

# The Neuroscience of Social Vision

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Humans display impressive fluency in perceiving and understanding one another. Through our senses, we are able to discern the identities, social categories, traits, and minds of our conspecifics. These perceptions are often performed accurately, rapidly, automatically, and simultaneously. This feat is especially impressive considering the complexity of social stimuli. A large body of literature has made great progress in documenting how we infer social information from complex perceptual cues, including both static and dynamic information gleaned from a target's face and body. Nonetheless, it is impressive that this information could be perceived efficiently, especially when it is often ambiguous or buried in noise. Since social stimuli are among the most consequential for perceivers, it is important they still efficiently extract this information.

Increasingly, research has documented the role of top-down forces in assisting and biasing social perceptions.<sup>1,2</sup> Such work argues that our context, culture, prior knowledge, emotional, and motivational states can all have great weight in shaping visual perceptions. While social psychological research has documented the perceptual

impact of many of these factors, the emergence of social neuroscience has proven vital in understanding the mechanisms involved and the extent of their influence, guiding and constraining theoretical development. In this chapter, we review the current scope of this contribution and discuss its trajectory moving forward. Given the lion's share of this work has regarded visual social perception, this chapter will focus on discussion of top-down influences in social vision.

The theory that top-down forces influence perception is not new, dating as far back as Helmholtz.<sup>3</sup> The empirical start of this approach was carried out by "New Look" researchers in the mid-twentieth century. The New Look saw perception as shaped by top-down factors such as motivations and expectations.<sup>4</sup> For instance, seminal work by Bruner and Goodman<sup>5</sup> found that children's size estimations of coins were biased by the value of the coins and the wealth background of the children.

Though the New Look eventually tapered off due to criticisms of its methodological and inferential rigor,<sup>6</sup> the ubiquity of twenty-first century top-down perception research in social psychology and neuroscience is

of no surprise. If perception is inferential, the role of top-down factors in *social* perception is even more plausible, given the consequential and ambiguous nature of social stimuli. Perceptions of others determine whom we trust and how we navigate interpersonal interactions. The information gleaned from a face is not always as clear-cut as objects and categories in the nonsocial world. For instance, there is large variation in cues that convey our age, sex, and race. Furthermore, these ostensibly independent categories often overlap in their cues and must all be extracted simultaneously. Cues may also be very ambiguous and fleeting in the decoding of transient aspects of a target, such as their current emotional state, beliefs, and intentions. In addition to the clear, adaptive function top-down factors would have in facilitating accurate perceptions, it may even be adaptive to have slight inaccuracies in perception if those inaccuracies facilitate adaptive behavior, such as erring on the side of caution to rapidly avoid potentially dangerous stimuli (e.g., mistaking a stick for a snake).<sup>7</sup> From the social psychological standpoint, such work has thus taken a functionalist perspective—where top-down influences on social vision streamline or alter visual processing to aid adaptive needs—which has proven productive.<sup>1,2</sup>

Another reason for the ubiquity of this work is due, in part, to current knowledge of pervasive top-down feedback processing in visual perception and the brain.<sup>8–10</sup> Research has identified white-matter feedback projections both within low- and high-level visual processing in the occipito-temporal cortex<sup>11</sup> and between many levels of visual processing and top-down regions, such as afferents from the amygdala, prefrontal, and orbito-frontal cortex to the occipito-temporal cortex.<sup>12–14</sup> Furthermore, functional neuroimaging has documented top-down shifts in visual representation reaching as far upstream as early vision in V1,<sup>15</sup> where a striking proportion of input is from higher-level regions.<sup>16</sup> Integrative work in perception has since benefited from this knowledge and advances in cognitive models, producing productive theories and research.<sup>17,18</sup> Such findings have been pivotal in both galvanizing and constraining theory into how top-down mechanisms may inform perceptual processing.

With its roots in both social perception and cognitive neuroscience, social neuroscience has quickly integrated this knowledge to produce valuable insights into these processes. In the current chapter, we will first review current knowledge of the functional neuroanatomy of social perceptual processes. We will then focus upon literature in social neuroscience regarding how social factors influence the visual perception of other people. We will also discuss research from the vision and cognitive neurosciences that provide valuable insights that may inspire future inquiry and observations from social perception ripe for exploration. Lastly, we will discuss the

implications of this research for discourse into the origins and function of top-down influences in social vision.

## 1. SOCIAL (VISUAL) PERCEPTION

Humans are lay experts in predicting many aspects of one another from mere appearance and behavior. Consider an encounter with any stranger on the street. Visual information alone can make apparent another's current emotions, beliefs, and desires, and it can bring to mind stereotypes and traits belonging to that person, in spite of their personalities and histories as we know them. Often these inferences and recollections are achieved from thin slices of another's nonverbal behavior in extremely brief time frames and are impressively accurate.<sup>19</sup> On the other hand, these perceptions are also prone to processing idiosyncrasies and our biases, which can leave them systematically inaccurate. The study of social perception has a long history, which has unearthed much about these processes. Born and raised in social psychology, social perception research focused predominately on how initial perceptions impact our inferences, evaluations, and behaviors toward others. For example, such work has long shown that particular types of information, such as an individual being recognized as a friend or an individual being recognized as a Black male, guides our evaluation of and behavior toward that individual, often in unconscious and unintended ways.<sup>20</sup>

With the increased integration of social, cognitive, and neural sciences in the twenty-first century, more attention has been placed on understanding the processes that give rise to initial social perceptions. Such work has pored over what happens between the reception of sensory input and the experience of a final social percept, such as how the flood of visual information on the retina is transformed into the happy, familiar face we interpret and act upon. Such work has made much headway, documenting how specific face, body, and voice cues assist in our recognition of others' identity, social category membership, traits, and mental states.<sup>21–23</sup> Such work has also taught us much about the cognitive and neural mechanisms underlying these perceptual processes.<sup>24,25</sup>

In social neuroscience, the bulk of research on top-down influences has explored how they modulate or control evaluative or behavioral responses, such as the regulation of stereotypes or negative attitudes in response to out-group members.<sup>26,27</sup> In this chapter, we focus our attention on how top-down processes impact the initial social perceptions themselves, which in turn trigger those stereotypes and attitudes. We will focus upon how social factors influence the visual processing of faces, including social categorization,

trait judgment, emotion recognition, and identity recognition. To lay out a foundation for our discussion of the social cognitive impact on processes on face perception, first we review current knowledge of their functional neuroanatomy.

### 1.1 Identity Recognition

Any story of face perception typically begins with the recognition of identity, as clearly, the successful recognition of familiar others is fundamental to life quality and survival. Identity recognition is a first necessary step in recalling crucial knowledge necessary to successfully navigate social interaction, and accordingly, face recognition has been a focal topic of research. Although a seemingly straightforward process, the computations required to recognize a face's identity and rapidly integrate configural integration of a complex, dynamic stimulus whose features vary across space and time are quite complex. The same individual face can appear different due to attire, age, facial expression, angle, and lighting. Nevertheless, human face recognition is remarkably accurate and efficient against all odds.

Prominent models of face perception put forth core and extended systems responsible for face recognition. These models carve the face perception process into two paths, one for the processing of dynamic features, such as emotion expression, and one for the processing of static features, such as face identity (as well as social categories, discussed below).<sup>24,25</sup> Convergent evidence from functional neuroimaging<sup>28</sup> and lesion patients with face-recognition deficits<sup>29</sup> (prosopagnosics) suggests key contributions of several regions to successful recognition. The primary system for processing static features, such as face identity, is dominant in the right hemisphere and is located along the hierarchical ventral-visual "what" stream responsible for visual stimulus recognition. In this hierarchical processing stream, stimulus representation begins in its retinotopic visual configuration and becomes increasingly more complex and conceptually constrained along the ventral-visual stream. Specific to faces, early feature processing occurs in regions such as the occipital face area (OFA). This information is then used to form higher-order representations, such as the holistic percept of a face, represented further downstream in the ventral temporal cortex (VTC), including the fusiform gyrus (FG) and fusiform face area (FFA) within it.<sup>30</sup> Such higher-order representations are thought to integrate information about a face into a more visual-independent representation. Interestingly, recent perspectives have argued that visually-independent, abstract representations of a face's identity are housed in the right anterior temporal lobe.<sup>31</sup> Most relevant to our discussion in this chapter, however, is how the extended social brain as a

whole is also suggested to play important roles in face recognition.<sup>32</sup>

