



Functional neuroanatomy of racial categorization from visual perception: A meta-analytic study

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ABSTRACT

We effortlessly sort people into different racial groups from their visual appearance and implicitly generate racial bias affecting cognition and behavior. As these mental activities provide the proximate mechanisms for social behaviours, it becomes essential to understand the neural activity underlying differences between own-race and other-race visual categorization. Yet intrinsic limitations of individual neuroimaging studies, owing to reduced sample size, inclusion of multiple races, and interactions between races in the participants and in the displayed visual stimuli, dampens generalizability of results. In the present meta-analytic study, we applied multimodal techniques to partly overcome these hurdles, and we investigated the entire functional neuroimaging literature on race categorization, therefore including more than 2000 Black, White and Asian participants. Our data-driven approach shows that own- and other-race visual categorization involves partly segregated neural networks, with distinct connectivity and functional profiles, and defined hierarchical organization. Categorization of own-race mainly engages areas related to cognitive components of empathy and mentalizing, such as the medial prefrontal cortex and the inferior frontal gyrus. These areas are functionally co-activated with cortical structures involved in auto-biographical memories and social knowledge. Conversely, other-race categorization recruits areas implicated in, and functionally connected with, visuo-attentive processing, like the fusiform gyrus and the inferior parietal lobule, and areas engaged in affective functions, like the amygdala. These results contribute to a better definition of the neural networks involved in the visual parcelling of social categories based on race, and help to situate these processes within a common neural space.

1. Introduction

Social categorization is probably the most widely investigated process by social psychologists (Allport, 1954; Tajfel et al., 1979; Macrae and Bodenhausen, 2000; Tajfel, 1970). It is believed to reflect a natural tendency to sort the world into categories that “provide maximum information with the least cognitive effort” (Rosch, 1978). In the case of other people, such categorization appears inevitable and activates stereotypes and attitudes that influence social behavior, as we tend to spontaneously categorize others as members of social groups and to behave accordingly (Dovidio et al., 1997; Macrae and Bodenhausen, 2000; Tajfel, 1970). Social categories, such as age, gender or race, are

typically conveyed by visual traits that are primarily displayed in the face and perceived effortlessly (i.e. eye shape, jaw’s size, skin colour or body shape) (Freeman and Johnson, 2016; Celeghin et al., 2017; Costa et al., 2014; Freeman and Johnson, 2016; Ito and Urland, 2005; Negro et al., 2015; Van Bavel and Cunningham, 2011).

Intergroup bias denotes the systematic tendency to prefer an in-group over an out-group member, and is a major consequence of the social categorization (Hewstone et al., 2002). The integration of bottom up visual cues and top-down social factors seems pivotal in generating intergroup biases, particularly racial bias, as visual perception and behavioural responses depend on the interaction between the group membership of the observer and the stimulus characteristics (Bagnis

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et al., 2019; Van Bavel and Cunningham, 2011; Correll et al., 2015; Craig et al., 2012; Hu et al., 2017; Hugenberg and Bodenhausen, 2004). For example, individuals tend to show more accurate or faster face recognition, better recall, and to have more prosocial behaviors toward in-group than out-group members, whereas out-group faces tend to be perceived more homogeneously (Elfenbein and Ambady, 2002; Hewstone et al., 2002). Racial bias is a specific instance of intergroup bias and refers to the tendency to categorize people according to racial cues, and to behave differently with same-versus other-race individuals (Walker and Hewstone, 2006). In prior literature on racial bias, as well as throughout this paper, the terms “same-race”, “same-group”, “own-race” and “in-group” are used interchangeably to indicate people who belong to the same race (e.g. both White), and vice-versa.

Racial bias is affected by rather basic visual attributes (e.g. skin colour or typical facial features), and by attitudes and prejudices, owing to higher-order cognitive processes and social factors. On the one hand, own-race faces are perceived and recognized more accurately and faster than other-race faces because of familiarity with some physical facial features (Elfenbein and Ambady, 2002; Walker and Hewstone, 2006). Also, emotional expressions displayed by own-race faces tend to cause a more coherent reaction and to induce greater affective physiological responses, such as facial mimicry and skin conductance (Brown et al., 2006; van der Schalk et al., 2011). On the other hand, visual perception of, and attention to, racial stimuli seem to be facilitated by stereotypical associations, e.g. between anger and Black men (Dickter et al., 2015; Trawalter et al., 2008), danger and Black people (Correll et al., 2007, 2015; Eberhardt et al., 2004), or contextual elements such as face-body compounds and low-vs. high-status attire (Freeman et al., 2011).

In recent years, a number of studies have investigated the neural correlates of racial bias using functional magnetic resonance imaging (fMRI) (Kubota et al., 2012). Some of these studies have focused primarily on visual aspects of race perception, others delved into the socio-emotional component or looked at higher-order cognitive processes shaping race perception. Specifically, research focusing on differences in visual encoding have shown greater activations in fusiform and occipital areas for own-race faces when the faces were unfamiliar (Kim et al., 2006), and in individuals with stronger implicit racial bias (Brosch et al., 2013), thereby suggesting a greater involvement of sensory regions when processing own-race than other-race stimuli (Feng et al., 2011; Golby et al., 2001; Natu et al., 2011). Analysis of the socio-emotional factors revealed that other-race face perception is correlated with greater amygdala activity, indicative of enhanced emotional responses to out-group members owing to the link between racial prejudice and affective reactions (Cottrell and Neuberg, 2005; Cunningham et al., 2004; Forbes et al., 2012; Hart et al., 2000; Lieberman et al., 2005; Phelps et al., 2000; Richeson et al., 2008; Ronquillo et al., 2007; Stanley et al., 2008; Wheeler and Fiske, 2005). Moreover, activity in the amygdala is also associated implicit measures of out-group bias, including the eyeblink startle index (Phelps et al., 2000) and reaction-time scores on the Implicit Association Test (Cunningham et al., 2004; Greenwald et al., 1998; Krill and Platek, 2009; Phelps et al., 2000).

Studies addressing higher-order cognitive processes involved in race perception report anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (dlPFC) activity, and interpreted the findings as suggesting a role on these regions in conflict monitoring and inhibition of prejudice towards other-race stimuli, respectively (Forbes et al., 2012; Knutson et al., 2007; Richeson et al., 2003). Furthermore, greater activity in a neural network encompassing medial prefrontal cortex (mPFC), ACC and insula (INS) has been observed in response to own-race faces, especially in painful contexts, suggesting a greater role of empathic processes during in-group than out-group perception (Azevedo et al., 2013; Cheon et al., 2011; Contreras-Huerta et al., 2013; Freeman et al., 2010; Harris and Fiske, 2006; Wang et al., 2014; Xu et al., 2009; Zuo and Han, 2013).

Current inconsistencies in the areas involved in same- and other-race categorization dampens generalizability of results, and previous summaries of published studies have provided valuable, but qualitative,

reviews of the reported activation sites. Coordinate-based Meta-analytic approaches to neuroimaging data have become increasingly important to complement individual studies and contribute to partly overcome these limitations, as they offer a valuable tool to synthesize quantitatively the functional neuroanatomy of a given phenomenon in a common space. This can be achieved by filtering-out idiosyncrasies of individual studies, owing to a variety of task demands, difficulties in the inclusion and balancing of multiple races, as well as their interactions with the experimental stimuli, thus contributing to the unbiased identification of convergent brain activations across specific results (Eickhoff et al., 2009; Fox et al., 2014). Moreover, this data-driven neural taxonomy can be further qualified investigating long-range connections with functionally co-activated areas, their clustering and hierarchical organization, and the primary contribution of underlying cognitive dimensions to same-vs. other-race categorization.

