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Toward an integrative science of social vision in intergroup bias

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Highlights

- Social categories and intergroup bias can be derived from face perception.
- Social categorization is sensitive elemental visual features in the face.
- Prior knowledge and expectations modulate facial representations.
- This evidence challenges accounts based on hierarchical brain organization.
- A new model building on recursive dynamic interactions is proposed.

Abstract

Social neuroscience is unveiling how the brain coordinates the construal of social categories and the generation of intergroup biases from facial perception. Recent evidence indicates that social categorization is more sensitive and malleable to elemental facial features than previously assumed. At the same time, perception of social categories can be crafted by top-down factors, including prior knowledge, motivations, and social expectations. In this review, we summarize extant wisdom and propose a model that goes beyond traditional accounts that have conceived stereotypes and prejudices as the end result of "reading out" social categories in the face, and have assumed a hierarchical brain organization. Our model proposes recursive and dynamic interactions amid distant brain regions. Accordingly, the reciprocal exchange of sensory evidence and predictions biases and "explains away" visual input in face perception regions until a compromise is achieved and social perception stabilizes. Ideally, this effort would contribute to shape a research field at the interface between neural and social sciences, which is often referred to as social vision.

Keywords

intergroup bias; social vision; stereotypes; prejudices; predictive coding; biased competition; face perception; emotion.

1. Introduction

Social neurosciences are probing the neural underpinnings of social behavior as well as the impact of social factors on brain functioning. In recent years, a burgeoning area at the interface between neural and social sciences has begun to investigate the mutual interactions amid visual perception of social cues, how these perceptual features are used to derive social categories such as gender and race, and the way in which these processes are integrated in stereotypes and prejudices that guide interpersonal behaviors (Martin and Macrae, 2007). Traditionally, social beliefs or expectations forming prejudices and stereotypes have been considered as the final result of categorization processes operating after invariant representations of relevant visual dimensions in the sensory input are formed (e.g., black, female, angry face) (Brewer 1988). Mounting evidence is instead revealing that the perception of social categories from visual cues like faces is far more complex and dynamic than previously assumed (e.g. Freeman et al. 2015; Haxby et al. 2000; Stolier et al 2016; for a review see Freeman and Johnson, 2016). We propose that social categorization from faces occurs iteratively at multiple processing stages, with social beliefs influencing and updating also elemental aspects of visual processing, therefore contributing to stabilize perceptual representations in areas involved in face processing along the ventral occipito-temporal stream.

This new approach is breaking the traditional disciplinary divides between social psychology, neuroscience, vision and cognitive sciences. Therefore, theoretical and empirical advancements that are gaining traction in one discipline and can be useful to foster further cross-fertilization may not be fully familiar to scholars active in another field of social and cognitive (neuro)sciences. Moreover, the inter-disciplinary investigation of intergroup bias seems uniquely posited to enable knowledge transfer, whereby basic advancements in these fields can be applied to deal with real-world societal issues. This would promote adaptive expression of social behavior in intercultural environments, where prejudices and stereotypes still foster intergroup conflicts.

Specific aspects of social perception are garnering attention and have been summarized in previous reviews (Amodio 2008, Amodio 2014, Freeman and Johnson 2016). These former papers were guided by a social psychology perspective (Amodio 2008) or concentrated on particular neuroimaging methods (Ito and Bartholow 2009). Recently, Freeman and Johnson (2016) proposed an intriguing model on how visual cues from the face are integrated with, and shaped by, social processes such as stereotypes and attitudes to derive social categories. Their view incorporates general principles of functioning also endorsed in the present proposal, but without direct reference to specific intergroup biases and focusing essentially on the role of three brain regions: the fusiform gyrus (FG), the orbitofrontal cortex (OFC) and the anterior temporal lobe (ATL) (Freeman and Johnson 2016). Hence, time seems ripe to make an additional effort to integrate views within a single and compact format, and to outline a more extended neural model that can provide traction for further empirical inquiry. Accordingly, in this short review we will summarize some of the key findings, extant limitations, and future directions that are collectively shaping a unifying approach to visual perception of social categories and intergroup bias that is sometimes referred to as *social vision* (Adams et al. 2011, de Gelder and Tamietto 2011, Freeman and Johnson 2016). We focus predominately, but not exclusively, on race and gender bias based on face perception, as most of the literature concerned the use of faces to delve into these forms of prejudice. Nevertheless, some of the principles and mechanisms reviewed here may likely underlie other forms of prejudices and stereotypes, like those related to political partisanship.

