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Multimodal investigations of emotional face processing and social trait judgment of faces

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Abstract

Faces are among the most important visual stimuli that humans perceive in everyday life. While extensive literature has examined emotional processing and social evaluations of faces, most studies have examined either topic using unimodal approaches. In this review, we promote the use of multimodal cognitive neuroscience approaches to study these processes, using two lines of research as examples: ambiguity in facial expressions of emotion and social trait judgment of faces. In the first set of studies, we identified an event-related potential that signals emotion ambiguity using electroencephalography and we found convergent neural responses to emotion ambiguity using functional neuroimaging and single-neuron recordings. In the second set of studies, we discuss how different neuroimaging and personality-dimensional approaches together provide new insights into social trait judgments of faces. In both sets of studies, we provide an in-depth comparison between neurotypicals and people with autism spectrum disorder. We offer a computational account for the behavioral and neural markers of the different facial processing between the two groups. Finally, we suggest new practices for studying the emotional processing and social evaluations of faces. All data discussed in the case studies of this review are publicly available.

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INTRODUCTION

The human face is a critical channel for social communication and social interaction. This point has been well accepted in popular culture: numerous movies and TV shows such as *Inside Out* and *Lie to Me*, and the widely used emojis, all assume that emotions are expressed in and perceived from specific facial configurations; caricaturists create their art by exaggerating the link between certain social traits and the appearance of faces. Psychologists and cognitive neuroscientists have investigated the neurocognitive basis of the perception of others' momentary emotions and stable social traits from faces for several decades (for reviews, see Refs. 1–3). The ability to accurately perceive and interpret affective and social information from faces is vital for effective communication and even survival. Many of these judgments are made automatically and rapidly.[3–6] They inform a range of real-world decisions, such as dating and hiring,[7] approachability,[8] elections,[9–12] and sentencing decisions[13,14] (see Ref. 15 for a review). However, inferences of affective states and social traits from faces alone are often inaccurate and susceptible to biases in society.[16] For example, juries' decisions are influenced by their perception of the facial expression of guilt/remorse from defendants' faces.[17] Social traits judgments, such as competence and moral character, are biased by the perceived social identity of the faces and the stereotypes associated with it.[18] Thus, the emotional and social information from faces plays an important role in shaping social interactions and social decisions.

It is worth noting that although facial emotional expressions are momentary and state-dependent while social traits are long-term and stable, they are not entirely separate. Instead, they are intricately linked in the way humans perceive and interact with each other. Our perception of social traits can be influenced by the emotional expressions we observe on people's faces.[19] For instance, individuals with facial structures that resemble happy expression may be perceived as more trustworthy or sociable. Furthermore, the neural and cognitive processes involved in decoding facial emotional expressions and inferring social traits may overlap or interact.[20] For instance, people perceive a greater degree of anger from less trustworthy-looking faces. Investigating how the judgments of emotions and social traits interact and potentially influence each other can provide insights into shared behavioral and neural mechanisms and help us better understand the broader picture of human social perception and cognition.

Primates have evolved a specialized visual system to process faces.[21–24] The amygdala is an essential component of this network, playing a critical role in the processing of faces.[25] For a long time, the human amygdala has been linked to the recognition of facial emotions.[25–28] Studies have shown that individuals without a functional amygdala may have difficulty recognizing fearful faces.[29–31] Functional magnetic resonance imaging (fMRI) has demonstrated that the amygdala is most active in response to fearful faces.[32–34] While

most research has focused on fearful faces,[27] the amygdala has also been found to respond to neutral or happy faces in both fMRI[35] and single-neuron recordings.[36–39] However, some studies suggest that the amygdala still shows a greater response to facial expressions related to threat, such as fear and anger, than neutral or happy faces.[40] Researchers have used single-neuron recordings from the human amygdala to demonstrate that these neurons encode subjective judgments of facial emotions[41] and the content of emotions.[42] Furthermore, amygdala neurons encode social trait judgments and a comprehensive social trait space that establishes the basis of first impressions from faces.[43,44] In addition, amygdala neurons encode important facial features such as the mouth and eyes that may have a significant role in facial emotion and social trait judgment.[45]