### 1.2 Social Categorization

Social categorization is the process through which we group individuals based upon social information. The "Big Three" are sex, race, and age, but numerous other dimensions are categorized as well, such as social status, occupation, and even perceptually ambiguous categories such as sexual orientation.<sup>33,34</sup> Once determined, our social categorizations of others shape downstream evaluation and behavior, often without awareness.<sup>35,36</sup> This can occur largely through stereotypic associations, which can result not only in harmful biases, such as a tendency to accidentally shoot individuals who belong to racial groups stereotyped to be hostile,<sup>37</sup> but also ostensibly trivial biases, such as assumptions about the physical strength of young and elderly adults. Social categorizations also elicit evaluative biases and activate related attitudes (e.g., negative attitudes about Black individuals), which can exert strong impacts on behavior often in unintended ways.<sup>35</sup> Somewhat surprisingly, the neural architecture supporting social categorization has been largely unexplored, in part because much interest in social categorization has focused on the outcomes following the categorization process (e.g.,<sup>38,39</sup>). Indeed, for over half a century, social categorization has been considered a precursor to stereotyping and prejudice.<sup>40</sup> Recent models, however, propose that the reverse may also be true. As a social percept is processed in real time, stereotype and attitude structures may begin to spontaneously activate that in turn shape how that percept is even visually processed, molding it to conform to expectations derived from those stereotypes and attitudes.<sup>36</sup> We explore such reciprocal social categorization processes in this chapter.

The features that give rise to social categorizations are often static, such as the shape of facial features, hair, and skin color. Accordingly, the social categorization of faces is undertaken primarily by the ventral-visual stream, including the OFA and FG/FFA.<sup>24</sup> Corroborating this perspective, research has consistently found unique neural patterns for different races and sexes in these regions,<sup>41-43</sup> and these patterns are highly sensitive to natural gradations in such social category cues.<sup>44</sup> A large network of brain regions respond differentially to different visual social categories, but current knowledge indicates the regions in VTC play a central role in social category representation, consistent with their general role in visual categorization.<sup>45</sup> Given the wide impact of social categorizations, stereotyping, and prejudice on evaluation and behavior, different social categories also elicit unique responses in a number of cortical and subcortical regions, such as those involved in conflict

monitoring (anterior cingulate cortex), regulation (dorsolateral prefrontal cortex), and evaluation (amygdala, OFC) (for reviews, see Refs 26,27). While these regions are highly responsive to different social categories, this chapter is concerned more with the visual representation of social categories and how social cognitive processes fundamentally mold that representation, rather than downstream evaluative or regulatory processes.

### 1.3 Emotion Recognition

Recognition of emotion from facial and body expressions is crucial to adaptive social behavior. Emotion recognition guides response and action toward potential friendly or threatening others. As well, emotion recognition is paramount to successful communication between individuals. In order to identify emotions, we process both static and dynamic cues, such as facial expressions and bodily gestures. To make matters more complex, in naturalistic encounters, these emotional expressions are often quite ambiguous<sup>46</sup> and occur rapidly (even without our awareness) and therefore depend upon one another and context to be accurately identified.

While involving static features, emotion recognition differs from face recognition and social categorization in its dependence upon dynamic cues that are often configural. Dynamic cues processing is considered mostly separate from the static cue system discussed earlier. The independence of two systems involved in decoding static versus dynamic cues is an integral aspect of the functional architecture laid out in the Bruce and Young<sup>25</sup> model of face perception, and current neural models consider dynamic cue processing dependent primarily upon the superior temporal sulcus (STS).<sup>24</sup> Multivoxel pattern analyses have lent support to this model, finding the STS to carry categorical information about multiple emotion expressions (potentially right-lateralized).<sup>47,48</sup> While much work has focused on the role of the STS in emotion recognition, recent studies also suggest that ventral-temporal regions, such as the FG, are involved in carrying information about emotion expression categories as well.<sup>49</sup>

That recognition of and responses to emotion expressions depend on both static and dynamic information evokes questions about if and how this information is integrated. Investigations of face processing white-matter tracts found substantial connectivity between the OFA and FG, but no connections between the OFA/FG and STS.<sup>50,51</sup> Transcranial magnetic stimulation (TMS) delivered to the OFA reduces FFA responses to static and dynamic face stimuli, yet only reduces STS responses to static faces.<sup>52</sup> These results bolster a dissociated network in processing static versus dynamic features, yet refine and complicate its structure. It seems that the STS receives dynamic information from early visual regions

outside of static face processing regions (e.g., OFA), whereas it does receive static information from the OFA. Future research will be needed to understand if, where, and how this information is integrated to form emotion expression representations in the STS, as well as how the STS receives static information if not through direct white-matter tracts.<sup>50</sup> Furthermore, a critical question to emotion perception is to what degree static and dynamic emotion computations are integrated, and what contributions do each together or separately make to visual experience and behavioral responses. The susceptibility of emotion expression representations in these regions to top-down factors may come to inform their integrated and separable roles.

### 1.4 Trait Attribution

Among many other dimensions of social perception, humans naturally infer a wide range of traits from the mere appearance of another's face. These judgments tend to be consensual in that perceivers strongly agree in their evaluations, even with very limited exposure to a face,<sup>53</sup> and in some cases, these judgments can be surprisingly accurate.<sup>19</sup> Whether accurate or not, these perceptions may yield important consequences, such as differential outcomes in court for baby-faced as opposed to mature-faced defendants.<sup>54</sup> Overgeneralization theory accounts for many of these judgments, whereby trait judgments are extracted from facial features that associate with them.<sup>22,55</sup> For instance, neotonous features signal submissiveness and innocence due to their similarity to infants, or features on a neutral face similar to positive emotions signal trustworthiness due to their association with positive interaction.

Research into the brain regions underlying trait representation is still in its infancy, but consistent with the discussion so far of static features, evidence implicates the FG to be generally responsive to various trait attributions. Thus far, studies have found the FG to be responsive to baby-facedness<sup>56</sup> and trustworthiness,<sup>57</sup> though the extent of its involvement is still undetermined. Trustworthiness judgments have received considerable attention in the neuroimaging literature, due to their consequential nature and primacy as a dimension in social perception.<sup>22</sup> While static feature and trait representation may be housed primarily within the ventral-visual stream, the process of overgeneralization requires the involvement of many additional mechanisms. For instance, if trustworthiness judgments are the by-product of subtle emotion perception, they likely involve the interaction of face representation (e.g., FG), emotion expression processing (e.g., STS), and evaluative regions responsive to emotional expression (e.g., the amygdala). A series of studies have substantiated the finding that trustworthiness cues are implicitly tracked

by the amygdala,<sup>58</sup> even when faces are presented without subjective awareness.<sup>59</sup> However, while activity in both the fusiform and amygdala may underlie trait attribution processing, recent research has also found that these regions may be responding to the typicality of faces, which covaries with trustworthiness cues.<sup>60</sup> Such findings suggest that some of the curvilinear effects of trustworthiness in the amygdala (i.e., higher responses to faces appearing either more untrustworthy or trustworthy, relative to neutral) may possibly be accounted for by mere typicality effects, where deviations from the “typical” face elicit higher amygdala responses. However, such findings do not account well for the negative-linear effects of trustworthiness (i.e., higher responses to more untrustworthy faces) that also exist in the amygdala in different subregions.<sup>59,61</sup> Nevertheless, such findings suggest that there may be multiple component processes underlying the processing of facial traits, such as emotion overgeneralization and face typicality.<sup>62</sup>

## 2. SOCIAL INFLUENCES ON VISUAL PERCEPTION

The influence and fundamental role of top-down factors in social perception has received profound attention in social vision research.<sup>1,2</sup> Social perception is susceptible to countless social factors, including familiarity and prior knowledge, stereotypes and attitudes, group motivations and biases, emotion, and social context. Social perception is also malleable to the myriad “nonsocial” top-down influences that impact perceptual processing, such as expectation, processing goals, and attention,<sup>8</sup> in ways that are likely to be quite socially consequential.