2. Social categories are influenced by elemental facial features and contextual cues

Face perception is often pivotal in social contexts, as faces convey important elements to shape efficient interactions. In the blink of an eye people can recognize emotions, race, gender, age, familiarity and other socially relevant cues in another person's face (Celeghin, Diano, Bagnis, et al. 2017, Costa et al. 2014, Freeman and Johnson 2016, Ito and Urland 2005, Negro et al. 2015, Van

Bavel and Cunningham 2011). This process appears to unfold effortlessly, and traditional accounts assume indeed that we read-out and classify others from faces as members of social categories, thereby activating attitudes, stereotypes and prejudices associated to that category (Macrae and Bodenhausen 2000). As a consequence, we distinguish between in-group members, if they belong to our own group, and outgroup members, if they belong to another group. This tendency leads to the so-called intergroup bias; that is, a tendency to prefer members of the own in-group at the expense of out-group members. For example, people tend to show more accurate or faster face recognition, better recall, and to have more prosocial behaviors or empathic responses toward in-group than outgroup members, whereas out-group faces tend to be perceived more homogeneously (Elfenbein and Ambady 2002, Han 2018, Hewstone et al. 2002).

However, faces, just like objects, are encountered as part of a natural scene and are embedded in a typical visual context (Bar 2004, de Gelder et al. 2006). It has long been established that common associations between faces and environmental contingencies influence what is "seen" in the face, and that perceptual context is routinely encoded during face processing to form the "social gist of a scene". For example, the same fearful or happy facial expression is perceived differently if it is displayed along with an (in)congruent bodily expression, voice, or within a natural scene (de Gelder et al. 1999, de Gelder et al. 2000, Kret et al. 2013, Massaro and Ellison 1996, Pourtois et al. 2000, Poyo Solanas et al. 2018, Righart and de Gelder 2006, Van den Stock et al. 2014). Moreover, different information about fine details or global orientation and proportions are simultaneously conveyed differentially by high and low spatial frequencies, respectively, which in turn engage partly segregated neural pathways, such as parvocellular (P) and magnocellular (M) pathway (Burra et al. 2017, Mermillod et al. 2009, Oliva and Schyns 1997, Vuilleumier et al. 2003). A recent hypothesis also suggests that these parallel channels, with their characteristic processing phases, play distinct roles in the integration of social information (Carretié et al. 2007, Im et al. 2017, Kveraga 2014). Initial and reflexive processing of multiple congruent social signals from the face (e.g., emotional expression and gaze direction) would be predominantly associated with the phylogenetically older and action-oriented M pathway that feeds information primarily to the dorsal visual stream, whereas more reflective and sustained processing of ambiguity or incongruences would engage preferentially the slower and analysis-oriented P pathway that dominates in the ventral stream.

Although we are beginning to unveil how face perception influences the construal of social categories and the generation of related intergroup biases, we know very little about how simultaneous visual features are integrated and coexist in the formation of multiple social categories (e.g., a happy young Africano-American female). Initial evidence is suggesting that category formation is sensitive to elemental cues or basic features in the faces and in the surrounding visual context (Freeman et al. 2015). For example, fearful or sad faces are recognized by western culture observers more readily and correctly when covered by an Islamic headdress (e.g., niqab or turban), therefore in a visual context creating an out-group condition, than when covered by a cap or scarf, hence in the in-group condition. Conversely, recognition of happiness is more accurate when the face is covered by a Western compared to Islamic headdress (Kret and Fischer 2018, Liedtke et al. 2017). Categorization of race from faces is influenced by contextual attire, so that face-body compounds in a high-status attire (e.g., shirt, tie and jacket) bias responses toward “white” categorization, whereas the same face is more often perceived as “black” when presented in a lower-status or blue collar uniform (Freeman et al. 2011).

Finally, contextual cues can be embedded within the face itself and are part and parcel of social perception along multiple categories. For instance, an emotionally ambiguous facial expression tends to be perceived as angry when displayed by a man and as happy when female, due to stereotypes associating men to aggressive and women to joyful expressions (Hess et al. 2004, Kret et al. 2011, Stolier and Freeman 2016). Moreover, faces that are more difficult to decode and thence to categorize, either because of greater perceptual ambiguity or reduced familiarity, lead to more negative evaluations and enhance prejudices independently of the final outcome of the categorization process (Freeman, Pauker, et al. 2010, Hugenberg 2005, Hugenberg and Bodenhausen 2003, Hugenberg and Bodenhausen 2004, Hugenberg and Sczesny 2006, Lick and Johnson 2013, Lick and Johnson 2015). Mixed-race or gender-atypical faces produce a more unstable perception that bends categorical decision toward prejudices and negative outcomes, owing to stereotypical associations with out-group race or gender.

Collectively, these findings indicate that the formation of social categories from facial appearance is not simply a late process that occurs extrinsically after individual facial features are analyzed independently and then linearly assembled in an invariant or context-independent visual representation. Rather, visual perception and social categorization from faces are more malleable and context-sensitive than previously assumed, thus implying recurrent interactions at multiple processing stages. As it happens, some forms of prejudice seem liable to perceptual congruency between face and visual context, to stability of, and familiarity with the stimulus itself. Social behaviors and their interpersonal consequences also reflect the mutual interaction and inherent intersection of multiple social categories, whereby socially invariant categories like age, gender and race intrinsically interact with socially variant categories like emotional expressions (Freeman and Johnson 2016).