Individuals with autism spectrum disorder (ASD) experience extensive challenges in social functioning, especially in recognizing emotions.[46,47] While some studies have identified deficits in recognizing emotions from facial expressions in individuals with ASD,[48–51] others have not observed such deficits[52–54] (see Ref. 55 for a review). Impaired emotion recognition may arise from atypical fixation onto faces, which has been reported in many studies,[54,56–58] but again the literature is mixed.[59] Additionally, individuals with ASD make social trait judgments from faces differently compared with neurotypicals.[52,60] Notably, the differences in both emotion perception and social trait judgment between ASD and neurotypicals have been linked to the two groups' differences in amygdala function.[46]

In this review, we demonstrate how multimodal approaches, including human single-neuron recordings, electroencephalogram (EEG), fMRI, and computational modeling, together advance a richer understanding of perception of social affective information from faces, in both neurotypicals and individuals with ASD. We first discuss a relatively underexplored facet of neural encoding of emotion, emotion ambiguity, and subsequently provide a comprehensive analysis of social trait judgments from faces. Finally, we discuss future directions and new perspectives to investigate facial emotions and social trait judgments from faces. We acknowledge that emotion and social trait are just two, among many other, types of information people perceive from others' faces. Other types of information, such as identity[61,62] and attractiveness,[63–66] are also critical for our understanding of person perception, but are beyond the scope of the present review.

EMOTION AMBIGUITY

When making perceptual decisions, we encounter situations where the mapping of a stimulus category to a choice is uncertain. Facial expressions of emotions are a stimulus category in which we frequently encounter pronounced ambiguity, as different emotions can be difficult to distinguish from one another.[67] It is important to note that the term "ambiguity" in decision-making studies usually refers to an absence of information about a stimulus beyond categorical uncertainty, while in the perceptual domain, it refers exclusively to categorical uncertainty, where all information about the stimulus is available and the task is deterministic. In this review, we define facial emotion ambiguity as the degree of uncertainty that arises when making a categorical decision between two emotional facial expressions that are close to the perceptual boundary.

In this section, we first describe a physiological signature that indexes emotion ambiguity using EEG.[68,69] EEG source location indicates that this signature originates in the cingulate cortices, with corroborating BOLD-fMRI activation in the same areas.[69] These cingulate cortices are functionally connected to the amygdala,[70] and functional MRI also demonstrates amygdala activation.[42] Notably, single-neuron activation in the amygdala to the same stimuli aligns with these neuroimaging results.[42] Furthermore, the amygdala's involvement in social dysfunctions in ASD is evident,[25,71] and indeed atypical emotion judgment has been observed in individuals with ASD.[59] Finally, we present a computational account that elucidates ASD behaviors using single-neuron data from the human amygdala.[72]

EEG reveals a physiological signature that encodes facial emotion ambiguity

A significant amount of research has been conducted on the neural mechanisms that encode ambiguous information related to perception and emotion. A specific area of interest is the late positive potential (LPP), which occurs around 400 ms after stimulus onset and is primarily associated with evaluating ambiguous information. The LPP has been found to be sensitive to various types of ambiguity, including ambiguous facial expressions,[73] racially ambiguous faces,[74] and stimulus uncertainty.[75] The LPP plays a critical role in perceptual decision-making by accumulating sensory information and determining choices.[76–78] It indexes perceptual decision-making processes that involve gradually accumulating evidence until a specific threshold is reached.[79] Given the LPP's role in coding faces, emotion, uncertainty, and combinations of these attributes, Sun et al. proposed that the LPP may serve as a physiological signature encoding facial emotion ambiguity and they systematically investigated how the LPP responds to ambiguous emotional faces, the specific attribute it encodes, and how accumulating sensory information can be dissociated from determining choices, shedding light on how the LPP encodes perceptual ambiguity.[69]