The present study provides the first quantitative meta-analysis of the available neuroimaging literature, involving more than 2000 healthy participants of 3 different races (Black, White, Asian). Our aim was to delineate with a bottom-up meta-analytical framework the neural fingerprint of areas involved in race bias, thereby revealing convergent and divergent areas engaged in same-vs. other-race visual categorization. In fact, racial categorization largely rests on the primacy of visual traits, like skin colour or eyes shape, that we can “read-out” effortlessly as reliably indicators of racial membership. Accordingly, the wide majority of the literature sampled race bias using visual stimuli; a focus reflected also in the present study. Additional analyses assessed the behavioural profile of regions identified in the ALE meta-analysis through the functional decoding of each of these structures across the largest-scale database of fMRI studies (i.e. BrainMap; Lancaster et al., 2012). Finally, we profiled the functional connectivity of structures involved in same- and other-race categorization with the rest of the brain using a Meta-Analytic Connectivity Modeling (MACM) (Laird et al., 2009), and we examined their intrinsic organization and hierarchical clustering. This enabled us to shift the focus from individual structures to inter-regional connectivity patterns, which is a more plausible approach to study how complex functions such as intergroup categorization map into brain activity.

2. Methods

2.1. Literature search and study selection

We performed a systematic literature search in several databases and search engines, including Google Scholar, PubMed and Scopus using specific keywords such as “race”, “racial bias”, “racial categorization”, “intergroup” combined with “fMRI”, “functional MRI”, “neuroimaging” to identify peer-reviewed neuroimaging studies. Moreover, articles were also identified from a previous meta-analysis (Shkurko, 2013), other reviews (Bagnis et al., 2019; Mattan et al., 2018; Amodio, 2014; Chekroud et al., 2014; Molenberghs, 2013; Natu and O’Toole, 2013) and by searching through the reference lists and citation indices of studies obtained during the initial search. The literature search ended in June 2019. Then, articles were assessed according to the following inclusion criteria, previously established as best-practice recommendations for neuroimaging meta-analyses (Muller et al., 2018):

- 1) Only fMRI studies were included, while MEG, EEG, TMS and connectivity studies were excluded.
- 2) Results had to be based on whole brain analyses, while studies based on region of interest (ROI) analyses were excluded to avoid inflated significance and overrepresentation of a-priori selected brain areas.
- 3) Only studies reporting neural activations in a standard stereotaxic template (i.e. Talairach and Tournoux or MNI) were included.
- 4) Only tasks using visual stimuli were included.
- 5) Studies had to investigate specifically racial categorization (e.g. not cultural or social differences), thus reporting comparisons that

distinguished between same- and other-group categorization based on race.

- 6) Only studies on healthy adult participants were included, whereas studies including only children or patients with neurological or psychiatric disorders were excluded.

According to these inclusion/exclusion criteria, a total of 57 fMRI studies were finally selected for the meta-analysis (Fig. 1).

2.2. Study categorization and extraction of coordinates

Firstly, we organized a database to code the information extracted from each article, including sample description (sample size, average age, gender distribution, sample race), experimental setting (type of paradigm, contrast details, stimulus categories, stimulus race, task instruction) and MRI data (coordinates, numbers of foci, fMRI design and analysis). The overall meta-analysis on intergroup perception consisted of 94 experiments, 1072 foci across 2071 subjects. Subsequently, we performed two separated meta-analyses categorizing all the information according to interaction between the group membership of the subjects included in the sample and that displayed in the visual stimuli (e.g. in-group categorization in case of White participants exposed to White people stimuli, out-group categorization in case of White participants presented with Black people stimuli, and so on; see Tables 1 and 2). We extracted the brain coordinates of significant peak activations, as reported in each study and contrast, relative to same-group or other-group perception. Specifically, 51 experimental contrasts (including a total of 489 foci) across 1162 subjects were included in the same-group meta-analysis. The other-group meta-analysis included 43 experimental contrasts (involving a total of 583 foci) across 909 subjects.

2.3. Meta-analyses

2.3.1. Activation likelihood estimation (ALE)

Data were examined according to a quantitative voxel-wise meta-analysis of 57 neuroimaging studies on racial bias. We used an approach based on coordinates, i.e. the revised activation likelihood estimation (ALE) algorithm, to estimate on each voxel the probability of regional brain activations (Eickhoff et al., 2012, 2009, Tatu et al., 2018; Turkeltaub et al., 2012, 2002).

Because of its high anatomical precision, this approach allows to evaluate the consistent activations from the statistically significant foci reported in the same standard stereotaxic space (Laird et al., 2010). These activation foci are considered as the centre of a 3D Gaussian probability distribution to create a Modeled Activation (MA) map for each study weighted for sample size (Eickhoff et al., 2009; Turkeltaub et al., 2012). Then, the ALE maps across all the experiments are calculated and compared with a null-distribution in order to control the noise through a random-effect analysis. The resulting nonparametric p -value maps were then thresholded at Cluster-Level $p < 0.05$ (Eickhoff et al., 2012), with 1000 threshold permutations for uncorrected $p < 0.001$.

All the statistical analyses were performed with the GingerALE software (version 2.3.6, <http://www.brainmap.org/ale/>). The meta-analysis results were overlaid onto a standard anatomical template and displayed using MRICroGL (<http://www.mccauslandcenter.sc.edu/mricrogl/>).

2.3.2. Functional decoding

In order to evaluate the cognitive-functional roles of brain regions characterizing same-group and other-group perception, we conducted a functional analysis using the Behavior Analysis 2.2 plug-in in Mango Software (http://ric.uthscsa.edu/mango/plugin_behavioralanalysis.html).

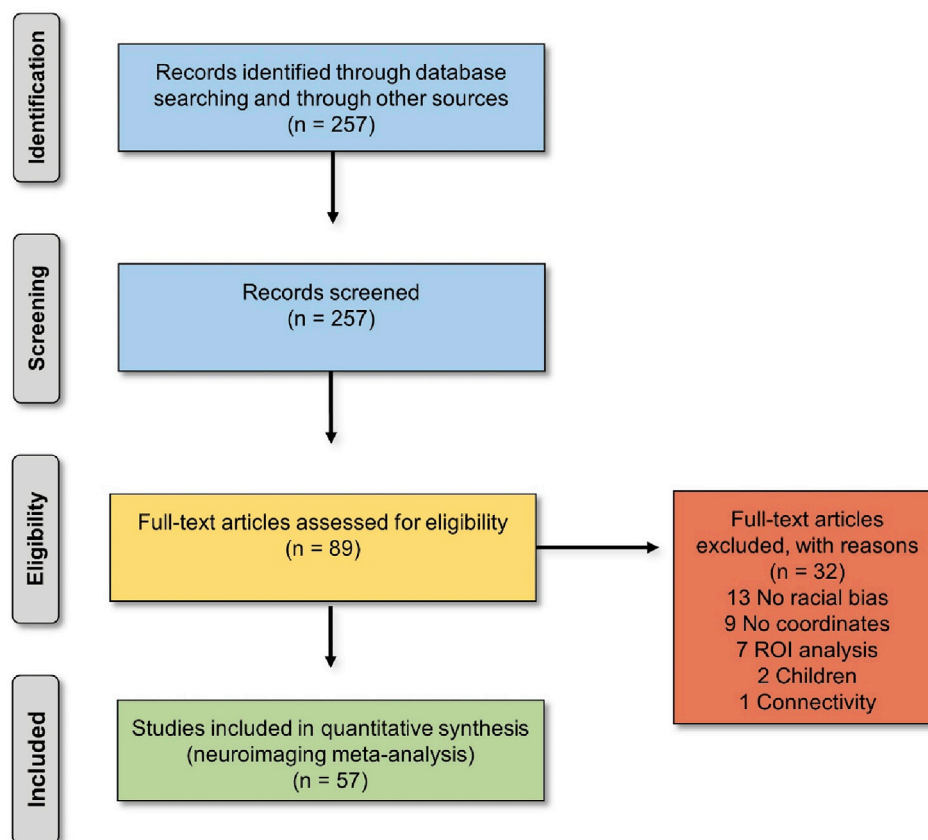


Fig. 1. PRISMA flow chart of study selection process (Moher et al., 2009).