3. Prior knowledge and social-cognitive factors modulate face perception

Perception of social attributes is not only sensitive to basic visual features in the face and surrounding context, but also depends on prior knowledge, motivations, and higher-order social and cognitive factors. Although this principle is generally valid for any type of perceptual judgment, the inherent ambiguity of sensory input bearing social meaning, as reviewed above, leaves more room to top-down influences from processes and brain areas typically considered to operate after face representation stabilizes (Pavlova et al., 2017, 2018). For instance, political partisanship influences people's visual representations of a biracial political candidate's skin tone (Krosch et al. 2013). In fact, when pictures of candidates were manipulated to appear lighter or darker than the original, lighter photographs were judged as more veridical and representative if the observer's voting intentions were in favor of that candidate, whereas participants whose partisanship did not match that of the candidate showed the opposite pattern.

These high-level beliefs and expectations influence basic aspects of visual perception and dovetail with behavioral data showing that social factors like political affiliation and ideology permeate even downstream and largely unintentional behaviors, such as gaze following of in-group and out-group voters (Cazzato et al. 2015, Liuzza et al. 2011, Liuzza et al. 2013, Porciello et al. 2016). Gaze following, which is a reflexive oculo-motor behavior, is indeed significantly and positively correlated with the Implicit Association Test (IAT) (Greenwald et al., 1998). These two measures portend voting intentions and account for different aspects of the attitudes towards candidates. While IAT scores are predicted by explicit emotions toward the candidate, gaze following is predicted by the candidates' perceived influence within their political affiliation. Other higher-order social factors in the "eyes of the perceiver", such as stereotypical expectations in social status (Freeman, Penner, Saperstein, Scheutz and Ambady 2011), beliefs about economic scarcity (Krosch and Amodio 2014), or social dominance (Ho et al. 2013) impinge on the race or gender that is seen in the face.

Noteworthy, racial bias impacts not only on perceptual categorization of faces and facial attributes, but also reduces empathic resonance to pain (for a review see Han 2018). This has been measured as decreased response in area related to empathy, such as the anterior cingulate cortex (ACC), supplementary motor area (SMA) and anterior insula (AI) (Xu et al., 2009) or by reduced sensory-motor reactivity in the corticospinal system for observing pain in different-race individuals (Avenanti et al. 2010). Lastly, language and prior knowledge, including that derived from gossip, manifest themselves in shaping perception, including whether a face is consciously perceived or not (Anderson et al. 2011), akin to what has been previously shown for facial expressions in affective sciences (Barrett et al. 2007, Gendron et al. 2009). For instance, the temporary reduction in the accessibility of an emotion word's meaning, owing to semantic satiation procedure, leads to slower and less accurate perceptions of that emotion in the face (Lindquist et al. 2006). Likewise, presenting faces that vary in racial ambiguity with race-congruent or incongruent semantic labels shifts the threshold at which perceivers distinguish between racial groups. Therefore, semantic information offered by the verbal labels influences the categorization of race by creating a context for the interpretation of perceptual cues during social categorization (Tskhay and Rule 2015).

Evidence that the assignment of faces to social categories can be crafted by top-down factors, such as expectations or stereotypes that are traditionally considered extrinsic to the visual analysis of facial features, shares insightful analogies with the neuroscience of perceptual decision making; i.e. the study of processes involved in gathering and combining sensory information to choose one option from set of alternatives (Heekeren, Marrett, and Ungerleider 2008). For example, perceptual ambiguity can be resolved using “predictive coding”, whereby the brain anticipates the sensory environment by generating expectations that are based on prior probabilities of stimulus occurrence (Summerfield and de Lange 2014). Accordingly, perceptual predictions are repeatedly compared with, and gradually refine, the representation of sensory evidence until the visual system settles on the most likely interpretation of the input, and categorical perception is achieved (Esterman and Yantis 2009; Bar et al. 2001). For example, during a face detection task, Summerfield et al. (2006) found a neural representation of predicted perception in the medial frontal cortex (MFC) that occurred before actual stimulus presentation. This activity could be dissociated from responses in visual brain regions such as FG responsible for detecting the physical presence of the stimuli. Furthermore, top-down functional interactions from medial frontal cortex to FG increased during perceptual decisions about faces, thus support the idea that perceptual decisions are derived by matching expected with observed sensory evidence (Summerfield et al. 2006). These and other findings (e.g. Heekeren et al. 2004) suggest that areas in the lateral intraparietal area (LIP) and prefrontal cortices are particularly well suited to harbor expectations, whereas neurons in face selective visual areas mainly encode physical properties of the stimuli. Under predictive coding framework, parietal and prefrontal regions perform at least three different operations. First, they integrate noisy sensory information over time and compute a decision by comparing the different outputs of neurons in ventral visual areas. Second, they engender expectations or perceptual inferences that trigger the formation of specific stimulus templates against which incoming sensory evidence is matched. In fact, changes in neural activity in these regions occur independently of actual stimulus evidence or physical presence (Kok et al. 2014). Third, fronto-parietal areas modulate neural activity in ventral visual cortex through re-entrant projections to bias interpretation of sensory information towards one perceptual hypothesis.