Specifically, Sun et al. utilized EEG and fMRI with three types of ambiguous stimuli to examine the neural representation of perceptual decisions under ambiguity (Figure 1A,B).[69] The LPP was first shown to differentiate levels of ambiguity (Figure 1C), and notably, the LPP was shown to be specifically associated with behavioral judgments about choices that were ambiguous (Figure 1D). Through mediation analyses and a series of control experiments, the LPP has been shown to be generated (1) only when decisions are made (not during mere perception of ambiguous stimuli) (Figure 1E), (2) only when decisions involve choices on a dimension that is ambiguous (Figure 1F), and (3) more strongly in the presence of ambiguous stimuli compared to when only unambiguous stimuli are present (Figure 1G).

Earlier notions that the LPP might be specialized in processing affective pictures[80–82] have been supplemented by accounts that the LPP is not specific to fear-happy emotion ambiguity, but also encodes emotion ambiguity along the anger-disgust dimension (Figure 1H) as well as morphed animals (Figure 1I).[68] Therefore, it is a general neural signature for perceptual ambiguity, not specific to facial expressions of emotions or even faces. Furthermore, using task instructions with different levels of ambiguity, it has been shown that the LPP is modulated by task instructions and has the maximal response when the dimension of stimulus ambiguity is task-relevant.[68] The LPP is specifically associated with response latency and confidence rating, and it can be explained by direct behavioral ratings

of task ambiguity and difficulty but not eye movement patterns.[68] It is worth noting that in the field of perceptual and cognitive neuroscience, different terms have been used to describe this event-related potential (ERP) component (e.g., P300, centro-parietal positive potential, and late positive deflection). The manipulation of attentional locus and stimulus-reward association drives this ERP component,[83–86] consistent with its role in coding stimulus ambiguity and task uncertainty.

Research employing source modeling, a technique used to estimate the location and activity of brain sources contributing to EEG-recorded electrical signals, has identified the anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), and insula as the origins of the LPP.[87–89] This has been confirmed by fMRI and fMRI-guided ERP source prediction (Figure 1J,K).[69] The dorsal ACC (dACC) is thought to be involved in the detection of performance errors and the monitoring of conflict.[90–94] Meanwhile, the ventral ACC (vACC) is associated with fear extinction[95] and emotion regulation.[96] In particular, studies using ambiguous face stimuli have shown that the negativity bias, which is the tendency to interpret ambiguous stimuli as negative, is positively correlated with vACC activity when ambiguous faces are perceived as sad.[97] The ACC has functional segregations (see Refs. 92 and 96 for details), but most of its functions involve processing ambiguity in some form, which requires conflict resolution, ongoing action monitoring, dynamic adjustments in cognitive control, and inversely correlates with confidence in judgment. Studies have shown that both dACC and vACC are activated during ambiguous decision-making.[98] Ambiguous emotional faces relative to unambiguous emotional faces activate the dACC, whereas ambiguous affective decisions relative to ambiguous gender decisions activate the vACC.[99] Together, the functional localization in the ACC corroborates the role of the LPP in encoding facial emotion ambiguity.

Neuroimaging and human single-neuron recordings reveal encoding of emotion ambiguity in the human amygdala

The amygdala is particularly important in detecting ambiguous stimuli and modulating vigilance and attention accordingly.[100–102] Research has shown that the amygdala is capable of differentiating between stimuli with varying degrees of perceptual ambiguity. Notably, highly trustworthy and untrustworthy faces elicit the strongest response from the amygdala, while the response is weaker for faces that are perceived as intermediate (i.e., ambiguous) in terms of trustworthiness.[103–105] This phenomenon has been observed even when the faces are unconsciously perceived.[103] Additionally, the amygdala shows the strongest response to the anchor faces for both faces varying in valence and faces varying in nonvalence dimensions.[106] Furthermore, emotional stimuli, regardless of valence, lead to greater amygdala activity compared to neutral stimuli.[107] These findings suggest that the amygdala plays a crucial role in processing the categorical ambiguity of the dimensions represented in faces.