Table 1
Overview of the studies included in the meta-analysis on same-group perception.

Year	First author	N (M)	Race sample	Paradigm	Stimulus	Race stimulus
2001	Golby	19(19)	W + B	Detection	Faces	W + B
2004	Cunningham	13(9)	W	Backward masking	Faces	W
2005	Lieberman	20(10)	W + B	Perceptual/verbal discrimination	Faces	W + B
2006	Kim	12(6)	A	Social categorization	Faces	A
2007	Ronquillo	11(11)	W	Social categorization	Faces	W
2008	Beer	16(8)	W	Social categorization	Faces	W
2008	Chiao	20(10)	A + W	Social categorization	Faces	A + W
2008	Richeson	9(3)	W	Perceptual discrimination	Faces	W
2009	Adams	28(10)	A + W	Social categorization	Eyes	A + W
2009	Krill	14(3)	W	Cyberball	Faces	W
2009	Xu_exp 1	17(8)	A	Pain – empathy	Faces	A
2009	Xu_exp 2	16(8)	W	Pain – empathy	Faces	W
2010	Adams	32(16)	A + W	Passive viewing	Faces/gazes	A + W
2010	Freeman	16(8)	W	Social judgment	Faces/words	W
2010	Mathur_exp 1	28(5)	W + B	Pain – empathy	Complex scenes	W + B
2010	Mathur_exp 2	14(4)	B	Pain – empathy	Complex scenes	B
2010	Mathur_exp 3	14(1)	W	Pain – empathy	Complex scenes	W
2011	Cheon_exp 1	27(15)	A + W	Pain – empathy	Complex scenes	A + W
2011	Cheon_exp 2	14(7)	W	Pain – empathy	Complex scenes	W
2011	Cheon_exp 3	13(8)	A	Pain – empathy	Complex scenes	A
2011	Feng	30(19)	A	Social categorization	Faces	A
2011	Liew	18(10)	A	Social judgment	Faces/hands	A
2012	Derntl	24(12)	W	Social categorization	Faces	W
2012	Gilbert_exp 1	16(12)	W	Social judgment	Faces	W
2012	Greer_exp 2	23(7)	W	Social judgment	Faces	W
2012	Greer_exp 3	27(7)	B	Social judgment	Faces	B
2012	Losin	20(10)	W	Imitation – passive	Faces/hands	W
2012	Mathur_exp 1	10(4)	B	Pain – empathy	Complex scenes	B
2012	Mathur_exp 2	10(1)	W	Pain – empathy	Complex scenes	W
2012	Mathur_exp 3	20(5)	B + W	Pain – empathy	Complex scenes	B + W
2013	Azevedo	27(11)	W + B	Pain – empathy	Hands	W + B
2013	Contreras	17(8)	W	Social categorization	Faces	W
2013	Contreras-Huerta	20(8)	W	Pain – empathy	Faces	W
2013	Zuo	20(8)	A	Pain – empathy	Faces	A
2013	Earls	20(20)	W	Imitation	Faces/hands	W
2014	Cloutier	45(21)	W	Working memory	Faces	W
2014	Kramer	22(11)	W	Social categorization	Faces/gazes	W
2014	Losin	20(10)	B	Imitation	Faces/hands	B
2014	Sheng	21(10)	A	Pain – empathy	Faces	A
2015	Cao	30(12)	A	Pain – empathy	Faces	A
2015	Chen	22(11)	A	Backward masking	Faces	A
2015	Li_exp 1	40(19)	A	Pain-empathy	Faces	A
2015	Li_exp 2	20(11)	A	Pain-empathy	Faces	A
2015	Luo	30(16)	A	Pain-empathy	Faces	A
2015	Molapour	20(10)	W	Conditioning	Faces	W
2015	Rauchbauer	41(23)	W	Imitation	Faces/hands	W
2016	Berlinger	25(12)	W	Pain – empathy	Faces/hands	W
2016	Li	44(20)	W	Social judgment	Faces	W
2017	Brown	19(19)	W + B	Perceptual discrimination	Faces	W + B
2017	Fourier	38(21)	W + B	Pain – empathy	Faces/visual scenes	W + B
2017	Watson	21(8)	W	Social categorization	Bodies	W
2017	Firat	13(7)	W	Social categorization	Complex scenes	W
2018	Mattan	60(60)	W	Social judgment	Faces	W

Abbreviations: A = Asian; B= Black; W= White.

). The analyses of this plug-in are based on behavioural and coordinate data included in the BrainMap database. Functional decoding is, in fact, a data-driven approach that investigates the association between activation in a given brain region and mental/cognitive functions associated to that region across the fMRI studies in healthy subjects stored in this database (Lancaster et al., 2012). This approach can therefore elucidate the contribution of areas engaged in either same- or other-race perception to a variety of behavioural/cognitive functions, thus enabling comparisons of the same brain structure (or cluster or areas) across functions, but not otherwise. This because the association of different brain areas to the same cognitive/behavioural domain may simply reflect the overall number of studies that investigated one specific brain area.

At the time of analysis, the functional database contained information about more than 15000 neuroimaging experiments categorized using five behavioural domains; that is, cognition, action, perception, emotion, and interoception, and their related sub-categories (Fox et al., 2005). A

comprehensive list of behavioural domains of the BrainMap taxonomy is available at <http://brainmap.org/taxonomy>. The analysis was performed on selected brain seeds, as identified by each cluster resulting from the ALE meta-analysis. Only z-scores ≥ 3.0 were considered significant ($p \leq 0.05$ with Bonferroni correction for multiple comparisons).

2.3.3. Meta-Analytic Connectivity Modeling (MACM), network similarities and hierarchical clustering

A MACM was also performed in order to assess the co-activation patterns associated with the regions identified in the ALE meta-analysis. Specifically, MACM provides a meta-analytic estimate of functional connectivity by modeling the probability that different brain regions are active simultaneously. This is achieved assessing the covariance between regions that determines co-activation profiles across all the experiments stored in BrainMap (Laird et al., 2009; Robinson et al., 2010). The method assumes that voxels are functionally connected if they

Table 2
Overview of the studies included in the meta-analysis on other-group perception.