In the context of intergroup bias, activity in frontal regions may help to situate face processing within a broader social context of predictions derived from prior person-knowledge, stereotypes or expectations, and induce final social categorizations to align accordingly. In fact, stereotypes can be conceived as implicit expectations generated during perception, thus influencing categorization from faces, similar to other types of prior knowledge (Mason et al. 2006). This hypothesis has been recently bolstered by an elegant study investigating the intersection of different social categories, during which participants viewed faces varying in gender, race and emotion. In a two-choice mouse tracking response task, the perceptual categorization along one dimension (e.g., male vs. female) became biased by task-irrelevant dimensions (e.g., black vs. white, or angry vs. happy), owing to stereotypical associations linking one category to another (e.g., black, male and angry stereotypes tend to overlap and intertwine). Notably, the pattern of interdependence between social categories during subjective perception of faces paralleled that assessed independently at the abstract level of conceptual knowledge. In this latter task, stereotypes concerning the same categories were measured presenting traits (e.g., “aggressive”, “intelligent”) and asking subjects to indicate whether the trait was stereotypic of the male or female category, black or white, angry or happy.

Finally, biased perception of faces owing to stereotypical associations was reflected at the neural level in the multi-voxel representation of the same categories in the FG and orbitofrontal cortex, i.e., in visual areas contributing to configural face perception and in the representation of social knowledge, respectively (Stolier and Freeman 2016).

In summary, traditional models treat stereotypes and prejudices as the end result of social categorization, which in turn derives from reading out face features in visual areas along the ventral stream. Mounting evidence about intergroup bias from faces offers a perspective that challenges some classic assumptions. The hierarchical architecture, with a serial progression of information and linear integration from lower-level face processing to higher-order social cognition, is leaving room to a heterarchical model of parallel processing and recursive dynamic interactions. In a heterarchy, ascending and descending pathways allow higher-level systems to be connected directly with lower levels. Also, integration within levels is ensured by lateral interactions providing horizonal relations (Crumley 1995; Bruni and Giorgi 2015; Heekeren et al. 2008). Accordingly, extraction of facial cues, social categories formation, and the semantic associations in related stereotypes, mutually constrain one another and recurrently interact until a compromise is achieved and social perception stabilizes.

4. Neural networks for intergroup bias

The quest to characterize the neural signature of intergroup bias has recently come under extensive scrutiny. Extant research concurs to support a network-based and dynamic approach to social brain functions, thus shifting the focus toward inter-regional connectivity patterns (Diano, Tamietto, et al. 2017, Pessoa 2014, 2017, Sporns 2014). Here we sketch a dynamic and interactive model that might serve as a framework into which different aspects of social perception and intergroup bias can be integrated (Figure 1). Core principles are derived from the *biased competition model*, which has been initially advanced to account for attentional functions (Desimone and Duncan 1995) and then readapted in the context of interactions between emotion and attention (Pessoa et al. 2002). According to the model, neural resources for stimulus representation are limited; thence a competition between multiple concurrent stimuli is purported. In the present case, the stimuli are the manifold visual cues bearing social meaning, whereas the ultimate outcome of this competition is a stabilized neural representation of the social category that is formed in the visual cortex based on perception and integration of these multiple facial and contextual features. As discussed in the previous sections, the competition takes place because: 1) social category formation from faces is inherently ambiguous, owing to high degree of within-category variations (e.g., more or less prototypical gender, race or emotion faces), thereby impacting differently on stereotype activation and social evaluations (Freeman, Schiller, et al. 2010, Freeman and Ambady 2009, Freeman et al. 2008, Mason, Cloutier and Macrae 2006, Pavlova et al., 2014); 2) social cues inhabit multiple social categories simultaneously (e.g., young and joyful Asian female), which coexist and interact dynamically until the formation of the dominant dimension.