Using a unique combination of human single-neuron recordings from the amygdala and functional neuroimaging, it has been shown that the human amygdala encodes facial emotion ambiguity, in addition to emotion degree (Figure 2).[42] Specifically, fMRI shows that the left amygdala is activated by emotion degree and that the right amygdala is activated

by levels of emotion ambiguity (Figure 2A). Single-neuron recordings show that there are two separate populations of neurons, one whose response correlates with the gradual change of fearfulness or happiness of a face and a second whose response primarily correlates with a decreasing level of categorical ambiguity of the emotion (Figure 2B,C). Together, this study has shown convergent evidence from human single-neuron recordings and fMRI that the amygdala encodes facial emotion ambiguity.

Computational approaches and clinical populations reveal behavioral and neural markers of facial emotion processing

Several studies find reliable, but weak, differences in the ability to recognize emotions from facial expressions between neurotypicals and individuals with ASD,[48–51] although others do not.[52–54] The discrepancies in these findings may be due to the heterogeneity of ASD participants, differences in the stimuli and tasks used in the various studies, ceiling effects, and the compensatory strategies used by individuals with ASD. However, it has been suggested that as long as the measures used are sensitive enough, behaviorally or biologically based measures can usually detect group differences in facial emotion recognition.[55] To enhance sensitivity and avoid ceiling effects, two main methodological approaches have been proposed: modifying task demands, such as by using difficult or unfamiliar tasks, and manipulating stimuli, such as using face morphing.[49,51] Along this line of reasoning, one study used a two-alternative forced-choice task with a gradient of morphed faces along the fear-happy dimension to investigate the sensitivity and specificity with which people are able to distinguish ambiguous emotions in facial expressions (the same task and stimuli as in Figures 1A,B and 2). It has been shown that people with ASD demonstrate reduced specificity to emotions (Figure 3A,C), although their eye movement patterns are remarkably similar compared to neurotypicals and they have normal thresholds to report fear (Figure 3A,B). In addition, in this task, people with ASD demonstrate reduced pupil oscillation when judging faces with ambiguous facial expressions (Figure 3D,E).[108]

Inferences about differences in facial emotion judgments between neurotypical and autistic adults typically rely on high-level categorical descriptors of stimuli (e.g., happy vs. sad, or levels of happiness, etc.), neglecting image-by-image variations (Figure 4A) and neural sensory representations of each stimulus being tested. To address this issue, one can leverage computational models that characterize specific features within an image. These models have been developed through recent advances in computer vision and computational neuroscience.[109–111] In a recent study,[72] Kar utilized a data-driven approach to discover trial-by-trial (i.e., image-by-image) behavioral differences between neurotypical and autistic individuals. The author then utilized computational models trained to represent primate vision to investigate the underlying neural mechanisms that could drive the two human groups' behavioral differences. The results revealed that artificial neural networks (ANNs) that have been developed to achieve various primate vision-related objectives[109–111] could be fine-tuned to make facial emotion judgments like humans (Figure 4B,C). Interestingly, the ANN's image-level behavioral patterns better matched neurotypical participants' behavior than autistic individuals' behavior (Figure 4D). This behavioral mismatch was most remarkable when the ANN was constructed from units that correspond to the primate inferior temporal (IT) cortex (Figure 4E). Further analyses revealed that the behavioral

variance explained by human amygdala responses could be significantly explained by ANN-IT responses. The study also revealed that additional noise in sensory representations is a likely mechanism implicated in the different facial emotion processing in individuals with ASD than neurotypicals (Figure 4F).