Year	First author	N (M)	Race sample	Paradigm	Stimulus	Race stimulus
2000	Hart	6(2)	W + B	Social categorization	Faces	W + B
2000	Phelps	14(7)	W	Working memory	Faces	B
2003	Richeson	15(7)	W	Perceptual discrimination	Faces	B
2004	Cunningham	13(9)	W	Backward masking	Faces	B
2005	Lieberman_exp 1	11	W	Perceptual discrimination	Faces	B
2005	Lieberman_exp 2	20(10)	W + B	Perceptual/verbal discrimination	Faces	W + B
2005	Wheeler	7(3)	W	Social categorization	Faces	B
2006	Kim	12(6)	A	Social categorization	Faces	W
2007	Ronquillo	11(11)	W	Social categorization	Faces	B
2008	Beer	16(8)	W	Social categorization	Faces	B
2008	Richeson	9(3)	W	Perceptual discrimination	Faces	B
2008	Van Bavel	17(7)	W	Social categorization	Faces	B
2010	Adams	32(16)	W + A	Passive viewing	Faces/gazes	W + A
2010	Mathur	28(5)	W + B	Pain – empathy	Complex scenes	W + B
2011	Cheon	27(15)	A + W	Pain – empathy	Complex scenes	A + W
2011	Liew	18(10)	A	Social judgment	Faces/hands	W
2011	Masten	18(9)	B	Social categorization	Faces	W
2012	Derntl	24(12)	A	Social categorization	Faces	W
2012	Greer	27(7)	B	Social judgment	Faces	W
2012	Korn	19(12)	W	Perceptual discrimination	Faces/words	B
2012	Losin	20(10)	W	Imitation – Passive	Faces/hands	B + A
2012	Mathur	20(5)	B + W	Pain – empathy	Complex scenes	B + W
2013	Contreras	17(8)	W	Social categorization	Faces	B
2013	Zuo	20(8)	A	Pain – empathy	Faces	W
2014	Cloutier	45(21)	W	Working memory	Faces	B
2014	Hehman	20(4)	W + A	Perceptual discrimination	Faces	B
2014	Kramer	22(11)	W	Social categorization	Faces/gazes	A
2014	Losin	20(10)	B	Imitation	Faces/hands	W
2015	Cao	30(12)	A	Pain – empathy	Faces	W
2015	Li	20(11)	A	Pain – empathy	Faces	W
2015	Liu	26(13)	A	Passive view	Faces	B
2015	Luo	30(16)	A	Pain – empathy	Faces	W
2015	Molapour	20(10)	W	Conditioning	Faces	B
2015	Rauchbauer	41(23)	W	Imitation	Faces/hands	B
2015	Senholzi	16(7)	W + A	Perceptual discrimination	Complex scenes	B
2015	Telzer_exp 1	26(13)	W + A	Social judgment	Faces	W + A
2015	Telzer_exp 2	13(7)	A	Social judgment	Faces	W
2015	Terberck	20(9)	W	Social categorization	Faces	B
2016	Berlinger	25(12)	W	Pain – empathy	Faces/hands	B
2016	Cassidy	30 (13)	W	Social categorization	Faces	B
2016	Li	44(20)	W	Social judgment	Faces	B
2017	Brown	19(19)	W + B	Perceptual discrimination	Faces	W + B
2017	Watson	21(8)	W	Social categorization	Bodies	B

Abbreviations: A = Asian; B= Black; W= White.

are statistically co-activated above chance in functional neuroimaging studies (Robinson et al., 2012, 2010). Initially, we determined by mean of Sleuth package all experiments in the BrainMap database activating every seed region, as resulting from our previous ALE analysis. As suggested in the guidelines, we included the Experiment-level search criteria of “Context: Normal Mapping” and “Activations: Activation Only”. Next, co-activation coordinates were extracted and imported in GingerALE in order to perform a quantitative meta-analysis that enabled us to assess areas of convergence representing functional connectivity of every seed with other brain sites.

From the resulting MACM maps, we extracted the maxima ALE values associated with each co-activated region. This resulted in a normalized matrix where the rows represent the brain areas found in the ALE meta-analyses for same-group and other-group perception, and columns represent the co-activated regions. Based on these co-activations, we measured similarities between the same-group and other-group neural regions, which were represented spatially by computing square distance matrices using Spearman metric, where higher values indicate closer similarity in a scale ranging from 0 to 1. The matrix was then reoriented to minimize cross-correlation of diagonal values and submitted to a hierarchical clustering to obtain a dendrogram of networks based on the average distance between entries. According to this method, data were grouped in a multi-level hierarchy, where clusters at root levels are linked to the clusters at the next levels, and so on until the highest level in

the hierarchy is reached (Celeghin et al., 2019).

3. Results

3.1. ALE results

Ninety-four experimental contrasts across 2071 subjects were included in the overall intergroup meta-analysis. The average age of participants was 22.80 years and 50% were females. Concerning race, 47% were White, 22% Asian, and 7% Black people, while 24% of studies used mixed samples (e.g. Asian and White together). The tasks most common were social categorization (25%), perceptual discrimination (12%), pain-empathy (29%) and social judgment (13%), and faces were projected as stimuli in 64% of the studies.

Perception of the racial traits, regardless of their membership or their same/different relation with the observers’ racial category, was associated with a range of cortical, subcortical and cerebellar structures. Specifically, significant brain activity was observed in cingulate and frontal cortices, encompassing the left cingulate gyrus (CG), the right superior frontal gyrus (SFG) and the bilateral inferior frontal gyrus (IFG), in the occipital and parietal cortices including the right lingual gyrus (LG), the left middle occipital gyrus (MOG) and the left inferior parietal lobule (IPL). We found bilateral activity in the amygdala (AMG), INS, hippocampus (HIP) and in the parahippocampal gyrus (PHG) at limbic level,

and in the declive and culmen at cerebellar level.

3.1.1. Same-group perception

Same-group meta-analysis included 51 experimental contrasts across 1162 subjects. The average age of study participants was 23.94 years and 48% were female. The sample included 46% White, 23% Asian, 6% Black, while 24% were mixed (e.g. Asian and White together in the same sample). Overall, the most frequently used tasks were the pain-empathy paradigm (37%), the social categorization (22%) and the social judgment (14%). Faces were most common stimuli (59%), followed by complex visual scenes (16%).

ALE results showed that same-group perception was characterized by significant activity in the cingulate and frontal cortices, encompassing the medial frontal gyrus (mFG). There was also enhanced activity in subcortical regions such as the left INS and the right striatum, including the putamen and the medial globus pallidus (Fig. 2).

3.1.2. Other-group perception

Other-group meta-analysis involved 43 experimental contrasts across 909 subjects. The average age was 22.80 years and 53% of participants were female. Concerning race, 48% were White, 21% Asian, 7% Black, and 24% of the studies used mixed samples (e.g. Asian and White together). The most common tasks were social categorization (30%), perceptual discrimination (18%), pain-empathy paradigm (18%) and the social judgment (12%). Stimuli were prevalently faces (70%).

Other-group perception was associated with activity in a right-lateralized cluster, encompassing INS and IFG. Moreover, we found enhanced activation in the occipital lobe spanning the right fusiform

gyrus (FG) and the left MOG and in the parietal lobe specifically in the IPL. Finally, significant activity was also identified in the right AMG (Fig. 2).

3.2. Functional decoding results

3.2.1. Same-group perception

Across all experiments included in the BrainMap database, the mFG was significantly associated with cognition (chiefly, with aspects of language, attention and memory), with perception (somesthesia and pain) and with domains related to emotion and action. The left INS/IFG showed significant associations with emotional and cognitive profiles, whereas the right striatum was uniquely associated with emotional functions.

Altogether, the whole network was generally associated with the functional domains related to emotion, cognition, action and perception (Fig. 3).