[Insert Figure 1 here]

There is general consensus that different facial features are represented in visually responsive areas of the occipito-temporal cortices within a division of labor that reflects different functional specializations (Bernstein and Yovel 2015, Haxby et al. 2000, Pitcher et al. 2011). The occipital face area (OFA), in the lateral occipital complex, preferentially represents face parts, including the eyes, nose, and mouth, thus concurring to early, local and lower-level aspect of face processing that are particularly sensitive to physical variations. The fusiform face area (FFA) (Kanwisher et al. 1997) in the ventral-orbital portion of the temporal lobe encodes more global and invariant visual features, such as identity, gender or race. FFA activity is more linked to subjective perception than to physical attributes, and its responses are shaped by socio-cognitive processes, including stereotypes (Stolier and Freeman 2016) and implicit biases (Kaul et al. 2014, Van Bavel et al. 2008). For example, research demonstrated greater FFA activity in response to faces of one's own race; an effect associated with better recognition of in-group than out-group faces (Golby et al. 2001). Larger N170 component is found in event-related potentials (ERP) when white people with strong implicit prejudice view black versus white faces. This ERP component indexes configural face encoding and its neuronal generator is likely located in the fusiform gyrus (Ofan et al. 2011). Furthermore, neural representation of race in FFA, as determined by multi-voxel pattern analysis, reflects behavioral indices of prejudice and stereotyping (Brosch et al. 2013, Contreras et al. 2013, Ratner et al. 2012, Stolier and Freeman 2016). Finally, the posterior portion of the superior temporal sulcus (pSTS), in the lateral surface, processes changeable facial aspects, such as expression, and identity from dynamic features of familiar faces (Bernstein and Yovel 2015, O'Toole et al. 2002).

Competition for neural representation of social categories in visual areas can be biased by two functionally different and anatomically segregated mechanisms. One way is by bottom-up sensory mechanisms, such as reflex-like attribution of stimulus salience, associated affective judgments or visceral emotional reactions. For example, implicit prejudice may stem from reflexive threat responses to the perception of out-group members and is rooted in mechanisms similar to those governing fear conditioning and expression that are largely independent from selective attention or awareness (Amodio and Hamilton 2012, Amodio et al. 2003, Amodio and Ratner 2013, Hart et al. 2000, Kawakami et al. 2007, Olson and Fazio 2006). These bottom-up mechanisms are implemented in phylogenetically ancient subcortical structures such as the amygdala, which exerts a modulatory influence on visual areas (Blair 1999, Vuilleumier 2005, Vuilleumier et al. 2004). This re-entrant feedback enhances processing of affectively loaded stimuli that are thus endowed with a competitive advantage. Likewise, the insula seems to contribute 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 experiences 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).

Another way to bias face representation is by top-down processing that sustain social knowledge, impression formation, semantic memory, or that govern conflict monitoring and response selection. For instance, stereotype associations are posited to involve the anterior temporal lobe (ATL) that stores social knowledge helpful to predict and interpret facial information based on prior semantic associations (Eifuku et al. 2010, Olson and Fazio 2006, Ross and Olson 2012, Zahn et al. 2007). Trait (e.g., intelligent or athletic) and evaluative judgments (e.g., loyal or honest) indexing stereotyping and racial attitudes, respectively, correlate with activity in ATL (Gilbert et al. 2012). Also, when ATL normal functioning is temporarily disrupted by transcranial magnetic stimulation (TMS), the expression of implicit gender stereotype measured with IAT is attenuated (Gallate et al. 2011). In a similar way, the dorsal compartment of the medial prefrontal cortex (dmPFC) has been associated with gender and racial stereotypes in fMRI experiments, in agreement with the role of dmPFC in social cognition, mentalizing the formation of socially relevant impressions. A recent TMS study demonstrated the causal role of dmPFC in creating coherent impressions based on the integration of face and verbal description of social behaviors (Ferrari et al. 2016). Participants were required to form socially relevant impressions about other individuals on the basis of text descriptions of their social behaviors, and to decide whether a face alone, a trait adjective (e.g., "selfish"), or a face presented with a trait adjective was consistent or inconsistent with the impression they had formed. TMS interference with dmPFC selectively delayed responses about whether a face-adjective pair was consistent with the impression participates had previously formed.

Additive to the bottom-up/top-down dimension, a fuzzy distinction between emotional and cognitive components involved in intergroup bias can prove useful to further synthesize the different contribution of various neural areas. Although we treated intergroup bias as a rather unitary phenomenon, emotional and cognitive functions may impinge differently on prejudices and stereotypes, respectively, which are integral components of intergroup biases. In fact, prejudices entail positive or negative emotional evaluations related to a social category, whereas stereotypes reflect beliefs and conceptual associations related to a social category or group as defined in a given society or culture. We agree that the distinction between affective and cognitive functions is not categorical, and that complex behaviours such as those treated here emerge from the coalition of network of brain areas whose individual functions can be hardly conceptualized as specifically affective or cognitive (Pessoa 2008; Pessoa 2017). Likewise, prejudice and stereotyping operate in concert to determine intergroup biases in daily life. The cognitive aspects of stereotypes clearly include positive or negative attitudes toward these attributes, as much as prejudices involve mentalizing or perspective taking, which are typically considered cognitive functions. We therefore refer simply to the prevailing mode of functioning, acknowledging that the role of a given structure in a complex mental function is ultimately determined by the dynamic interactions it entertains with other regions (Pessoa 2014).