### 2.1 Stereotypes and Attitudes

One abundant source of social information highly likely to guide social perception is stereotypes and attitudes. An impressive literature documents the myriad intergroup stereotypes and attitudes individuals form and their robust influence in social cognition and behavior (e.g., Ref. 38). Stereotypes are trait and behavioral ascriptions generalized to a social category, such as hostile stereotypes of African Americans in the United States. Stereotypes are nuanced, and their precise content guides cognition in specific ways.<sup>38,39,63</sup> We may come to avoid or overcome those we see as dangerous or pity and assist those we positively regard and believe unfortunate and helpless. We also may come to associate perceptual features of a target with stereotypes, such as Afrocentric facial features<sup>64</sup> or trustworthiness cues.<sup>65</sup> These associations make clear the expectations we may accrue about one another based upon stereotypes. Our stereotypes of race, sex, and age, among others, all elicit

associations with the many dimensions of social perception, such as facial features and traits, voice, and body language.

Race and sex categories are strongly associated with stereotypes and emotional responses tied to approach-avoidance behaviors, and in the presence of sufficient feedback structures, stereotypes may play a crucial role in driving even the visual perception of those categories. A rapidly growing body of behavioral studies has begun to document an interesting source of stereotype feedback in social category perception. For instance, different social categories that incidentally share stereotypes facilitate recognition of one another.<sup>36</sup> One example of this process is where one category (e.g., male) is perceived more efficiently if it happens to share stereotype contents (e.g., “aggressive”) with a presumably unrelated category (e.g., Black), and that “unrelated” category becomes activated. This leads to a number of perceptual effects, such as male categorizations of Black faces being especially facilitated, female Black faces partially activating the male category, and gender-ambiguous Black faces being overwhelmingly categorized as male.<sup>67</sup> Such intercategory relations are even found to drive an array of behaviors from interracial marriage to leadership selection.<sup>66</sup> The initial findings came from social categorization work, where categorization along one social dimension facilitated and inhibited categorizations along other categories. This has been shown to occur for race and sex (Black male, Asian female),<sup>67,68</sup> race and emotion (Black anger),<sup>69,70</sup> and sex and emotion (male anger, female joy),<sup>71,72</sup> among others. For instance, categorization efficiency of Black faces increases when they have an angry expression, a relationship that increases with racial prejudice.<sup>69,70</sup> Recent theoretical work has integrated these and other findings into a computational model, proposing stereotypes as one route through which this intercategory facilitation occurs. By this account, the processing of facial features (e.g., skin tone) begins eliciting category activation (e.g., Black), which in turn begins automatically activating associated stereotypes (e.g., hostile). With stereotypes activated, they become an implicit expectation that then guides the categorization process. The recurrent feedback naturally part of this dynamic system thereby allows activation of stereotypes to return upstream and shape other category activations, including those that did not initially activate the stereotype. Thus, for example, when processing a Black face with a happy expression, race-triggered stereotypes may become activated that then place an immediate top-down constraint on the perception of the face’s emotion, leading its perception to be biased toward anger. Overall, this work suggests that the visual perception of social categories is the end-result of a dynamic and malleable process wherein bottom-up facial cues and top-down stereotypes form a “compromise” over

time, in some cases biasing perceptions in accord with one's expectations.

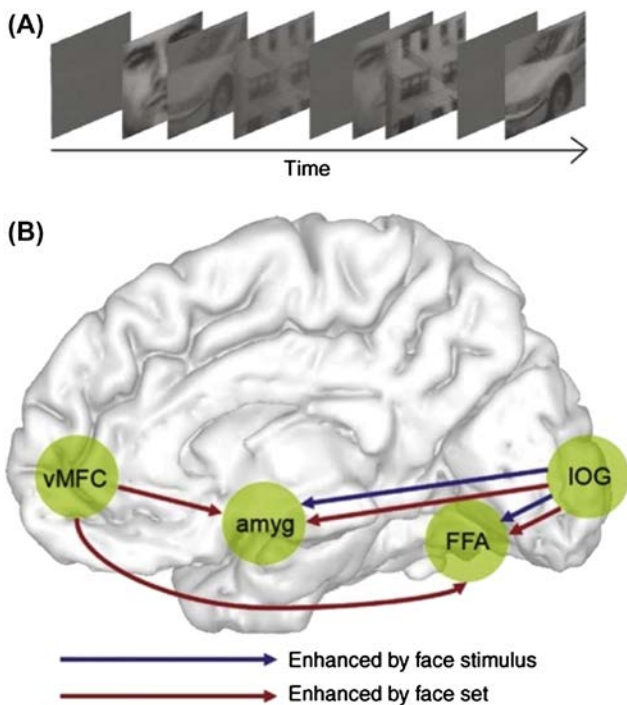
We recently conducted an fMRI study to examine the neural mechanisms underlying this dynamic process, specifically in the context of race and emotion.<sup>73</sup> In the scanner, subjects passively viewed faces independently varying along race (from White to Black) and emotion (from happy to angry). Following the scan, they completed a mouse-tracking task that measured individual differences in stereotype associations linking Blacks to anger and Whites to joy. In a mouse-tracking task, mouse trajectories are recorded as participants categorize a stimulus along a particular dimension by clicking on one of two responses in either top corners of the computer screen (e.g., Black versus White, anger versus joy). As participants head toward one response option (e.g., joy), their mouse trajectory may initially curve toward the other response option (e.g., anger) if that response option is stereotypically associated with one of the face's task-irrelevant category memberships (e.g., race is Black). For instance, while categorizing a Black face with a joy expression, participants may initially curve toward the "anger" response before ultimately selecting "joy," due to stereotypes associating Black with hostility and anger. In this particular study, the researchers used this task as an index of individual differences in stereotypes linking race and emotion (Black anger, White joy).

As faces became more stereotypically incongruent, we found that the anterior cingulate cortex (ACC), a region important for conflict monitoring,<sup>74</sup> showed linearly increasing activation. The ACC also showed increased functional connectivity with the FG. They argue that, when viewing a face, the ACC may have been involved in resolving conflicts between the bottom-up cue-driven interpretation (e.g., happy Black face) and the top-down stereotype-driven interpretation (e.g., angry Black face). This, in turn, may have led to greater communication with the FG, either for receiving more perceptual evidence to resolve the conflict, contributing notice of the conflict back to the FG, or both. Furthermore, the dorsolateral PFC (dlPFC), a region implicated in inhibiting prepotent responses,<sup>75</sup> showed heightened responses to stereotype-incongruent targets (e.g., happy Black face) in individuals with stronger stereotypic associations (as assessed using the postscan mouse-tracking task). Thus, one possibility is that the dlPFC, through functional connectivity with the ACC,<sup>76</sup> may have served the function of suppressing a stereotype-driven interpretation to make way for the veridical, cue-based interpretation (also see Ref. 77). It is noteworthy that these results were obtained when subjects were merely viewing faces passively in the scanner. Thus, the findings suggest that conflict monitoring and inhibitory mechanisms may help automatically clear inappropriate, stereotype-driven interpretations from the processing landscape,

ultimately allowing us to see faces for what they really are through the veil of stereotypes.<sup>73</sup>

Such results are informative as to the mechanisms underlying our ability to resolve the natural inconsistencies often encountered between our stereotypical expectations and another's actual face. Such stereotypical expectations can become activated by simultaneous category memberships, as with race and emotion above, but also by numerous other sources. Although these results implicate several brain regions in an overall sensitivity to stereotypic incongruities, we were also interested more directly in the representational structure of a face's social categories. Specifically, we were interested in how that structure can become altered by one's stereotypes at multiple levels of cortical processing, in turn reflecting a bias in visual perceptions. In a recent fMRI study, participants viewed faces crossed on gender, race, and emotion categories in the scanner.<sup>78</sup> Participants also completed a postscan mouse-tracking task assessing the degree to which the targets activated similar social categories due to shared stereotypes (e.g., to what degree Black targets are implicitly perceived to be more similar to male than female targets, due to overlapping stereotypes). Such stereotypically biased similarities between categories (e.g., Black and male) in subjective perceptions were reflected in the similarity of the categories' multivoxel representations in the FG and OFC, even while controlling for any possible featural similarities. These results suggest that these regions were involved in representing a face's multiple social categories, and importantly, in a manner systematically biased by stereotype information. It is possible that the OFC may be involved in spontaneously retrieving stereotype knowledge and generating implicit expectations (e.g., Blacks are hostile; men are hostile), congruent with prior lesion work.<sup>79,80</sup> Following stereotype retrieval, the OFC could then provide feedback to the FG to bias social category representations of a face, consistent with top-down feedback models in visual object recognition (Figure 1).<sup>13,17,18</sup> Such findings suggest that visual representations of faces' social categories in the FG may be biased systematically by one's stereotypical expectations, which may be imposed by the OFC.

