR may engage different processes (see following section), which may or not contribute to the ORE in their specific way.

One somewhat unexpected region responding to OR faces is the cerebellar declive. The cerebellum is not typically included in models of face processing, but two previous meta-analyses suggest its role in face perception (Fusar-Poli, Placentino, Carletti, Allen, et al., 2009; Fusar-Poli, Placentino, Carletti, Landi,

et al., 2009; Zinchenko et al., 2018) and another one indicates its sensitivity to 'race' (Bagnis et al., 2020). Zinchenko et al. (2018) hypothesize that this region might work as an updater for facial feature changes, similar to the cerebellar role in the motor domain. As a cautionary note, being close to the FG, its activity might be due to smoothing in the original studies.

Implications of our findings for the ORE

In line with recent conceptualizations (Bagnis et al., 2019; Young et al., 2012), our findings underscore the complexity of 'race' processing. Occipito-temporal activations to OR faces could indicate that OR faces are visually demanding. However, some of the same regions also process visual categories, indicating that OR faces are processed at that level. Other processes (e.g., like mentalizing, behavioural regulation, memory) could eventually accompany the ORE. Thus, our findings seem to provide support for hybrid models (for review, Young & Hugenberg, 2012), rather than any of the two traditional theories. The hybrid categorization-individuation model posits that OR faces are difficult to recognize because they are processed categorically, but both perceptual expertise and motivational/situational factors contribute to OR recognition performance (Hugenberg et al., 2010). When considering common activations, both low expertise (reflected in higher visual effort) and categorical processing (reflected in activation of category-sensitive regions and the DMN) could simultaneously hamper individuation. Then, depending on the task, the OR, and the individual's goals, other regions might contribute socio-affective aspects, not necessarily related to the ORE.

A further interpretation concerning the reduced motivation hypothesis (Bernstein et al., 2007; Hugenberg et al., 2007, 2010; Brebner et al., 2011; but see also Wan et al., 2015) remains open. Although the reviewed data does not seem to support it, we cannot refute this idea completely at present. To test its prediction of attenuated neural responses to OR faces in regions associated with attention and task engagement, it would be necessary to systematically assess the opposite contrast (i.e., SR > OR).³ However, we still put forward a few observations. First, some of these regions we found in response to OR faces of all subgroups, such as the MCC, the caudate and the MFG, are also part of the executive control network (Petersen & Posner, 2012; Shen et al., 2019), which does not suggest reduced engagement while perceiving OR. Second, the recruitment of the MOG, the FG and the PCC could indicate that OR faces elicited increased individuation and memory efforts (Denkova et al., 2006; Elfgrén et al., 2006; Kim et al., 2019; Mason & Macrae, 2004; Nielson et al., 2010). Third, when disregarding the Asian subgroup, the MFG, the MedFG and the insulae are the most frequently reported regions. These are generally involved in high-order cognitive and attentional processes (Chayer & Freedman, 2001; Stuss, 2011). Thus, it arguably is unlikely that, when presented with OR faces, participants' engagement was reduced.

While these frontal activations conform to the meta-analysis by Bagnis et al., 2020, the functional role of these regions in OR face processing—and potentially the ORE—is less clear. The MFG is part of the core network for person recognition, and responds to familiar (or learned) faces as well as voices (Zäske et al., 2017), while the medial PFC might encode stable personal traits (Kovács, 2020). Moreover, activity in these regions may support stereotype suppression (see below). Instead, although the insula has been related to negative prejudice towards outgroup members (Lieberman et al., 2005; Richeson et al., 2003), we suggest that this region could merely support increased saliency of OR faces (Menon & Uddin, 2010).

³The same analysis on the opposite contrast would have highlighted regions that tend to respond to SR faces, across comparisons with different OR faces, i.e. the opposite effect to that studied here. Since the same brain regions cannot be significantly activated for a functional contrast and its opposite simultaneously (with same tasks and participants) we imagine that this analysis would reveal a substantially different pattern, as compared to the one presented here for OR faces. Indeed, Bagnis et al. (2020), who performed a meta-analysis on a conceptually similar contrast, report widely different convergence patterns for OR and SR stimuli. This analysis could further confirm our interpretations about the meaning of our results for the theories of the ORE, for instance by showing that little visual effort is required to process SR faces; but they could also question our claims, e.g. in case they showed a larger engagement of occipito-temporal regions for SR faces, as compared to that for OR faces. The investigation of the contrast SR > OR with a similar method to that used here can be an important research question for future studies.

Regions preferentially responding to faces of different OR

Our second main finding is that African and Caucasian OR faces also seem to preferentially engage different regions. This finding is robust to the inclusion of studies reporting non-significant results (Figure S3). As the subgroups contain similar task proportions (also cf. Table S2), it seems unlikely that such differences reflect task effects. Note that since we merged participants of different ‘races’, it is similarly unlikely that this result reflects ‘race’-specific differences in global face processing styles (Hayward et al., 2013) or in scanning patterns (Blais et al., 2008). Regarding differences between observers of different OR subgroups in socio-economic status and provenance, we provide additional relevant data (where available) in the Supporting Information (Table S2). Although we found no stark differences in our dataset, the reporting of socio-economic status is limited, such that this variable may deserve further research. We hypothesized that the ‘race’-preferential activation profiles could likely be due to an *appearance effect*, in the sense that OR-preferential neural responses are elicited by relatively homogeneous visual representations, OR-preferential stereotypes, or both. So far, these differences between OR faces have been rarely addressed. A notable recent exception is a recent multi-method neuroimaging study, which reports that repetition suppression (RS) occurs in different regions for different ‘races’ (Zhou et al., 2020, cf. Exp. 5a and 5b with Chinese observers). In line with the literature we reviewed, the middle PFC seem to be responsive to African OR faces (together with the PCC, which we found in response to all OR faces). While different regions exhibited RS for Asian *SR* faces, no significant RS effects were found for Caucasian OR faces.