As discussed previously, structures like the amygdala or the insula seem predominantly linked to prejudices and negative attitudes toward out-group members, and exert their influence in a reflex-like and bottom-up fashion. Other areas such as the OFC are the source of top-down modulations that support flexible evaluative representations involved in intergroup prejudice (Bar 2004). In fact, the OFC links reward to hedonic experience (Kringelbach 2005) and contributes to the formation of perceptual priors that modulate activity of perceptual regions (Knutson et al. 2001, O'Doherty et al. 2004, Stanley et al. 2012). A meta-analysis of neuroimaging studies on the OFC also showed two prevalent axes of functional distinction. A medial-lateral distinction accounts for the representation and evaluation of reinforcers and punishers, respectively. Similarly, a posterior–anterior distinction indicates that less complex reinforcers such as taste are represented more posteriorly in the OFC than more complex or abstract reinforcers, which play a major role in prejudices (Kringelbach and Rolls 2004).

As for the contribution of areas prevalent in cognitive functions, the inferior frontal gyrus (IFG) in the lateral prefrontal cortex is associated with selection of concepts into working memory and to sustain actions (Miller et al. 2002). Besides the contribution of ATL and dmPFC already discussed, an interesting distinction relates relatively bottom-up versus top-down functions to the left versus right IFG, respectively. Building on hemispheric laterality also observed during action execution and inhibition (Aron 2007), it is suggested that the left IFG is more involved in the retrieval and activation of prejudices, whereas the right IFG contributes more to its control and inhibition (Amodio 2014). For example, when judging whether gender stereotypes (e.g., “enjoys shopping” or “likes action movies”) apply to target male of female faces, activity in the right IFC increased differentially if participants used the stereotypes rather than avoided using it (Mitchell et al. 2009). This has been interpreted as reflecting an effort to inhibit the impact of stereotypes on behavior, also based on the fact that IFG activity correlates negatively with amygdala response during perception of black faces in white observers (Cunningham et al. 2004, Lieberman, Hariri, Jarcho, Eisenberger and Bookheimer 2005). Other regions involved in more bottom-up versus top-down cognitive influences on stereotyping are the anterior cingulate cortex (ACC) and the dorso-lateral prefrontal cortex (dlPFC). The ACC is implicated in monitoring and detection of response conflict, which are needed to curb the influence of intergroup bias on behavior. Inhibiting the expression of racial stereotypes, which requires cognitive control, is associated with greater ACC activity (Amodio et al. 2004, Beer, Stallen, Lombardo, Gonsalkorale, Cunningham and Sherman 2008). While the conflict signal in the ACC arises, the dlPFC increasingly engages to select the appropriate response and guide behavior. For example, increased dlPFC activity is associated with better behavioral control of stereotypes (Amodio 2010) and prefrontal lesions impact on stereotypical gender attitudes (Gozzi et al. 2009), thereby contributing to identify the PFC as a site that guides the control of intergroup bias.

We are cognizant that "all models are wrong but some are useful" (Box 1979). With due limitations, we tend to think that the framework described above can accommodate most known functions of neural structures involved in intergroup bias and social perception from face. Briefly, the model proposes a dynamic integration and reciprocal exchange of bottom-up and top-down influences biasing and "explaining away" visual input in face perception regions, with a further distinction between affective and cognitive components.

5. Concluding remarks: current limitations and future challenges

Different areas of social and affective neuroscience deal with the effects of social and emotional factors on neuronal functioning. The social vision approach to intergroup bias seems uniquely situated to furthering our wisdom in this endeavor of investigation for several reasons. First, it focuses more on the dynamics that characterize the process of social perception rather than on the outcomes of this categorization. Second, by considering the role of attitudes, associative knowledge or social norms in relation to complex interpersonal behaviors, it fosters the cross-talk amid social psychology, neurosciences, cognitive and vision sciences. In doing so, the social vision approach contributes to contrast a reductionist attitude in neuroscience and portends a more pluralistic outlook to the relationship between brain and behaviors that accounts for the multidimensionality of complex social phenomena (Diano, Celeghin, et al. 2017, Krakauer et al. 2017). Neuroscience is indeed replete with examples illustrating the overt difficulty of deriving processes from processors. In other words, it seems epistemologically problematic and methodologically incomplete to infer the mapping between brain and behavior by looking exclusively at lower-level properties, as when relying only on neural data, with over-simplistic experimental designs, or with behaviors "incorporated as an after-thought" (Krakauer, Ghazanfar, Gomez-Marin, MacIver and Poeppel 2017). Finally, concepts recently introduced in neuroscience, such as brain's degeneracy (i.e., a psychological function or behavior may result from more than one neural circuits (Edelman and Gally 2001; Friston and Price 2003) and pluripotentiality (i.e., the same neural structure may have multiple functions and generate different behaviors (Anderson 2016; Gallese and Lakoff 2005; Pessoa 2008, 2014) are deep-seated in the social vision approach, and are fostering present-day advancements on our understanding of intergroup bias in social behavior (Celeghin et al. 2018, Celeghin, Diano, de Gelder, et al. 2017).