In addition to stereotypes, individuals also develop strong attitudes and evaluative biases toward others that are typically positive or negative in nature.<sup>81</sup> These attitudes often manifest at an implicit level,<sup>82</sup> especially negative ones, and such implicit negative attitudes often predict less successful intergroup interactions in spite of individuals' explicit goals.<sup>83,84</sup> There are many aspects of visual perception that are likely to be influenced by attitudes. Among them is the perceived similarity of in-group and out-group members, as well as liked and disliked others in general. Out-group members are typically considered more dissimilar than in-group members.<sup>85</sup> One



**FIGURE 1** Schematic of how top-down feedback regarding expectations is contributed to visual processing of faces.<sup>17</sup> (A) In this study, participants viewed face and house stimuli during sets in which they were to identify one or the other. (B) Connectivity patterns enhanced by face stimuli and face sets. While seeking face stimuli, the OFC (vMFC) showed functional connectivity with the fusiform face area, putatively providing predictions to assist in target recognition. *Adapted from Summerfield and Egner.<sup>17</sup>*

fascinating study explored the neural correlates of this biased tendency, where participants viewed White and Black faces during fMRI, after which they completed an implicit measure of racial attitudes.<sup>86</sup> The authors found that participants with higher pro-White bias held more unique multivoxel representational patterns for White and Black faces in the FFA, suggesting that visual representations of White and Black faces in the FFA were more distinct for those with more biased attitudes. One likely explanation for these effects is the learning and formation of neuronal population codes in the FFA associated with White and Black faces that become more distinct and sharpened over time (or in less biased individuals, they become less distinct and more overlapping over time). In future work, it will be interesting to directly study the tuning of such stereotypically or attitudinally biased face representations over time (whether developmentally or via manipulations), as well as to explore the relevant moderators to better understand these patterns' flexibility and boundary conditions.

Although the effect of social experience and biases on the visual representation of social categories is quite new, there is a rich literature examining their effect on visual representations of a face's identity. The cross-race

effect (or own-race bias) is a consistently replicated and highly robust phenomenon whereby own-race faces are better recognized than other-race faces. Its causal mechanisms have been widely documented, extending from perceptual expertise<sup>87</sup> to motivational and cognitive differences in out-group face perception, such as increased individuation toward own-group faces.<sup>88</sup> One such difference in perceptual processing, whether due to perceptual expertise with the out-group or intergroup motivations, is decreased configural face processing.<sup>89</sup> Configural processing of faces is largely dependent on face-specialized regions in the right FG, such as the FFA.<sup>90</sup> To investigate its role in the cross-race effect, a behavioral study presented White and Black faces to the left and right visual fields of participants during a recognition task and found increased cross-race effect for faces presented in the left visual field.<sup>91</sup> Because information presented to one side of the visual field in each eye is routed to the contralateral visual cortex, faces presented to the left visual field were routed to the right visual cortex. The increased cross-race recognition deficit during left field presentations may therefore be explained by right visual cortex dependence on configural processing of faces. It is likely the left visual cortex employed a more similar, featural strategy to face processing and thus processed both races similarly. Thus, configural processing mediated by right visual cortical mechanisms seem to play a particularly important role in the cross-race effect.

To examine the neural correlates of this effect more directly, a seminal study using fMRI found increased bilateral fusiform activity to own-race, compared to other-race, faces during initial encoding, suggesting enhanced processing in face-selective regions may underlie better encoding.<sup>92</sup> Interestingly, as neural responses in the left FG responded more strongly to own- than other-race faces, the cross-race effect increased. That is, larger differences in left FG activity related to better performance for own-compared to other-race faces. However, the lack of right FG correlation with recognition performance is puzzling, due to its primacy in configural face processing. Though inconclusive, findings within the left FG raise interesting questions about its role in face recognition. A related study looking at cross-race deficits in race categorization (better race categorization of own-race faces) have found similar, though opposite, results and suggested featural processing dependence in the left FG to play a part.<sup>93</sup> An event-related potential (ERP) adaptation study has since shed further light on the neural processes underlying the cross-race effect. The N170, a face-selective ERP involved in configural face encoding, showed adaptation (reduced amplitude) to repeated identities in the right hemisphere.<sup>94</sup> These results suggest that other-race faces are perceived as more similar, supporting accounts of the other-race effect as relating to the extent of individuation or categorical perception.<sup>88</sup> These findings may also be

due to differences in perceptual expertise, among other factors, but importantly, they show this modulation to occur at core, early stages in perceptual face processing.

We have discussed several ways in which stereotypes, attitudes, and other social biases between groups may influence the visual perception of faces. Stereotypes are a rich source of expectations, and intergroup attitudes may motivate us to see others as dissimilar from ourselves or fail to individuate one another. Although the pronounced impact these factors have on downstream evaluation and behavior has long been recognized, it has only recently been considered that social biases can trickle down to affect lower-level visual processes, shaping our earliest visual perceptions of other people. The nascent study of these topics has left many questions open about the structure and function of these top-down effects on visual perception, which future work in this burgeoning area will need to explore.

## 2.2 Person Knowledge and Familiarity

Our experience and knowledge of one another are replete with expectations. One expectation is of course appearance, particularly the features and their configuration with which we identify an individual. As we have discussed, a single identity varies in its diagnostic features over space and time. Therefore our familiarity with a face can be crucial to its detection despite shifts in appearance. There is no stimulus with which humans are more adept and experienced than the face, and thus a large volume of research has investigated familiarity in face perception. In one behavioral study, face identities were morphed between two identities, creating a continuum of faces varying between the physical features of both identities.<sup>95</sup> Participants perceived face identity categorically, with an abrupt boundary between morph levels discriminating the two identities from one another. Importantly, participant familiarity with the faces positively predicted the degree of categorical perception. The more familiar a participant was, the more morphed faces were perceived as a specific identity. Another study investigated this during fMRI by looking at stimulus adaptation effects, where neural responses decrease in a region sensitive to properties of a repeated stimulus.<sup>96</sup> Using a morph continuum between Marilyn Monroe and Margaret Thatcher, participants were shown sequential pairs of the morphs, always varying in the same degree of featural changes. They found that the OFA showed similar adaptation to all morph-pairs, implying these regions process featural aspects of the face. However, the FG and FFA showed increased adaptation to morph-pairs recognized as the same identity, implying these regions are sensitive to the identity of a face. Importantly, the degree of these regions' adaptation to identity related positively with participants'

familiarity with Monroe and Thatcher before the experiment. These findings suggest that visual FG face representations exist at a higher level than their mere visual features, specific to knowledge about the identities of the targets. While identity and representation of a face depend on visual stimulus features, our familiarity with an individual can constrain these representations and identify faces that do not match perfectly as belonging to the same stimulus. However, an open question remains as to how this learning and modulation occurs.

The neural process underlying familiar face recognition is likely exceedingly more complex. A prominent view now assumes familiarity effects to rely partly upon higher-level knowledge about the target.<sup>32</sup> However, investigation of this is difficult, as familiarity may be due to visual or social experience with the target. Furthermore, the influence of social familiarity is likely manifested through various routes, as social familiarity depends on person knowledge as well as evaluation and attitudes toward that individual. To dissect this process, experiments have often contrasted different forms of familiarity. Adaptation studies have failed to reliably show familiarity effects independent of stimulus features (for a review, see Ref. 97). Therefore it is possible that familiarity effects in the FG are dependent on visual familiarity with the stimulus alone.<sup>96</sup> We may come to better understand exactly how familiarity assists face perception through the study of identity population codes and focus on the extent of the VTC, including anterior regions that may more uniquely represent identity.<sup>31</sup>

A recent study addressed this question by presenting participants with faces of individuals, some of whom were associated with biographical information.<sup>98</sup> These faces varied in orientation to control for visual familiarity. While multivoxel identity patterns were not modulated by the biographical information specifically associated with the target, targets associated with biographical information increased in representational similarity to one another. Similar coding of targets associated with person knowledge suggests social information biases fusiform representations of identities, but the underlying process remains elusive. Nonetheless, this study depended on person knowledge gained through relatively superficial impressions, and the modulatory effects of different forms and degrees of familiarity remain to be seen. If person knowledge does have a unique contribution to visual processing, interesting questions will concern the dynamics of its influence and how it shifts representational structure. For instance, it is possible that familiarity and prior knowledge is fed back to the fusiform online to guide representation.<sup>99</sup> It is also plausible that experience with familiarity of the target structures more permanent population codes in the FG, and familiarity affects the criterion a stimuli must meet to activate this population.