3.2.2. Other-group perception

The right INS/IFG was associated with cognition (attention, memory and language), emotion, perception (somesthesia and pain) and action (inhibition). The right AMG was linked with emotion in general and with fear specifically. Cluster in the right FG, left MOG and left IPL did not reach standard statistical threshold for the association with specific behavioural domains, possibly because of the small size of the clusters resulting from the ALE. Nonetheless, the domains approaching standard significance in z-scores for FG and the left MOG were perception (vision) and cognition (attention), whereas the left IPL was related to cognition

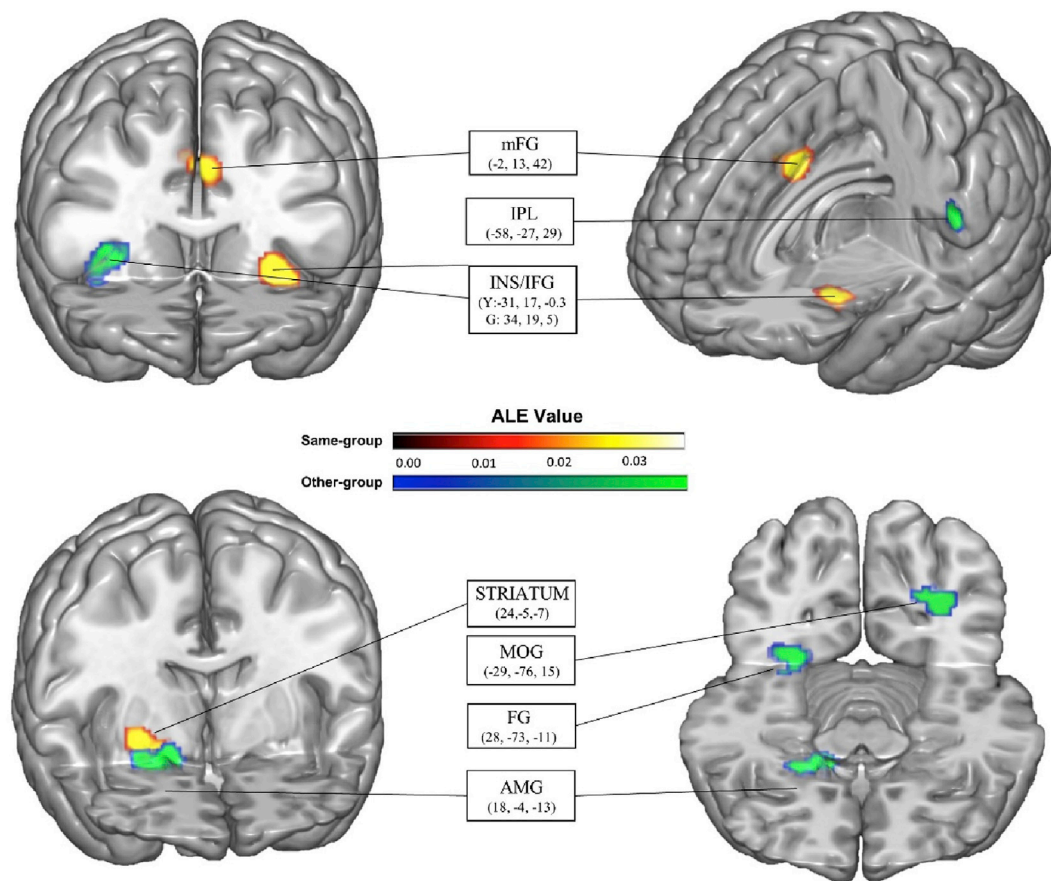


Fig. 2. Anatomical 3-D rendering of the ALE maps. ($p < 0.05$ corrected for multiple comparisons at the Cluster Level, minimum cluster size of $K > 100 \text{ mm}^3$). Coordinates (x, y, z) represent the weighted centre of each cluster, and the anatomical labels are those reported by GingerALE based on the location of the same cluster centres. AMG = Amygdala; FG= Fusiform Gyrus; G = Green; IFG= Inferior Frontal Gyrus; INS= Insula; IPL= Inferior Parietal Lobule; mFG = medial Frontal Gyrus; MOG = Middle Occipital Gyrus; Y=Yellow.

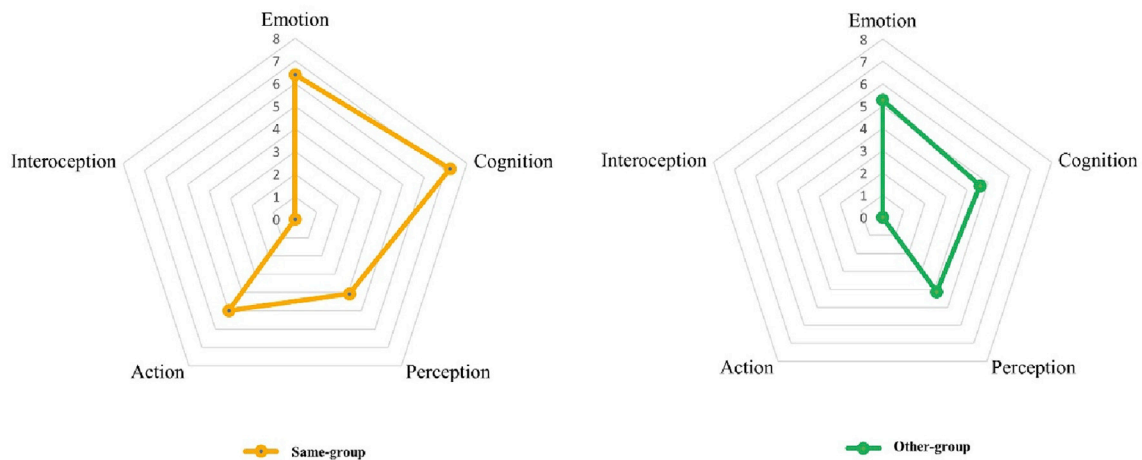


Fig. 3. Functional decoding associated with same-group (left panel) and other-group perception (right panel). The radar graph reflects the engagement of areas collectively underpinning race perception in other behavioural/cognitive functions, according to the categorization domains of BrainMap (the weighted probability of association to one domain is reported in z-scores).

(language) and action (execution).

At the network level, all these areas showed significant associations with emotion in general, and fear specifically, cognition (attention, memory and language) and perception (somesthesia, pain and vision) (Fig. 3).

3.3. MACM results

Neural structures do not have functions in isolation. To underscore the network properties and long-range functional connections of areas involved in same- and other-group categorization, we performed MACM analyses. Firstly, we identify all studies including activations in our seed regions using Sleuth. These regions were those found in the ALE analysis as distinctively involved in same- and other-group categorization. These structures were recruited in studies collectively involving a range of subjects between 7271 and 13633, including between 478 and 887 experiments, and returning between 7770 and 13821 additional foci. These activations were then further investigated by an ALE meta-analysis for each seed region across identified experiments.

3.3.1. Same-group perception

The MACM analysis indicated that the mFG, the left INS and the right striatum display a remarkable similarity in the recruitment of spatially remote regions. In fact, the patterns of functional connectivity were found in several common bilateral regions. The structures were functionally connected with the thalamus (medial dorsal nucleus), the caudate body and the putamen at the subcortical level. In the frontal lobe, significant interactions were found with the bilateral IFG and mFG, while inter-regional connections with the temporal lobe involved the left superior (STG) and middle temporal gyrus (MTG). Significant co-activations were also identified at level of superior parietal lobule (SPL), IPL and precuneus. Finally, the left cerebellum (declive and culmen) and the inferior occipital gyrus (IOG) were dynamically connected with seed regions (Fig. 4).

3.3.2. Other-group perception

Seed regions engaged in other-group perception entertained significant co-activations with several areas. In particular, all regions revealed significant connectivity with bilateral INS and thalamus, and with the dorsal striatum at the level of the caudate body, bilaterally, and the left putamen. At frontal level, we found co-activations with the bilateral IFG and mFG, the right SFG, the left MFG and the left precentral gyrus (preCG). Moreover, the bilateral IPL, the right SPL and the left post-central gyrus (postCG) were identified across all our seeds. In the

temporal lobe, significant co-activations were found with the left MTG and with the right STG. Interestingly, the right AMG showed co-activations specifically with the right FG (BA 19) (Fig. 4).