There are several limitations that are worth mentioning, which at the same time define just as many questions that remain outstanding. Most conclusions drawn from the extant literature on the neural bases of intergroup bias rely primarily on reverse inferences, where psychological processes are inferred from the observation of brain activity (Poldrack 2011). Moreover, the field has primarily focused on relatively basic responses to intergroup variations, such as passive viewing of racial group members, and concerned with racial prejudice, which is a specific form linked to highly identifiable physical attributes. Designing more complex tasks that also take into account and assess cognitive control of intergroup bias remains a future challenge. Also, social perception of traits and mental states warrants further investigation, as well as the study of whether principles of functioning discovered for facial features also hold for different social cues such as bodily expressions or vocal signals (Schrimer and Adolphs 2017). Indeed, we mainly focused on face perception since most studies on intergroup bias involved facial stimuli, and this modality has thus come to dominate our thinking. Concerning bodies, there are functional and anatomical analogies with mechanisms described above for face perception that may be intuitively accommodated within the proposed framework. For example, the congruence between bodily expressions and background scenes facilitates recognition of the target body (Kret and de Gelder 2010). Focal regions responding selectively to body parts and whole-bodies have been found in the lateral occipito-temporal cortex and labeled extrastriate body area (EBA) and fusiform body area (FBA), respectively (Downing et al. 2001; Greven and Ramsey 2017; Peelen and Downing 2005; Schwarzlose et al 2005; Urgesi et al. 2004; Peelen and Downing 2007). Functions of the EBA and FFA closely mirror those described for

OFA and FFA in face processing, while pSTS is involved in body recognition and action observations, thereby confirming its general role in processing changeable and dynamic aspects of social stimuli (de Gelder et al. 2012; Dolcos et al. 2011; Katsumi and Dolcos 2018; Puce and Perrett 2003). Lastly, there is initial evidence on the impact of stereotypes on body perception. In fact, during perceptual judgments, Black men were perceived as bigger, taller, more muscular and more physically threatening than White men in the absence of any actual physical differences in the stimuli (Wilson et al. 2017).

Other more specific questions remain unanswered. For example, the motor system is now considered an integral component of perceptual decision-making processes (Heekeren et al. 2008). How these structures contribute to decisions that are more complex and are not linked to particular actions is not yet clear. Equally unknown is how we trade off speed and accuracy in social decision making and categorization. Although studies on intergroup bias seem particularly ripe to expand our view on the neural and psychological processes involved in control and inhibition, this potential has not been fully exploited yet. However, it is noteworthy that psychological strategies that link a visual cue with a specific behavior are effective in facilitating the control and inhibition of implicit stereotypes (Mendoza et al. 2010). Visual expectation and attention seem intuitively related concepts, and disentangling these mechanisms in the context of social perception would contribute to better define their relationship in general (Summerfield and Egner 2009). Studies have found that expectations modulate neural activity also during states of inattention, thereby suggesting that attention is not a precondition for expectation to module perceptual decisions (Naatanen 1990; Feldman and Friston 2010).

Lastly, the translation of basic knowledge into intervention strategies is still in its infancy. For example, building on mechanisms of fear conditioning and extinction, images of racial outgroup individual were paired with positive images or counter-stereotypical concepts to contrasts intergroup prejudices and stereotypes (Kawakami et al. 2007, Olson and Fazio 2006). Furthermore, studies in infants and children investigating the ability to categorize faces by race or gender seem to provide further insights into interventions aimed at reducing discrimination (Lee et al. 2017). Indeed, although it has been shown that newborns and children are able to discriminate between faces from different ethnicities (Liu et al. 2015), later experiences with other-race people during childhood and adolescence appears sufficient to reduce the own-race bias in recognition (Goodman et al. 2007). Interestingly, this effect has been demonstrated not only at a behavioral level, but also at the neural level. For example, amygdala activity seems influenced by social interactions, as adults with more contacts with other-race people during childhood show lower amygdala responses to other-race faces (Cloutier et al. 2016). Also, amygdala response is affected by the internalization of cultural biases and social norms across development: as children get older, activity in this region increases in response to out-group faces (Telzer et al. 2013). Frequent contacts with both in-group and out-group members may reduce the stereotypical associations reflecting learned cultural knowledge towards out-group and, as a consequence, influence the reflexive affective judgments implemented in subcortical limbic regions. Consistent with our model, the IFG seems specifically recruited in adolescents, but not in children, to mediate evaluative and regulatory processes during perception of other-race faces (Telzer et al. 2013). Neuroimaging studies on intergroup bias in children are still scant, but these early findings suggest that some principles of the large-scale network organization neural proposed here arise from experience and can be subsequently refined through development.