Research outside of neuroimaging has provided convincing evidence that speaks to the role of person knowledge in early face processing. Specifically, individuals associated with negative behaviors are more likely to reach and dominate conscious visual perception.<sup>100</sup> Participants learned about different faces, paired with positive, neutral, or negative information. Participants then completed a binocular rivalry task. In binocular rivalry, different images are presented to both eyes of the participant, and one image comes to dominate conscious visual experience while the other is suppressed. The dominant image in binocular rivalry is largely dependent on competition in early visual processing, while top-down factors, such as attention, modulate this.<sup>101</sup> When different conditions were presented to both eyes, negative-associated targets were found to dominate in binocular rivalry. Impressively, this effect was driven specifically by social information. These results suggest that preconscious processing of the target elicits person knowledge that is fed back to enhance its visual representation. The primacy of negative-associated targets evokes interesting questions about the adaptive role of this feedback, for instance to promote vigilance toward threats (a topic we address later in the chapter).

Neuroimaging work examining the impact of person knowledge on social perception has focused on its impact on trait judgments and impression formation. One study found modulation of both amygdala and fusiform activity when subjects made personality judgments of faces with and without prior knowledge of the target.<sup>102</sup> With no prior knowledge, personality judgments elicited increased amygdala responses for making rapid judgments of faces. However, with prior knowledge of the target, although making the same judgments of faces, amygdala responses were absent with the activation of a cortical mentalizing network in their stead, including the STS and posterior cingulate cortex. These results suggest that prior knowledge modulated the role of the amygdala in personality judgments, supplanting it with mentalizing processes. This provides evidence that, although the amygdala's role in rapid trait inferences is quite spontaneous and can occur even without subjective awareness,<sup>59</sup> such processes may also be sensitive to context and top-down social factors. Future work will be tasked with investigating how these shifts interact with upstream visual processing, as well as possibly adopting neural decoding approaches to better understand the representational content of regional responses to personality traits.<sup>103,104</sup>

Modulation of social perceptual regions through prior knowledge about a target is a largely unexplored topic. The unique contributions of different sources and content of this information is critical to explicating this process. Therefore, future work would do well to consider these distinctions, such as visual and knowledge-based

familiarity (for a discussion, see Ref. 97). The contribution of person knowledge to face perception may depend on regions considered key in person knowledge, such as the medial prefrontal cortex (mPFC),<sup>105</sup> which has been shown to make unique contributions to familiarity effects in face perception independent of visual familiarity.<sup>106</sup> Investigation of the coupling between regions involved in person knowledge and face perception will be crucial to understanding the scope of familiarity's influence. Furthermore, the extent and function of this modulation may differ along the ventral visual stream, influencing earlier visual and later higher-level representation differently.

### 2.3 Motivation and Goals

In contrast to the specific knowledge and expectations provided by social group stereotypes, a number of motivational biases are inherent in merely categorizing ourselves and others as in- or out-group members. Perhaps one of the most consequential of human behaviors, humans are innately coalitional and come to support in-group members while being wary of or hostile toward out-group members. The biases that follow this tendency are comprehensively documented in social psychology and have an equally long history.<sup>107,108</sup> Prominent theories have studied how social identity with a group as well as minimal group categorizations bias cognition and behavior across a variety of domains. In contrast to familiarity, stereotypes, and attitudes learned through culture and intergroup interaction, these biases occur, importantly, in the complete absence of stereotypes and prior experience with both in- and out-group members. The neural substrates guiding in- and out-group categorization and underlying structural schemas that allow these biases to generalize still have yet to be investigated. However, research in social neuroscience has already begun to demonstrate the fascinating ways in which coalitional motivations influence social perception.

A powerful procedure for investigating unadulterated coalitional biases is the minimal group paradigm.<sup>107</sup> This method involves assignment of the participant to a "minimal" group, a group with which the participant has no prior experience or knowledge. Initial application of this in a neuroimaging context assigned participants to one of two arbitrary teams, the Tigers and Leopards.<sup>109</sup> During fMRI, participants learned, then viewed, the faces of both in-group and out-group members, with an equal number of White and Black faces assigned to both teams. In-group member faces elicited stronger bilateral FG responses than out-group members, an effect that was not moderated by target race. Increased in-group responsiveness in the fusiform is consistent with prior research, where such findings have occurred in the context of race.<sup>92,110</sup> Prior work interpreted this bias as

potentially reflecting learning and perceptual expertise with the in-group (e.g., cross-race effect, see above).<sup>92</sup> However, these findings support the perspective that increased FG activity corresponds to more effortful processing by the regions toward targets over and above target visual features, perhaps due to individuation processes withheld from out-group faces.<sup>88,94</sup>

The above research raises questions regarding the modulation of race representation in the fusiform. The mitigation of gross response increases toward own-race faces may be interpreted as the fusiform instead focusing on minimal group membership, consistent with behavioral studies finding race to be discounted to a degree when not diagnostic of in- or out-group membership.<sup>111</sup> Regional fMRI signal increases may be indicative of involvement during processing but do not necessarily reflect information represented within any set of voxels. In addition to general increased activity in the fusiform, later research investigated the informational content of the fusiform during a minimal group task. Similar to the study above, participants were presented with novel in- and out-group members, with both White and Black faces assigned to each team.<sup>43</sup> Replicating prior findings, the FG showed increased responding to the faces of in-group members. Despite the absence of race differences in regional activity, multivoxel patterns indicated that race was still represented in the fusiform cortex, even more so than earlier visual cortical regions. Such findings therefore suggest that group membership is unlikely to abate race representation itself, but it may mitigate cross-race perceptual differences through shifts in regional engagement in processing.

Nonetheless, there is much to learn about the impact of coalitional cognition on social perceptual mechanisms. The further exploration of how group membership alters the representation of others is an open area of inquiry, and it will also be important for research to identify how such top-down effects on visual perceptions relate to the robust biases observed in downstream behavior.

## 2.4 Emotional States

Emotions are internal states, defined by a conglomeration of physiological responses, which serve as powerful catalysts to adaptive cognition and behavior. These states inform us about the threats and affordances in the world around us, and our internal motivations and desires. Their nature is so intuitive that the study of emotion has maintained constructs derived from folk theories of emotion (e.g., fear, anger, and disgust). These internal states have an accordingly long history of functionalist accounts in modern science (e.g., Ref. 112). Traditional theories classified them as emotions with a focus on their functional role in human social and nonsocial behavior (for a review, see Ref. 113). Functionalist accounts

of emotion have been valuable to social psychologists interested in how social perception then predicts behavior toward targets, such as how emotion-specific stereotypes and prejudices drive intergroup behavior.<sup>38,63</sup> These theories parsimoniously capture how we avoid others who elicit disgust or fear (due to perceived disease or danger) and approach others who elicit positive emotions (due to perceived benefits) or anger (due to perceived threats that must be overcome).

At the psychophysiological and neural levels of analysis, biomarkers have been identified that reflect accounts of discrete emotional experience. Some physiological research conceptualizes emotions as the psychological categorization and cognitive elaboration of a more fundamental set of underlying physiological states.<sup>114</sup> “Core affect” models the variance in internal states in line with neurophysiological data, reducing them into two dimensions: arousal and valence.<sup>115</sup> For instance, an experience of intensely unpleasant arousal may be construed differently as fear or disgust dependent on the context. Moreover, these internal states show profound impacts on cognition and behavior and may play a crucial role in social perception through the extent of their modulation across the nervous system.<sup>13,116</sup>

Considerable research has focused on the role of the amygdala in processing the affective significance of social stimuli and serving as an important modulator of perception. One such line of work comes from an interesting series of studies exploring the conscious awareness of faces presented subliminally. An initial study presented participants’ happy, fearful, and neutral faces outside subjective awareness through a backward masking task.<sup>117</sup> Specifically, participants who were more often aware of the masked fearful faces showed enhanced amygdala activation to subliminal faces. The authors interpreted this as dependence of the amygdala response on conscious awareness of the fearful faces. However, an alternate interpretation was put forth, that only when amygdala responses occurred were participants consciously aware of the masked face.<sup>118</sup> Specifically, it was proposed that known afferents from the amygdala to the ventral-visual stream<sup>12</sup> continuously provide feedback that enhances visual processing to bring the target into awareness. That is, when the amygdala rapidly responds to the momentarily subliminal fearful face, affective information is fed back to enhance and sharpen face representation, increasing awareness.