3.3.3. Network similarities and hierarchical clustering

Distance matrix revealed a non-random aggregation of the brain regions found in the MACM analyses, resulting in a hierarchical clustering of these areas (Fig. 5). A first cluster included subcortical (right INS and right caudate), temporal (right MTG, left PHG and right FG) and parietal regions (right postCG, right IPL and left supramarginal gyrus). A second larger cluster comprised several regions in the frontal and parietal lobes such as the bilateral preCG, the right IFG, the bilateral MFG, the right SFG, the left postCG, the left precuneus, the left IPL and the right SPL. Also, this cluster included areas in occipital and temporal lobes, i.e. the bilateral LG, the right MOG, the left IOG, the left FG and the right STG, and subcortical regions such as the bilateral AMG and the left basal ganglia (putamen and caudate). Lastly, the third cluster comprised the left INS, the right IOG, the left mFG, the left IFG, the left SPL, the right precuneus, and the left MTG.

4. Discussion

The quest to characterize the neural signature of intergroup categorization has come under extensive scrutiny in recent years. In the present study, we provided the first meta-analysis of available fMRI studies addressing same- and other-group categorization from visual signals. Further analyses also gauged functional connections to provide a network-based and dynamic perspective. Besides specific differences that will be discussed below, racial perception is represented in several cortical areas including the left CG, the right SFG, in the INS, the bilateral IFG, the right LG, the left MOG and the left IPL. Other subcortical regions included the AMG, the PHG bilaterally, the left HIP, and the cerebellum.

Overall, these brain areas impinge on different aspects of categorization and evaluation of socially relevant stimuli (Bagnis et al., 2019). The occipito-temporal cortices are involved in visual perception of facial features and encode neural representations of face parts and invariant visual traits such as race (Haxby et al., 2000). Neural representations associated with the visual perception of a face, are boosted by both subcortical regions and by higher-order cortical regions. Coherently, we found activations in the AMG and the INS, which may exert a bottom-up influence on visual areas on the basis of the emotional and affective meaning conveyed by same- and other-group faces (Blair et al., 1999; Vuilleumier, 2005; Vuilleumier et al., 2004; Beer et al., 2008; Harris and Fiske, 2006; Knutson et al., 2007; Lieberman et al., 2005; Liu et al., 2015;

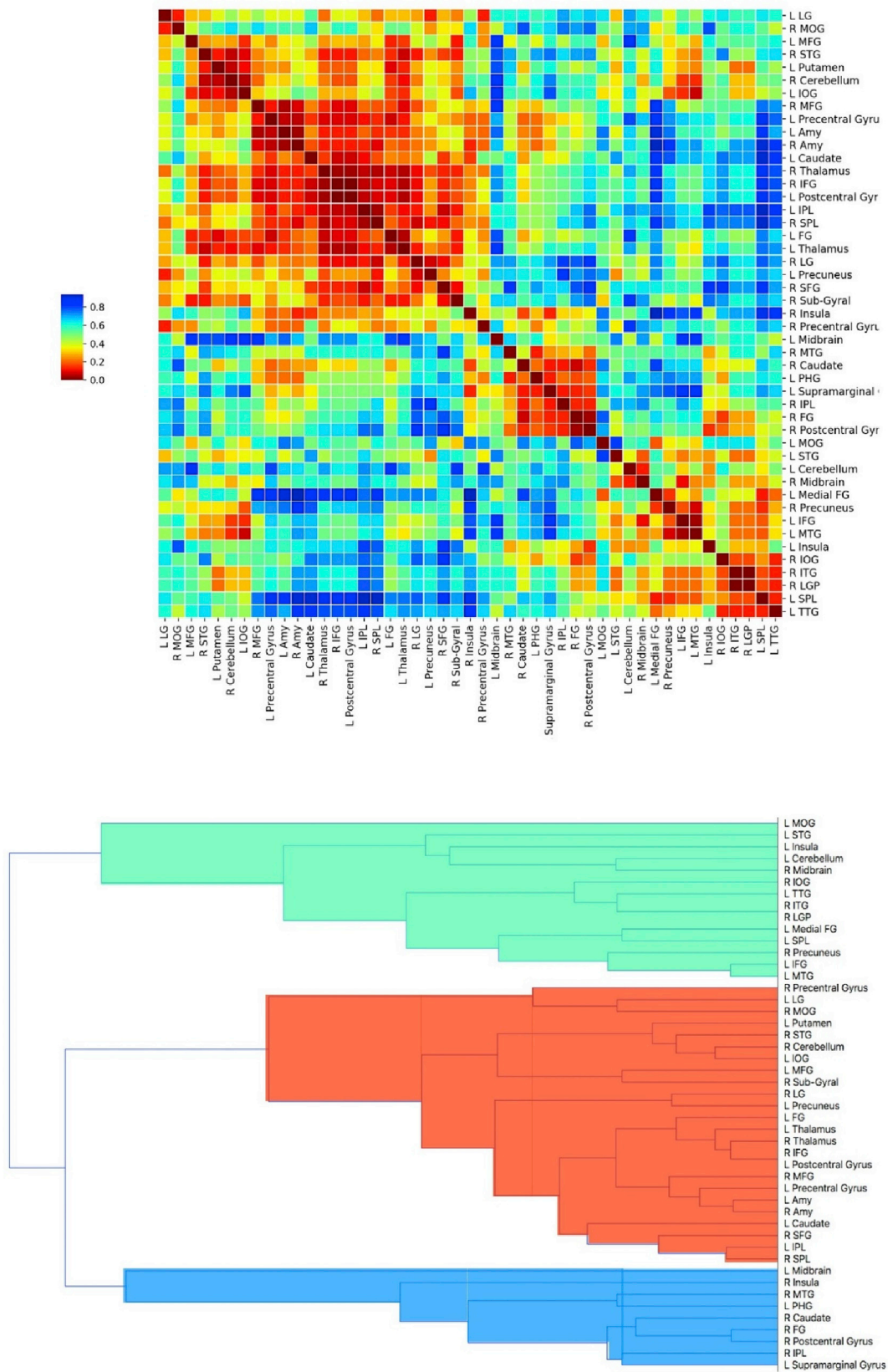


Fig. 5. Distance matrix and hierarchical clustering between brain areas found in the MACM analyses. The upper panel displays the square distance matrix amid co-activated brain areas, where higher values indicate closer similarities. The lower side reports a dendrogram of brain networks resulting from hierarchical clustering of the distance matrix amid co-activated areas.

CG and the mFG. There was also enhanced activity in the left INS and the right striatum. Overall, these brain areas seem to be associated with affective and cognitive empathy, self-referential evaluations and mentalizing about similar others, suggesting that same-race faces are mainly processed at a cortical level, relying on detailed mental representations of others and self-knowledge-based inferences (Amodio et al., 2008; Amodio and Frith, 2006; Bzdok et al., 2012). However, striatal activations suggest that these processes could be influenced by more basic encoding principles: interacting with same-group members strengthens the feeling of similarity and, vice versa, this feeling strengthens the will to have positive contacts with similar others (Mitchell et al., 2002; Singer et al., 2004; Wood et al., 2003; Xu et al., 2009). Consistently, functional decoding linked this same-group network mainly to emotion and cognitive domains such as attention and memory, suggesting that the typical advantage in memorizing and categorizing similar others could be influenced by affective and attentional processes (Elfenbein and Ambady, 2002).