SOCIAL TRAIT JUDGMENT

People not only infer others' moment-to-moment emotions based on faces, but also others' relatively stable social traits, such as whether someone is extroverted, trustworthy, or competent.[112–114] Despite the ongoing debate regarding the validity of these trait impressions, they can impact crucial decisions in real-life situations, such as voting or legal sentencing.[15] Various dimensional theories have been proposed to summarize people's social trait judgments of faces, such as the valence-dominance model,[115] the approachability-capability model,[116] the approachability-dominance-youthful/attractiveness model,[117] and the warmth-competence-femininity-youth model.[118] While some argue that the dimensions across these theories are similar (e.g., the valence dimension is similar to warmth, the competence dimension is similar to dominance), a recent work using quantitative methods demonstrates that these dimensions capture distinct aspects of social perception from faces.[118] Based on the findings from this most comprehensive analysis of social trait judgments of faces to date,[118] we have conducted a series of studies to understand the neural correlates of social trait judgment, its relationship with personality factors, and how people with ASD perceive social traits from faces compared to neurotypicals.

Specifically, in this section, we first describe the neural correlates of social trait judgment derived from neuroimaging and human single-neuron recordings. The amygdala plays a pivotal role in social trait judgment, as evidenced by both BOLD-fMRI[8,119] and single-neuron[43,120] activations. Remarkably, human amygdala neurons (along with adjacent hippocampal neurons) encode a comprehensive social trait space.[43] We then demonstrate that, besides individual differences in the brain, individual differences in personality traits can also explain how different people judge social traits from faces differently.[44] Finally, a comprehensive analysis of individuals with ASD reveals systematic differences in social trait judgment compared to neurotypicals.[121] Notably, these differences can be linked to amygdala activation and individual differences in personality.

fMRI and human single-neuron recordings reveal neural correlates of social trait judgment of faces

The functionality of face processing is supported by a dedicated neural system in primates.[21,24] Most of the existing studies focus on the recognition of faces and emotional expressions, but it remains unclear how the brain evaluates faces in general. Data-driven computational approaches have been used to study low-level facial features[62,122] and neural coding of faces,[123] but the neural correlates of higher-level social trait judgment remains relatively underexplored. A meta-analysis of 29 neuroimaging studies for the social evaluation of faces has revealed that across negative face evaluations, the most consistent activations are in the bilateral amygdala; whereas across positive face evaluations,

the most consistent activations are in the medial prefrontal cortex (mPFC), pregenual anterior cingulate cortex (pgACC), medial orbitofrontal cortex (mOFC), left caudate, and nucleus accumbens (NAcc).[124] Our own findings have further revealed context-dependent modulation of some of these brain areas during judgment of facial trustworthiness and dominance.[8,120] In particular, the human amygdala plays a critical role in social perception[28,125] and encodes various social trait judgments of faces, which has been supported by lesion studies,[126] fMRI studies,[8,105,119] and neurophysiology studies.[120] It is worth noting that these prior functional studies primarily focused on facial trustworthiness; however, humans use hundreds of different trait words to describe spontaneous trait judgments of faces[115,117,118] and automatically evaluate faces on multiple trait dimensions simultaneously. Therefore, a more comprehensive analysis is needed.

Our recent study has addressed this need, using a comprehensive face space (i.e., measuring trait judgments representative of the warmth-competence-femininity-youth model) (Figure 5A) and single-neuron recordings in the human amygdala and hippocampus.[43] Human single-neuron recordings provide unprecedented opportunities to investigate social trait judgment with the highest spatial and temporal resolution to date. We recorded from 490 neurons in the human amygdala and hippocampus, and we have shown that the correlation patterns of these neurons' activities are associated with the correlation patterns of human participants' judgments of faces on the representative set of social traits (Figure 5B,C). We have further shown that the activity of single neurons also correlates with judgments for individual social traits (Figure 5D). Encoding and decoding models reveal the most strongly neural-correlated social traits (Figure 5E,F). We also recorded from another 938 neurons and replicated our findings using a different set of social traits. Together, our results suggest that there exists a neuronal population code for a comprehensive social trait space (i.e., representing the warmth-competence-femininity-youth dimensions) in the human amygdala and hippocampus that underlies spontaneous first impressions. Furthermore, we have shown that encoding of facial features (e.g., eyes and mouth) may have a functional role in encoding social trait judgment (Figure 5G).[45]