Providing indirect evidence for this account, a later study had participants complete a binocular rivalry task with happy, angry, and neutral faces.<sup>119</sup> Participants were induced to experience positive, negative, or neutral affect. While negative affect induction exacerbated overall dominance of face stimuli during rivalry, congruency of affect and facial expression valence increased dominance of that facial expression (i.e., angry faces

exhibited dominance during negative affect and positive faces during positive affect). The general increase in binocular dominance of face stimuli during negative affect supports one interesting hypothesis, that negative affect states may promote vigilance in perceptual processing toward motivationally relevant stimuli. However, that affective congruence with the stimulus valence increases binocular dominance provokes additional fascinating questions about the role of affect and emotion in perception (e.g., dominance of happy face during positive affect). One possibility is that this effect is due to valence congruency between affect and the stimulus. By this interpretation, positive and negative affect facilitate processing of all congruently valenced stimuli. However, it remains to be seen whether there is a more nuanced functional specificity for individual emotions and motivational states. If emotions do each serve specific adaptive functions, we may expect specific emotions to enhance detection of specific emotional expressions. For instance, it is possible a fearful state shows enhanced facilitation toward threatening stimuli (e.g., anger expressions). Functional specificity of this mechanism would also provoke other interesting questions, such as enhanced processing of different aspects of a target (e.g., disgust enhancing processing of faces with pathogen cues).

Beyond the modulation of perception, emotions may play a more integral role in perception. In fact, research into their role has been the spark and paragon of social perceptual systems inexorable from their top-down contributors. Seminal work demonstrated that bilateral amygdala damage impairs the recognition of fear expressions.<sup>120</sup> From both lesion and fMRI studies, repeated observation of amygdala dependence in fear recognition suggests the affective response to a target plays a causal role in its recognition.<sup>121,122</sup> Lesion deficits may indeed be due to a lack of necessary feedback to visual regions such as the fusiform cortex. In one demonstration, amygdala and control lesion subjects were shown neutral and fear faces during fMRI.<sup>123</sup> Both control and lesion subjects showed face-selective activity in the FG. Intriguingly, while control subjects showed even higher responsiveness in the FG to fearful faces, those with amygdala lesions did not. Furthermore, increases in the extent of amygdala damage parametrically predicted decreases in FG responsiveness to fearful faces. These observations suggest that the amygdala plays a role in the modulation of responses in visual regions, perhaps through increasing responsiveness to certain stimuli. In addition to fearful expression recognition, amygdala damage has been found to relate to many emotion recognition deficits,<sup>121</sup> including an increased deficit toward social emotions (e.g., guilt<sup>124</sup>).

That said, there is still uncertainty concerning the role of emotion in these processes. This has become increasingly clear regarding its role as an essential component

in perception. While initial studies hinted at a perceptual system where the lack of emotional feedback to early visual regions precluded emotional expression recognition, later work provided an alternative that is rather compelling. Another potential route through which affective states could impair emotion recognition is through abnormal direction of attention to motivationally relevant stimuli.<sup>121</sup> This evidence comes from studies looking at fear recognition in a patient with complete bilateral amygdala lesions. In a first study, deficits in fear recognition were mediated by lessened attention to the eyes of faces; however, upon directing attention to the eyes, recognition accuracy returned.<sup>125</sup> A later study with the same patient showed normal detection of fearful faces during rapid presentation and masking tasks.<sup>126</sup> These studies therefore suggest the amygdala may only be involved in slow, deliberate, and conscious recognition of the emotional expression (e.g., where attentional search can impact decisions). Whatever the precise role of the amygdala is in modulating perception, Barrett and Bar<sup>13</sup> argue that emotions are predictive in nature and assist and guide perception. This perspective does not require that detriments in emotion preclude perception, but that they reduce its efficiency by preventing predictions of higher-order regions from feeding back to lower-level visual regions. Future research could explore how the lack of such predictions impacts perceptual responses.

## 2.5 Social Context

In the controlled environment of an experiment, individuals may categorize a cropped face superimposed on a white background. People in the wild are of course seen in meaningful contexts, such as the context of an organic grocery store, or the context of a political gathering. These contexts provide expectations about who we are to perceive within them, informing every facet of social perception. It is natural to anticipate someone's gender in a beauty parlor, emotion at a lively celebration, or identity in the living room of a close friend. In this sense, context is an aspect of the environment that activates expectations that elicit predictions about a target.

A large body of work has demonstrated how expectation influences perception through prediction,<sup>17</sup> and it has done so with the presentation of faces. While activity in the FG, a face-selective region, typically increases to face relative to house stimuli, this increase is also observed in the absence of any face stimuli when participants merely have the expectation that a face is to be presented.<sup>127</sup> FFA activation is also found in response to degraded face images once subjects have learned to detect the face, a process potentially recruiting parietal attention regions.<sup>128</sup> The influence of context as an expectation in perception has been a prominent topic in vision

research. As we will return to in our discussion, findings of its profound role in vision pioneered our understanding of prediction in perception and recognition.<sup>18</sup> A predictive account of context allows us to consider a much richer contextual environment (for discussion, see Refs 36,129). Here we discuss context as any aspect of the environment that provides expectations and predictions about the perceptual computation at hand. As we shall see, these contexts include the environment, as well as the body and face, and inferences made from them.

The most patent contextual influence is the scene in which we encounter someone. As we have considered, scenes are ripe with information that predicts who we are to perceive. Yet context is also ripe with information that predicts who we are *not* to see. For instance, one may expect a target to be Asian in the context of a market in the outskirts of Hong Kong. Or, one may expect a target to be White in the context of a corporate supermarket in the Midwestern United States. As comes to mind in consideration of these examples, we may also expect *not* to see a race in the scenic context of another. One line of research has documented how scenic context influences social categorization. In an initial behavioral study,<sup>130</sup> participants categorized faces varying on a White-Asian morph continuum. These faces were presented within scenes associated with each race, as well as a neutral context. Relative to the neutral context, congruent race-context trials facilitated race categorization (e.g., Asian face within Asian scenes), and incongruent contexts interfered with race categorization (e.g., Asian face within American scenes). These findings support a predictive role of context both guiding and limiting potential outcomes.

During fMRI, participants completed the same contextual race categorization task.<sup>131</sup> Both the OFC and retrosplenial cortex (RSC) linearly increased with congruency of face and context. That is, each region increased as facial and context cues became increasingly compatible and decreased as they became increasingly incompatible, all relative to neutral pairs. Prior work on scenic contextual influences in object categorization has documented contributions from the OFC and RSC.<sup>18</sup> The OFC is believed to update knowledge of current context provided by visual regions and play a role in feeding predictions back to early visual regions, such as the FG.<sup>17</sup> The RSC is involved in spatial processing and responsive to full scenes,<sup>132</sup> and increases in activity with contextual-target congruency may underlie contextual associations.<sup>18</sup> Consistent with this role, RSC activity mediated the impact of face-context congruency on reaction times in face categorization. Together with the behavioral findings, these studies show the nuances contextual predictions provide in social perception. Not only do contextually evoked expectations facilitate perceptions, but they can also inhibit perceptions that are incompatible with the context.

Research has extensively documented how context imbues emotional expressions with meaning, especially given the often ambiguous nature of emotional expressions.<sup>133</sup> Scene contexts provide obvious indicators of the emotional state of those around us. When confronted with a long line to the ticket counter for a social event, we have a clear and likely accurate expectation of the frustration on the face of our neighbor. Neuroimaging research into scenes' contextual influences on emotion recognition have shown context to influence processing in early visual regions. In one study, neutral and fearful faces were presented to participants with congruent or incongruent background scenes (e.g., fearful face depicted in front of a burning home).<sup>134</sup> Consistent with an account of contextual prediction influences perceptual processing, activity in the FG increased during congruent face-scene pairs. Also consistent with an account of context inhibiting unlikely outcomes, there was a decrease in FG activity during incongruent face-scene trials. Together, such studies exploring contextual impacts of scenes on social perception implicate a network of regions involved in expectation (OFC), scene perception (RSC), and face perception (FG).