4.1.1. Empathic and mentalization processing

As reported in a recent review (Han, 2018), empathic processes are crucial in encoding same-race and other-race faces. Indeed, empathy is important to understand the emotional states of others and to induce altruistic behavior in both interpersonal and intergroup context (Decety et al., 2016). Consistently, the present meta-analyses revealed the involvement of brain regions associated with affective and cognitive empathy. Specifically, the cingulate cortex is involved in affective component of empathy, i.e. the ability to vicariously experience others' emotional feelings (Fan et al., 2011; Gallese, 2003; Singer et al., 2004). Moreover, neural empathic activations seem to depend on the social relationship between the interactants (Singer et al., 2006; Hein et al., 2010; Avenanti et al., 2010). Indeed, the fact that cingulate activity is associated specifically to same-group stimuli suggests that sharing the same racial group could improve the empathy and the affective responses to others recognized as similar (Contreras-Huerta et al., 2013; Li et al., 2015; Luo et al., 2015; Sheng et al., 2014; Xu et al., 2009). Likewise, enhanced activity in response to same-group stimuli was found also in the insula. This region has been associated to integrative processes between relevant and irrelevant information (Critchley, 2005; Goll et al., 2015). More specifically, its activity portends the integration of motivational and social processes (Craig, 2003; Critchley, 2005). Although insular activation has been typically associated with negative emotions, such as disgust, in response to out-group stimuli (Harris and Fiske, 2006; see section 4.2.2), its significant activity during perception of in-group stimuli could reflect empathetic resonance toward similar others by contributing to the neural circuits underlying affective empathy (Fan et al., 2011; Singer, 2006; Singer et al., 2004). This interpretation is consistent with several studies reporting the INS during intergroup pain-empathy (Azevedo et al., 2013; Cao et al., 2015; Contreras-Huerta et al., 2013; Xu et al., 2009).

Prefrontal activity encompassing the mFG appears mainly involved in cognitive processing and in mentalizing based on self-knowledge used to understand the emotions of similar others. Indeed, several studies support the role of PFC in the humanization process because of its specifically greater engagement in judging and forming impressions about members of esteemed groups than about out-group members or objects (Cikara et al., 2011; Frith and Frith, 1999; Harris and Fiske, 2006; Mitchell et al., 2002). Moreover, it has been found that left IFG is specifically involved in the representation of social information, including personality traits as well as personalized details about others, especially when these others are members of the same group (Freeman et al., 2010; Heberlein and Saxe, 2005; Wood et al., 2003; Zahn et al., 2007).

4.1.2. Rewarding processing

Given the salience and motivational potential of social stimuli, it has been hypothesized that processing reward of same-group stimuli could motivate social behavior (Kelley and Berridge, 2002; Krach et al., 2010).

In keeping, we found the activation of the striatum, a region typically associated with reward and approach-related responses (O'Doherty et al., 2004). Its role during perception of same-group members could be related to an implicit preference based on positive bonding that reflects motivational consequences of continuing to interact and cooperate with same-group members (Amodio, 2014; Rilling et al., 2008; Van Bavel, 2008). Indeed, striatal activity has been found in several studies in association with reward-related responses toward same-group members, for example in case of prosocial and trust decisions (Knutson et al., 2001; Stanley et al., 2012; Telzer et al., 2015), suggesting that supporting people of their own group has positive consequences for themselves, as stated in the social identity theory (Tajfel, 1974).

4.2. Other-group perception

Other-group perception was associated with the right FG, the left MOG, the left IPL, the right INS and the right AMG. According to the functional decoding, these regions reflect a neural network involved in affective functions in synergy with attentional and visuo-perceptual processes.

4.2.1. Visuo-attentive processing

Owing to their social relevance and perceptual unfamiliarity, other-race facial cues summon attention, especially when combined with internal racial stereotypes (Correll et al., 2007, 2015; Dickter et al., 2015; Eberhardt et al., 2004; Trawalter et al., 2008). Selective responses in occipito-temporal and parietal cortices to other-race stimuli aligns with this view. More precisely, we found significant activation in the right FG, a crucial region in configural face perception (Haxby et al., 2000; Kanwisher et al., 1997; Kanwisher and Yovel, 2006). This result seems at odd with the literature on the expertise-based hypothesis. Indeed, some studies interpreted enhanced responses in the FG to same-group stimuli as expertise-based processing (Feng et al., 2011; Golby et al., 2001; Kim et al., 2006; Lieberman et al., 2005). However, other studies found no significant difference in the fusiform activity during the comparison between same- and other-race faces (Natu et al., 2011; Ratner and Amodio, 2013). Moreover, multivoxel pattern analysis (MVPA), revealed that FG activity is able to distinguish social categories, including race, mainly in participants with high levels of implicit racial bias, thereby suggesting a general influence of higher level social mechanisms on lower-level visual processing (Brosch et al., 2013; Contreras et al., 2013; Ratner et al., 2012; Stolier and Freeman, 2016; Terbeck et al., 2015). Consistently, the greater activity in right FG during other-group perception found in this meta-analysis could be interpreted as a neural representation of different race (Platek et al., 2008; Hughes et al., 2019).

Significant activity was found in the occipital and parietal cortices encompassing the MOG and IPL, in support of a greater visual activity and attentional resources engaged in processing other-group stimuli. This outcome is coherent with a socio-functional hypothesis about the strategic benefit of allocating attention towards socially relevant stimuli, such as threatening, competitive or unfamiliar stimuli (Öhman et al., 2001; Öhman and Mineka, 2001; Tamietto et al., 2005; Young and Claypool, 2010). Indeed, several behavioural and event-related potential (ERP) studies have shown that other-group members capture early attention more than same-group members (Bartholow and Dickter, 2008; Dickter and Bartholow, 2007; Ito et al., 2004; Ito and Urland, 2005, 2003; Trawalter et al., 2008). Although the association between race and threat due to negative stereotypes (e.g. Black and danger) is considered the main explanation of these findings, recent studies propose that other factors such as motivation and familiarity could play a role in driving attention to other-group members (Al-Janabi et al., 2012; Brosch and Van Bavel, 2012; Dickter et al., 2015; Dunsmoor et al., 2016; Richeson and Trawalter, 2008).

4.2.2. Affective processing

Other-group perception specifically involves subcortical areas

typically related to affective and emotional processes. Specifically, perception of social cues in other-race members was associated with activity in right AMG. This region seems to encode the emotional component of racial bias. Indeed, several studies showed that AMG activity is greater in response to Black versus White faces (Cunningham et al., 2004; Hart et al., 2000; Krill and Platek, 2009; Ronquillo et al., 2007; Wheeler and Fiske, 2005). AMG activity also correlates with indirect behavioural measures, such as high implicit prejudice and startle eye-blink responses, suggesting its role as a neural basis of implicit prejudice (Amodio et al., 2003; Phelps et al., 2000). Therefore, AMG activation could be interpreted as an instrumental response in order to rapidly direct the attention to potentially relevant stimuli, as other-group members in this case. The AMG sends feedback to visual extrastriate cortex in order to enhance efficient processing of affectively loaded stimuli that are thus endowed with a competitive perceptual advantage (Diano et al., 2017a; Morris et al., 1998; Pourtois et al., 2010, 2013; Sabatinelli et al., 2005; Vuilleumier et al., 2001, 2004; Vuilleumier, 2005). Another hypothesis is based on the link between AMG activity and anxiety (Bishop et al., 2004). Within the context of race perception, AMG responses could be related to the worries of showing prejudice toward other-group members (Amodio et al., 2003; Ofan et al., 2014; Richeson et al., 2008; Senholzi et al., 2015).