African OR faces mostly engage the anterior insulae, and the MFG and the MedFG. In our dataset, one study reports and discusses the result of the main effect of African OR passive observation (Richeson et al., 2003). Richeson et al. (2003) report activity in the MFG and the insulae, and interpret this as increased recruitment of cognitive control regions, independent of task demands. Apart from the typical regions of face processing (FG, inferior occipital gyrus, amygdala), the MFG also may be part of a network for face processing (Zhang et al., 2009) and face pareidolia (Liu et al., 2014). The MedFG may contribute to the anticipation of future faces (Mechelli et al., 2004), and its role in the extended face network was recently rediscovered (Kovács, 2020). Beyond face sensitivity, we speculate that MedFG activity might reflect down-regulation of stereotypes associated to African facial appearance (Amodio, 2014). Specifically, given awareness about the history of discrimination affecting people of colour (Lavalley & Johnson, 2020), participants might have tried to inhibit stereotype activation when seeing African faces (Forbes et al., 2012; Wheeler & Fiske, 2005). Instead, the anterior insula is a key hub of a network processing salience of stimuli (Seeley et al., 2007; Uddin, 2015). Its activation could indicate that African OR faces automatically capture attention, possibly driven by “race”-defining features (Levin, 2000). Skin pigmentation is a key ‘race’-defining feature for African faces in particular (Stepanova & Strube, 2012). Accordingly, pigmentation/texture information might be particularly helpful for categorizing, but unhelpful for identifying, individual African OR faces. While this idea is in need of empirical data, we note that a recent study suggests no differences in the use of texture/pigmentation information in memorizing Caucasian vs. *Asian* faces (Zhou et al., 2021).

The MFG also responds preferentially to Caucasian OR faces, but activation in the precuneus is far more prevalent. Why the precuneus is predominantly reported within this subgroup is unclear. We tentatively speculate that, since Caucasian faces are internationally well-represented in movies and TV, Caucasian face learning seems plausible for those exposed to such media (Michel et al., 2006; Wang & Zhou, 2016), potentially triggering memory retrieval (Bonni et al., 2015), or mental inferences (Abu-Akel & Shamay-Tsoory, 2011) more than other OR faces.

Limitations

First, although the labelling system in the Talairach Daemon allows to assign brain structure labels without terminological confounds, some of these labels identify rather extended brain regions (e.g., cingulate gyrus). For transparency, we report the raw output of the Talairach Daemon (cf. Appendix S1). Second, despite our efforts to locate unpublished analyses, these were not always available. This is a notorious

problem in systematic research, reflecting low response rate from contacted authors (Manca et al., 2018; Schroll et al., 2013) and uncommon open science practices in the past decades. Another limitation is that several studies tested 'racially mixed' samples, without reporting separate data for relevant subgroups. Thus, even when the data could have been included in principle, we were unable to do so without additional information from authors. The fact that different OR were unequally represented in our dataset also limits a subset of conclusions that could have been derived from the present design in principle. Specifically, we did not discuss in detail the Asian subgroup due to the small number of studies, which is in remarkable contrast to a wealth of EEG studies on Asian OR faces (e.g., Caharel et al., 2011; Caldara et al., 2004; Herrmann et al., 2007; Proverbio & De Gabriele, 2019; Stahl et al., 2008; Vizioli et al., 2010; Wiese et al., 2009). We expect that availability of future Asian OR studies will permit refined conclusions. We also acknowledge potential interpretative issues concerning the use of reverse inferences (Poldrack, 2006), which heavily rely on the literature found (and its biases) and on the assumption of strict structure–function relationships (Klein, 2010). Related to this, we considered the contrast $OR > SR$ as conceptually equivalent in all studies, across different tasks. However, due to low power, we cannot formally test for systematic differences in brain responses between tasks within this contrast. Moreover, our interpretations may be challenged by future studies analysing the opposite contrast. Finally, our findings are neither informative about how the reviewed regions are functionally connected nor about their temporal activation patterns during the perception of OR faces.

CONCLUSIONS

Based on this review, the perception of OR faces involves regions associated with visual expertise, category processing, mentalizing and behavioural regulation, but results also suggest a degree of OR-preferential activity profiles. Our findings are broadly consistent with the view that the ORE is related to visual expertise, categorical processing, and socio-affective processes. Accordingly, hybrid models of the ORE are likely to capture the phenomenon, although the idea that OR faces are poorly encoded due to low motivation was not supported. We consider OR-preferential brain responses as effects of the visual appearance of each racial subgroup. In particular, regions associated with stimulus-driven attention and cognitive control were especially engaged for African OR faces. Instead, regions associated with mentalizing and self-referential processing were involved in Caucasian OR face perception. We expect that future studies focusing on differences between different OR faces will shed further light on the neglected role of visual appearance for the ORE.

AUTHOR CONTRIBUTIONS

Linda Ficco: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; visualization; writing – original draft. **Veronika I. Müller:** Methodology; supervision; visualization; writing – review and editing. **Jürgen M. Kaufmann:** Conceptualization; supervision; visualization; writing – review and editing. **Stefan R. Schweinberger:** Conceptualization; investigation; methodology; project administration; supervision; visualization; writing – review and editing.

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Open Science Framework repository at: <https://osf.io/n8mt9/>. A selection of this additional information is already included in the Supporting Information files.

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