The context in which we perceive a target may also be situational. We would only expect a look of fear on someone in our social event line example if it was known that tickets were running low. One study has investigated how situational context impacts neural responding to emotion expressions, where participants viewed surprise (similar to fearful expressions) expressions in different contexts during fMRI.<sup>135</sup> Faces were preceded with sentences describing a positive or negative context, and faces in negative context evoked stronger amygdala responses. Importantly, these responses were seen in response to faces in context, but not to the contexts independently. Contrasts also found responsivity of the FG between negative and positive conditions. Future research will, however, be needed to fully characterize the mechanisms at play. In addition to exploring the role of situational context, this study provides evidence that context modulates evaluative processing in the amygdala, which as discussed earlier, may play an integral role in emotion perception.<sup>116</sup> Furthermore, in the study of emotion expression perception, increased amygdala responses are typically seen for facial expressions of fear,<sup>136</sup> making it possible that contextual information disambiguated the facial expression systematically due to fear-surprise expression similarity. Multivariate pattern analyses may lend themselves to investigating the neural underpinnings of such shifts more conclusively in the future.

In addition to the scenic and situational context, faces are of course typically atop an entire body. As visual context, the body is especially useful in providing predictions about a face, nonetheless about a target on their

own. Akin to the face, body cues convey diagnostic information that reveals a target's intent, experience, traits, and even identity, a process that relies heavily on body-selective regions such as the extrastriate body area (EBA) and fusiform body area (FBA) (for review, see Ref. 137). At the most fundamental level, the mere presence of a body predicts a face situated appropriately upon it. In one study, participants viewed images of faces degraded so as to be unrecognizable as faces and either embedded upon a body appropriately or placed separately elsewhere within the same image.<sup>138</sup> Embedded upon a body, degraded face stimuli elicited FFA activity comparable to nondegraded face stimuli, whereas in other conditions, the degraded face stimuli did not elicit FFA activity. General visual increases in activity to degraded faces upon a body evidences the body as a contextual predictor. Most impressively, this response in the FFA provides convincing evidence of the specificity of this prediction. That the FFA would respond as though a face present is fascinating, as FFA responses are often considered face-specific and are held in higher level regions typically associated with visual experience.<sup>139</sup>

Of course, there are more nuanced predictions the body provides about targets than their possession of a head. Humans, like all animals, behave differently in accordance with our motivations and emotions. The body thus provides a clear window into our internal states. Research into this matter has focused on the congruency of facial and body expressions. For instance, behavioral research has paired fearful and anger face and body stimuli during a face emotion categorization task.<sup>140</sup> Accurate emotion recognition was best in congruent pairs, and when face–body expressions were incongruent, the body expression largely drove emotional categorization of the facial expression. Another study used faces continuously morphed between happy and fearful with happy and fearful body stimuli, finding the body expressions to drive perceptions of the ambiguous facial expressions.<sup>141</sup> Recent research has reiterated the dominance of the body in face–body influences in emotion recognition, focusing even more broadly on valence judgment of emotional expressions.<sup>142</sup> This occurs strikingly to the degree that valence of high intensity natural facial emotional expressions were not discriminated above chance, whereas the valence of body expressions were discriminated accurately and drove valence judgments of facial expressions. Using event-related potentials (ERPs), the congruency of the face and body has been found to modulate neural responding as early as 115 ms.<sup>140</sup> Specifically, Meeren and colleagues found increased occipital P1 amplitude toward incongruent face–body pairs. The P1 is associated largely with attention, and its generator is potentially located in the ventral extrastriate cortex.<sup>143</sup> The response of the P1 to congruency of the face and body implies these separate aspects of the target impact one

another early in processing. The rapidity of this modulation leaves open the possibility that their interaction is dynamic and contributes to initial representations that are then fed forward.

Models of expectation and prediction in visual perception propose a predictive role of the OFC in guiding earlier OTC visual representation, especially via context.<sup>18</sup> It is still unclear to what extent these influences modulate visual representation as opposed to visual responding. The introduction of multivariate pattern analyses may serve as a powerful tool in explicating the outcome of these influences in OTC. In combination with research focused upon those percepts most malleable to context (e.g., emotion expression), pattern analysis tools may allow researchers to assess to what degree and how early visual representations are modulated toward those expected. Given its general role in expectation and prediction feedback in vision, the OFC, as we will continue to discuss, may play a general role across contexts.<sup>17</sup> In addition to a general OFC–OTC prediction loop, the nuances of different contextual sources likely depend on different associative cortical regions to exert their influence (e.g., such as scene or body-processing regions). Furthermore, if socially unique effects are continuously encountered in this research (e.g., Ref. 134), an important line of work may pursue the socially domain-specific nature of these effects.

### 3. MECHANISMS OF SOCIAL VISION

We believe findings in social psychology and neuroscience may provide new avenues for investigation to both extend and elaborate top-down influences in vision. Outside of social psychology and neuroscience, the vision sciences have investigated top-down influences in detail, providing compelling accounts of these processes that speak to their function and origins. At the neural level, top-down influences are likely to be enacted through a series of recurrent feedback connections. For instance, a considerable proportion of input in the visual cortex as early as V1 comes from higher-level regions, and observations of top-down modulation of V1 is accordingly ubiquitous.<sup>8,16,144</sup> Much of this input comes from within the extent of OTC.<sup>11</sup> A sizable amount of modulation also comes from nonperceptual regions of interest to social neuroscientists, such as the amygdala,<sup>12,145</sup> OFC,<sup>13,17</sup> and PFC.<sup>14</sup> While work has documented many direct anatomical sources of afferents in visual regions, much remains to be unveiled. In addition to direct connections, modulation is also likely enacted through successive processing and complex networks extending back to the visual cortex from various extraneous cortical and subcortical regions. Research in cognitive neuroscience has organized the top-down influences

of interest to the field predominately under the general processes of attention and expectation, among others less relevant to the current discussion.<sup>8,146</sup> Generally, the current perspective is that top-down influences shift properties of receptive fields as well as the information carried by neuronal populations.

There are findings in social vision and neuroscience that may not fall neatly within these existing frameworks.<sup>8,146</sup> Many of these findings are currently explained by motivational factors. Much recent research has found individual motivations and biases to impact processes such as categorization. One particularly interesting set of questions regards the impact of group membership on perceptual processing. For instance, does heightened FG activity to novel in-group members<sup>109</sup> reflect expectation or attention, or potentially a perceptual processing difference toward this group? Or are these effects merely postperceptual feedback or memory-driven? As well, how do implicitly prejudiced participants show sharpened or more dissimilar representation of in- and out-group races in the FG?<sup>86</sup> Does this reflect the above component processes of expectation or attention? Is this a difference in perceptual processing, or potentially a by-product of learning influenced by the top-down factors? It will be vital for future work in this vein to investigate these processes independently of the processes discussed here, as well as familiarity.

Another interesting avenue for research will be the differential perception of ambiguous stimuli. Much work in social categorization has asked how top-down influences impact category boundaries between stimuli, such as how political orientation, economic scarcity threat, or perceived social status impact the category boundary between in-group White targets and out-group Black targets.<sup>147–149</sup> These effects may reflect perceptual changes in nature or may not elicit differences in perceptual experience. Neuroimaging research can help investigate the extent to which these shifts occur in visual processing regions. An initial glimpse at this process has already been provided by work showing categorical representations of identity in the occipitotemporal cortex related to familiarity with the targets.<sup>96</sup> If there are indeed perceptual processes at play, it will be fascinating to explore how neuronal populations shift their receptive fields and thresholds to represent categories, and whether such shifts comprise a unique process of top-down influence on perception.

#### 4. AN INTEGRATIVE FRAMEWORK

The perceptual and top-down processes we have discussed are numerous. In addition to a more parsimonious account of top-down factors in social perception, recent computational accounts of person perception provide a possible integrative framework for these

perceptual and top-down processes and their interactions. The dynamic-interactive theory of person construal provides a connectionist model and dynamical systems approach to understand how the many levels of social perceptual processing functionally interact and develop dynamically.<sup>36</sup> The model is a recurrent connectionist network allowing large-scale interaction to play out over time between parallel and multilevel processes.