Consistent with AMG response, we also found activity in a right-lateralized cluster encompassing the INS and IFG. The INS contributes to the subjective feelings and negative visceral reactions, such as disgust, that are associated to negative attitudes towards racial out-groups and that are often experienced during prejudice response (Beer et al., 2008; Harris and Fiske, 2006; Knutson et al., 2007; Lieberman et al., 2005; Liu et al., 2015; Richeson et al., 2003; Ronquillo et al., 2007; Vercelli et al., 2016). Insular activity in response to other-group stimuli, similarly to AMG, has been associated with participants' implicit negative prejudice toward other-race groups (Lieberman et al., 2005; Richeson et al., 2003). In turn, IFG, especially in the right hemisphere, has been associated with the individuals' efforts to inhibit the influence of stereotypes (Aron et al., 2004). Because of the anatomical and functional connection between prefrontal cortex and the AMG (Ghashghaei et al., 2007; Pourtois et al., 2013), this inhibitory process could be associated with the anxiety of appearing prejudiced.

4.3. Functional connectivity analyses

MACM analysis enabled us to delineate differences in the functional connectivity pattern between same-group and other-group perception based on their co-activation profiles (Laird et al., 2009; Robinson et al., 2010).

Same-group regions were found to be functionally co-activated with several common brain areas, mainly in the frontal, parietal and temporal cortices, including the bilateral MFG and IFG, left SPL, bilateral IPL, right precuneus, left STG and MTG, and with subcortical structures, such as the INS, the thalamus and the basal ganglia, bilaterally. Consistently, these areas are typically involved in processes based on self-others distinctions, including auto-biographical memories and social knowledge, and play a role in attention and in guiding behavioural responses (Bonner and Price, 2013; Herrero et al., 2002; Igelström and Graziano, 2017; Shamy-Tsoory, 2011). Instead, other-group regions recruit a network involving subcortical regions including the AMG, thalamus and basal ganglia bilaterally, and the INS, which have an important role in emotion perception, attention and behavioural control. Indeed, MACM showed co-activation also with fronto-temporo-parietal areas, consistently with the well-known emotional cortico-subcortical networks and basal ganglia-thalamocortical circuits (Couto et al., 2013; Deshpande et al., 2011; Diano et al., 2017b; Herrero et al., 2002).

Altogether, inter-regional connectivity patterns of same- and other-group regions point to a non-random organization in distinct networks characterized by three hierarchical clusters. These three clusters showed some commonalities concerning occipital and temporal regions. This is

consistent with the intrinsic commonalities of race categorization, besides distinctions between same- and other-race membership, that shares in fact processes like visual encoding of faces and activation of social stereotypes (Bagnis et al., 2019; Freeman and Johnson, 2016; Mason et al., 2006). Indeed, brain regions such as IOG, MOG and FG are typically associated with representation of facial features, including facial parts (e.g. eyes, nose, mouth), lower level aspects of face processing (e.g. physical variations) and invariant visual traits (e.g. identity, gender and race) (Bernstein and Yovel, 2015; Kanwisher et al., 1997; Pitcher et al., 2011). Instead, STG and ITG, located in the anterior temporal lobe, have been shown to be involved in storing social knowledge about faces based on prior semantic associations (Eifuku et al., 2010; Ross and Olson, 2012) and specifically in expressing racial and gender stereotypes (Gallate et al., 2011; Gilbert et al., 2012).

Beside commonalities, the three clusters were characterized by regions reflecting different processes through which same-group and other-group faces are categorized and represented. The functional role of the first cluster seems related to bottom-up sensory processing of salient stimuli (Bagnis et al., 2019). In particular, the right INS contributes to subjective feelings and negative visceral reactions that are associated to negative attitudes toward racial out-groups and that are often experienced during prejudice responses (Beer et al., 2008; Harris and Fiske, 2006; Knutson et al., 2007; Lieberman et al., 2005; Liu et al., 2015; Richeson et al., 2003; Ronquillo et al., 2007). Likewise, the right IPL is involved in bottom-up attentional mechanisms in response to relevant stimuli. Studies of visual attention identified the IPL as a key region in detecting unattended stimuli in healthy subjects and neglect patients (Corbetta and Shulman, 2002; Tamietto et al., 2014; Thiebaut de Schotten et al., 2005). The second cluster comprised mainly structures involved in mentalizing and empathic processes. In addition to the contribution of the left INS and the mPFC already discussed, also the precuneus is involved in empathic responses, for example during observation of people suffering physically (e.g. painful stimulation) or socially (e.g. exclusion from a game) (Fourie et al., 2017; Han, 2018; Meyer et al., 2013). Finally, the third cluster was characterized by regions associated with motor processes. Neural activity in motor regions has been correlated with affective recognition based on simulation (Adolphs, 2002) and automatic preparation to act in response to relevant stimuli (de Gelder et al., 2004; Pichon et al., 2008). Consistently, this cluster comprised also the bilateral AMG, crucial for the perception of emotional stimuli or danger (Diano et al., 2017a; LeDoux, 2003). Another functional role could be associated to this cluster, as the motor system is considered an integral component of perceptual decision-making processes (Frith and Singer, 2008; Summerfield and De Lange, 2014). In the context of the intergroup bias, these structures could contribute to make decisions in social interactions. Interestingly, the right IFG, a region specifically involved in controlling and inhibiting stereotypes, is also part of this cluster (Amodio, 2014).

5. Conclusions

The present meta-analysis indicates that the brain engages partly distinct neural networks involved in the categorization of people into different racial groups, which is a crucial function for the living among different social groups and to maintain adaptive relationships (Zhou et al., 2019).

Same-group perception is characterized by empathetic and self-referential processes, whereas classification of other-group stimuli enhances attentional, visuo-perceptual and emotional processes. These findings suggest that group membership has important motivational consequence (Hugenberg and Bodenhausen, 2004; Rhodes et al., 1989). Indeed, same-group members tend to evoke greater feelings of empathy than other-group members, thus fostering cooperation with socially and biologically similar others (Brown et al., 2006; Cosmides et al., 2003). Classification of other-group members tends to recruit more attention demands, because the stimuli are less familiar and potentially

threatening, thereby leading also to greater involvement of affective areas (Dickter et al., 2015).

To conclude, the current study contributes to the mapping of complex psycho-social functions, such as racial categorization and inter-group bias, onto brain architecture. In fact, we have provided evidence for the heterogeneity of the brain bases of racial categorization from visual cues, as reflected in functional and connectional properties of brain activity. This knowledge capitalizes on an unprecedentedly large dataset of neuroimaging findings, and provides traction on several open theoretical issues, including the intersection of race-categorization with personal familiarity (e.g. friends, significant others) and frequency of exposure to other-race individuals. In fact, most of the studies included in our meta-analysis did not take into account the level of exposure to and/or familiarity with other-race individuals. Future inquiry on these factors will help to qualify how the brain copes with a more malleable society where racial groups are less segregated, and people can be frequently exposed to, and become familiar with, other-race individuals (Elfeinben and Ambady, 2003).

Data and code availability statement

Database of coordinates and code used to perform the meta-analysis are available upon request.

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CRediT authorship contribution statement

Arianna Bagnis: Conceptualization, Data curation, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Alessia Celeghin:** Writing - original draft, Writing - review & editing. **Matteo Diano:** Formal analysis, Writing - review & editing. **Carlos Andres Mendez:** Writing - review & editing. **Giuliana Spadaro:** Investigation, Writing - review & editing. **Cristina Onesta Mosso:** Writing - review & editing. **Alessio Avenanti:** Writing - review & editing. **Marco Tamietto:** Conceptualization, Writing - original draft, Writing - review & editing.

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