Personality-dimensional approach reveals individual differences in social trait judgment of faces

Idiosyncrasies in social trait judgments are well documented in prior research.[127–129] However, what individual differences (in perceivers' characteristics) are linked to these idiosyncrasies has only been examined for a small number of social traits (e.g., trustworthiness)[130,131] and for a limited range of individual difference factors.[47,132,133] In addition, some of these individual differences may meet the criteria of clinical diagnosis (e.g., ASD), but they also exist as a broader, subclinical spectrum in the neurotypical population (e.g., the Empathy Quotient and the Autism Spectrum Quotient [AQ] scores). Conducting a more comprehensive investigation of what individual differences are linked to idiosyncrasies in social trait judgments of faces, and more importantly, what neurobiological mechanisms underlie such associations, is critical not only for basic research but also for developing effective interventions to ameliorate the social-affective deficits in neuropsychiatric patients.[134] For example, people who score high on extroversion may perceive others as more approachable and outgoing, while people who score high on

neuroticism may perceive others as more anxious or distressed. People who score high on agreeableness may perceive others as more trustworthy and cooperative, while people who score high on conscientiousness may perceive others as more responsible and organized. It has been shown that the variability in the correlation structure between perceiver's social trait judgments of faces across 42 world regions can be explained by the variability in the actual personality structure of the people living in those regions[135] (see also Refs. 136 and 137).

Past research on individual differences typically relies on a handful of established personality questionnaires. However, any single individual difference measure is inevitably limited in its ability to capture the comprehensive range and dimensions of the construct of interest. In recent years, a new analytic tool, the transdiagnostic approach, has been developed and applied in personality science in order to address this limitation.[138,139] Essentially, this approach capitalizes on the power of statistically integrating multiple semantically related questionnaires to maximize the capacity to capture individual differences. Instead of using the score of each single questionnaire, this approach starts with an exploratory factor analysis of the items of multiple questionnaires and uses the factor scores as a more comprehensive representation of individual difference profiles.

Using this approach, our study has revealed a connection between personality factors and social trait judgment of faces.[44] Specifically, we conducted an exploratory factor analysis on the 33 subscales from 10 established personality questionnaires related to autistic traits, affect and social deficits, prosociality, and empathy. We identified a 4-factor latent structure that best characterized the variance in personality data (as shown in Figure 6A).[44] The four orthogonal personality dimensions were interpreted as autistic trait and social avoidance, empathy and prosociality, antisociality, and social agreeableness (Figure 6A). Critically, the individual differences in these personality factors' scores were significantly correlated with the individual differences in social trait judgments of faces (as depicted in Figure 6B).[44] Furthermore, this transdiagnostic approach indicates that the four personality dimensions (factors) show qualitatively similar association patterns with social trait judgments from faces in both people who self-identify as ASD and those who do not. However, a closer examination of the individual difference patterns reveals important quantitative differences between the two groups (see below). Together, these findings provide novel insights regarding the psychological mechanisms underlying the individual differences in social trait judgments of faces.

Computational approaches and clinical populations reveal behavioral, neural, and psychological markers of social trait judgments of faces

Processing faces is difficult for individuals with ASD. Yet, it remains unclear whether individuals with ASD make high-level social trait judgments from faces in similar ways as neurotypicals. Prior work has focused on a restricted set of social trait judgments of artificial faces. In particular, findings from prior research are discrepant. Studies using computer-generated faces generally find that individuals with ASD make similar trait judgments of faces as neurotypicals.[60,140,141] For instance, one study investigated seven social trait judgments (attractiveness, competence, dominance, extraversion, likeability,

threat, and trustworthiness) using computer-generated faces and found no group difference between ASD and neurotypicals in any of these trait judgments.[141] In contrast, studies using photographs of real people have revealed different social trait judgments by individuals with ASD.[52,60] For instance, one study investigated judgments of trustworthiness and approachability using black-and-white photos of real faces in natural poses and found that individuals with ASD gave more positive ratings to these faces on both traits than neurotypicals.[52] Yet, prior studies are limited in their conclusions by the narrow range of social traits that they investigated, and also by the often narrow diversity of the face stimuli, leaving their relevance to real-world social behavior unclear.