There are several key characteristics of the model that dovetail with our current discussion. The model includes multiple levels of processing, such as featural processing (e.g., face, body, voice, and contextual cues), social category representation (e.g., race, sex, emotion, and identity), and top-down factors (e.g., emotion, motivation, context, and prior knowledge). Connections do not only ascend the levels of the model, but feedback connections allow for top-down levels to influence lower-level processing. For instance, emotional states may reach down and activate category nodes relevant to them, facilitating their recognition when featural input activates them (e.g., Ref. 119). Information not only transfers one level at a time in the hierarchy but may also bypass adjacent levels when there is an association with further levels. This characteristic may account for some bottom-up cases where cues directly activate stereotypes<sup>64</sup> and reflects how certain top-down afferents extend directly to early vision.<sup>12</sup> Parallel nodes also interact laterally, allowing them to facilitate and inhibit one another. Therefore multiple inputs, for instance, received in parallel, such as facial features, may influence processing of one another.

These characteristics may sufficiently model expectation effects in social perception. In conjunction with expectation models,<sup>17,18</sup> top-down factors may not only facilitate activation of lower-level representations (such as context facilitating activation of congruent emotional expressions), but lateral interactions allow this activation to cascade and inhibit alternatives (e.g., angry expression inhibits happy expression). Furthermore, this model accounts for complex interactions, such as “bottom-to-top-down” influences, such as when social category interactions occur (for review, see Ref. 150). Cues may activate categories (e.g., Black), which in turn activate stereotypes (e.g., hostile) that wind up feeding back and activating ostensibly unrelated categories (e.g., male). Such category interactions have been observed between various social categories, such as race and sex,<sup>66,67</sup> emotion and sex,<sup>71,72</sup> and race and emotion,<sup>69,70</sup> and these are reflected in multivoxel representations of social categories in the FG and OFC.<sup>78</sup> However, currently the model does not specify how various forms of attention may select and filter information in earlier processing. As we gain insight into how the various forms of attention underlie social perception, future work may come to better integrate this into theoretical models.

## 5. THE ORIGINS AND FUNCTION OF SOCIAL VISION

As we discuss the myriad ways in which social factors influence perception, it is impossible not to often return to question why such a system would exist. For the social psychologist, functionalist perspectives have been central to theoretical development and have provided a parsimonious account of numerous phenomena. A perspective put forth by Gibson<sup>7</sup> echoes the William James<sup>151</sup> adage that thinking is for doing, in that perception is for doing. Gibson argued that ecological context shifts the affordance provided by any stimulus, and thus vision may guide action by modulating the perception of that stimulus in a way that facilitates appropriate action toward it. For instance, one may mistake a stick for a snake as to guide the less costly action of a false positive than negative. Fiske<sup>152</sup> paraphrased William James to argue that “social thinking is for doing” (p. 877), and in this vein, current work now extends Gibson<sup>7</sup> with the idea that social perception is for doing.

Psychological work in social perception has found supportive evidence in many domains, especially those social.<sup>1,2</sup> For instance, in the face of economic resource scarcity, White participants allocate lesser resources to out-group Black targets while perceiving their skin tone as darker, thereby increasing their out-group perception in a time where in-group favoritism is adaptive.<sup>147</sup> In addition, heterosexual individuals in romantic relationships perceive opposite-sex targets as less attractive, thereby lessening the threat to their relationship satisfaction.<sup>153</sup> Functionalist accounts also include general influences, such as context,<sup>133</sup> emotion,<sup>154</sup> and motivation.<sup>155</sup>

The consistency with which these influences have fit a functionalist framework naturally provokes questions about their adaptiveness and the role of evolution in their emergence. From this perspective, their phylogeny may have been guided by the adaptive benefits they afforded our near or distant ancestors. Mechanisms that allow shifts in perception that facilitate adaptive action, such as wariness of a potential threat or attraction toward a mate, may have been selected for. This evolutionary framing is quite appealing given it outlines one exception to a noteworthy concern with the idea of malleable perceptual experience—that action more often depends on accurate perception than not. An adaptationist account provides a plausible avenue through which a perceptual system that is suboptimal in certain domains (e.g., inaccurate distance perception while tossing an object<sup>156</sup>) may be adaptive in other domains that result in their selection (e.g., vigilance toward a threat by misperceiving its proximity<sup>157</sup>).

Alternatively, an interesting possibility is that social influences are mere by-products of mechanisms adapted for different functions. As has been observed

in vision research, many top-down influences in perception serve the purpose of increasing perceptual efficiency.<sup>8,17</sup> Expectation and attention filter and guide information processing in a system flooded with input. Therefore, it is possible that the evolution of these mechanisms put in place the architecture upon which social factors enact their influence as a by-product. By this perspective, allowing factors such as context and emotion to efficiently facilitate accurate perception may have put in place architecture that is subject to prediction errors, such as the misperception of distance or skin pigment. These perceptual errors are often in line with functionalist, adaptive predictions, as the errors facilitate behavior that may have been adaptive in certain contexts (such as exaggerated out-group perception that may cause one to distance themselves from potential threat). Such nonadaptive by-products of traits are discussed in evolutionary biology and are termed “spandrels” after the adorned spaces between indoor arches in architecture, which are not intentionally constructed but a by-product of arch shape.<sup>158</sup> In some cases, they may even provide more plausible accounts of certain phenomena, for instance how social and semantic categories may become entwined due to their overlapping perceptual and top-down features.<sup>36</sup>

There is of course little conclusiveness in the origin of these mechanisms, especially from their mere observation in humans. It is considerable, for instance, that these mechanisms evolved due to the adaptiveness of malleable perception, and their efficiency through prediction was a by-product. As well, they may both have been selected for independently due to adaptive benefits. These theories are also compatible, in that the underlying architecture of this system could have been evolved for perceptual efficiency, then co-opted for adaptive social functions (such as perceiving an object in a way that facilitates adaptive behavior, e.g., a stick for a snake). On the other hand, a malleable perceptual system may have been selected for, then co-opted for general perceptual efficiency purposes. The possibilities are numerous, and all fascinating. Their conclusion will likely rest upon anatomical evolutionary and cross-species research. Regardless, and importantly, these theories each provide fruitful avenues for hypothesis generation, whereby research may investigate where these influences are adaptive, make errors, or arise as by-products of the system’s architecture. One benefit of social neuroscience integrating models from cognitive neuroscience is that the complexity and constraints of these models may make apparent by-products that impact social cognition in a manner not intuitive via a functionalist perspective.

Regardless of its origins, the presence of these modulations across the brain provokes core questions

in perception and cognition. With the resurgence of research into top-down influences in perception, there has also been a resurgence of the debate as to whether evidence demonstrates top-down factors impact on perceptual *experience* per se.<sup>159,160</sup> The penetrability of conscious perceptual experience to these forces is a captivating question. Yet we must be cautious in interpreting the widespread modulation of activity across visual regions, as there is a lack of conclusiveness regarding neural substrates isomorphic with perceptual experience. For instance, visual activity as early as V1–V4 holds information about a visual stimulus held in working memory without the presence of the stimulus,<sup>161</sup> yet participants do not experience a perceptual experience of the stimulus. Therefore, despite the rich body of work discussed in this chapter, we yet lack conclusive evidence given the perennial challenge of measuring perceptual experience. Nonetheless, the research reviewed here and elsewhere does provide one convincing conclusion: that visual processing, at many levels bar the retina, is affected by the spectrum of top-down social and nonsocial influences. This work thus bolsters the reemerging perspective that fine lines between cognition and perception are worth scrutiny, and we hope its future development may come to bear on this debate.

## 6. CONCLUSION

Our knowledge of social perception was once limited to its downstream consequences, such as how categorization and perception influence stereotyping and behavior.<sup>40,152</sup> The past decade has seen unprecedented progress in unveiling the processes underlying initial percepts. Such progress has been driven by an equally unprecedented integration between disciplines, including the anticipated wedding of social-cognitive and neural sciences,<sup>162–164</sup> as well as social-cognitive and visual sciences.<sup>1,2,165</sup> Together, these perspectives have engendered productive theoretical accounts of social perception<sup>36</sup> and have galvanized research into its basis across levels of analysis. In this chapter, we have focused on the top-down influences in social perception, and importantly, the interesting and nuanced ways in which they interact with different levels of processing. Specifically, we have reviewed neuroscience research into top-down influences in social vision, a parsimonious account of these influences from the vision and neural sciences, and have discussed how these areas may inform one another and fit within current computational frameworks. We hope the current direction of this research forges a productive collaboration that informs each of the social, cognitive, and neural sciences.

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