In conclusion, the social vision approach to intergroup bias seems to offer a fruitful and timely ground for Tinbergen's seminal effort to go beyond the proximal causes of behaviors by considering also its real-world functions, evolution and development.

Author Contributions

AB, AC, CM, and MT performed bibliography search and discussed results. AB, AC, CM, and MT wrote the paper and approved final version for submission.

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Conflict of Interest

Declarations of interest: none

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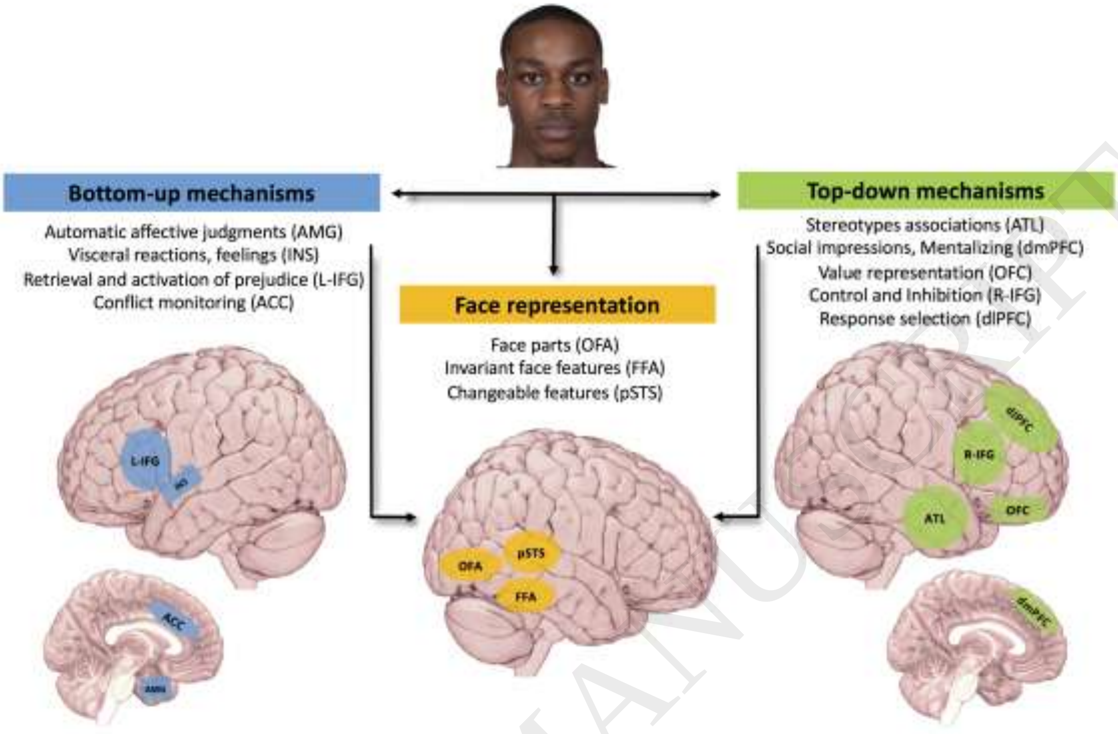
Figure Captions

Figure 1 (Color should be used for this figure)

Perception and integration of social categories. Visual representation (yellow) of social categories involves face-selective regions in occipital-temporal areas, including the occipital face are (OFA), fusiform face area (FFA) and posterior superior temporal sulcus (pSTS). Integration of visual cues is influenced by two functionally and anatomically segregated mechanisms. Bottom up mechanisms (blue) are implemented in subcortical and cortical structures, including amygdala (AMG), insula (INS) and left inferior frontal gyrus (L-IFG), whereas top-down mechanisms (green) involve mainly cortical areas, such as anterior temporal lobe (ATL), dorsal medial prefrontal cortex (dmPFC), orbitofrontal cortex (OFC), right inferior frontal gyrus (R-IFG), anterior cingulate cortex (ACC) and dorso-lateral prefrontal cortex (dlPFC). Square-shaped and oval-shaped areas distinguish areas predominantly involved in emotional and cognitive functions, respectively.


Bottom-up mechanisms
Automatic affective judgments (AMG)
Visceral reactions, feelings (INS)
Retrieval and activation of prejudice (L-IFG)
Conflict monitoring (ACC)
Face representation
Face parts (OFA)
Invariant face features (FFA)
Changeable features (pSTS)
Top-down mechanisms
Stereotypes associations (ATL)
Social impressions, Mentalizing (dmPFC)
Value representation (OFC)
Control and Inhibition (R-IFG)
Response selection (dlPFC)
L-IFG
INS
ACC
AMG
OFA
pSTS
FFA
dlPFC
R-IFG
ATL
OFC
dmPFC