Our recent study has addressed this prior limitation with a comprehensive investigation of the judgments made of naturalistic faces on a representative set of social traits by individuals with ASD.[121] There are several major findings. First, the correlational structure across trait judgments is similar between individuals with ASD and neurotypicals (Figure 7A). However, within each social trait, individuals with ASD show different rating patterns (Figure 7B) and reduced specificity (Figure 7C). Second, we used deep neural networks to show that these group differences are driven by discrepant judgments for different types of faces (e.g., younger male faces for the judgments of the trait *competent*) and differential utilization of features within a face (e.g., individuals with ASD pay less attention to the eyes when judging the trait *strong*) (Figure 7D,E). Third, we showed the specificity of our results for the diagnosis of ASD using additional comprehensive personality measurements. We validated our results with both a well-characterized sample of in-lab participants and another large sample of online participants using a different set of face stimuli (a preregistered study).

We further investigated the neural correlates of these group differences. Although much of the literature has investigated the impaired face processing in ASD,[142–145] few studies have shown the neural mechanisms underlying this impairment. To address this open question, we recently conducted two correlational studies,[43,44] focusing on the amygdala, which has long been hypothesized to underlie deficits in face processing in ASD.[146,147] We explored the association between social trait judgment from participants and the neural responses of the amygdala and hippocampus acquired from an independent group of neurosurgical patients without ASD, and whether this association is diminished in participants with ASD compared to neurotypicals.

First, we found that although the similarity structure of social trait judgments across faces by participants with ASD (Figure 7F) is similar to that of neurotypicals, the former is less correlated with the similarity structure of neural responses across faces by the neurosurgical patients than the latter (Figure 7G,H).[43] Second, in individuals with ASD, analysis of the judgments on each individual social trait has revealed a reduced correlation between judgments (*trustworthy* and *warm*) and neural responses.[44] Therefore, although we did not directly acquire neural responses from participants with ASD, we found that the judgments from participants with ASD are less explanatory of the neuronal responses in the amygdala and hippocampus. These findings suggest that the representation of social trait judgments in the amygdala and hippocampus may account for different social trait judgments of faces in ASD compared to neurotypicals.

Finally, we explored the underlying psychological mechanisms of social-affective difficulties in individuals with ASD. Prior research has put forward several theories. One of these is alexithymia, which refers to difficulty in recognizing and describing one's and others' emotional states,[148–150] and which has been suggested as a possible explanation for the observed difficulties in social interactions and emotional reciprocity in individuals with ASD.[151–154] Another proposed mechanism is deficits in empathy, which is the ability to experience others' feelings and show concern for their suffering.[155–158] This has been suggested as a possible explanation for the central impairments in social interactions in ASD, including difficulties with emotional engagement.[159]

In our recent study,[44] we explored a novel psychological account of social-affective difficulties in individuals with ASD, namely, the difficulty in social trait judgments. To this end, we used the transdiagnostic approach to individual differences (see above) and showed that individuals with ASD exhibit a weaker association between prosocial personality dimensions and social trait judgments of trustworthiness and warmth from faces compared to neurotypicals (Figure 7J). These results suggest that personality factors can explain some of the different social trait judgments and downstream behavioral difficulties in individuals with ASD.

CONCLUSIONS AND FUTURE DIRECTIONS

In this review, we have shown how multimodal approaches provide a richer understanding of emotional face processing and social trait judgment of faces, informing the psychological and neural underpinnings of face processing with different spatial and temporal resolutions. Specifically, we have demonstrated the benefits of using EEG, fMRI, single-neuron recordings, computational modeling, and a personality-dimensional approach to study emotion ambiguity and social trait judgment from faces. In particular, for each aspect of face processing, we have observed behavioral differences in individuals with ASD compared to neurotypicals. All data described in this review are publicly available (see Ref. 160 for emotion ambiguity and Refs. 44 and 161 for social trait judgment from faces). Below, we discuss some limitations in the existing research paradigm and advocate a few new perspectives to advance a generalizable understanding of emotional face processing and social trait judgment of faces.

Limitations of the existing paradigm for studying emotions and social traits judgments from faces

The empirical research reviewed so far by and large assumes that one's affective states and social traits can be inferred or decoded by a social interactant for communicative purpose or by a scientist for research purpose, through matching their facial configuration with the prototypical facial configurations of the basic emotions and social traits.[1,162] What this widely adopted approach primarily achieves is the description of associations between a narrow, researcher-dependent set of facial configurations and a small set of linguistic labels of emotion and social trait categories. This surface association is unable to directly address the deeper, mechanistic question of *what* specific information is encoded in and decoded from certain facial configurations that make social communication successful (in this case,

conveying an emotional state or a social trait). In other words, the underlying information ontology is unknown.

One way to address this information gap is to combine psychophysical approaches with facial configurations generated, with the help of computer algorithms, from higher-order axes of information.[162] For example, combining 42 static action units with six temporal parameters will give rise to a 252-dimension dynamic facial movement pattern space, which is far more comprehensive and less biased than the facial configurations posed by human actors used in the traditional research.[163] This approach can alleviate the potential misleading inferences of a high-dimensional structure based on its low-dimensional projection that the traditional research has risked committing.[164] Combining this more representative sample of dynamic facial movement patterns and psychophysical tasks, such as signal detection theory[165] and reverse correlation,[166] researchers are then able to identify diagnostic information underlying successful social communication via faces.

Another limitation of the traditional approach is the predominant use of static, decontextualized face images as stimuli. This is in stark contrast with what people experience in the real world—the faces people encounter in everyday life are dynamic, physically embedded, and socially situated. The movement and contextual information may fundamentally modulate the way we perceive and interpret the affective states and social trait information conveyed by the faces. For instance, studies have shown that the emotional valence of body gesture has a strong impact on how observers perceive the valence of accompanying ambivalent facial expressions.[167] In a similar vein, a face is perceived to belong to someone with high competence if the face is accompanied by richer than poorer clothes.[168] To address this limitation, recent research has incorporated dynamic facial movement and naturalistic face images as stimuli to study the perception of affective states[163,169] and social traits.[114,118,170]

Combining multimodal neuroscience approaches with these new ways of probing the naturalistic affective and social judgment processes will shed new lights on the understanding of the neurobiological bases of emotional face processing and social trait judgment of faces.

Multi-scale computational modeling of multimodal data

Multimodal experimental approaches generate data at multiple scales, including macroscopic fMRI and EEG data, mesoscopic intracranial EEG (iEEG) data, and microscopic single-neuron/local field potential (LFP) data. Given the complexity of multimodal data, we need powerful tools for data analysis. First, we promote the use of a unified computational model to explain multimodal data at different scales. For example, our ongoing work is establishing a unified drift-diffusion model that can explain data from different modalities (e.g., EEG, fMRI, and single-neuron data, as well as behavioral data from neurotypicals and individuals with ASD). Second, we promote the use of multimodal data fusion[171,172] to extract relevant information from each modality and combine it in a meaningful way to provide a more complete picture of the question under investigation. With multimodal data fusion, we can, therefore, gain a more comprehensive understanding of emotional face processing and social trait judgment of faces by combining information

from different sources. Although in this review we highlighted multimodal approaches to study emotional face processing and social trait judgment of faces and these studies pointed to coherent results, it is worth noting that these studies were not conducted in the same participants. Future studies are needed to understand how data from each modality are related to one another (e.g., how BOLD-fMRI is related to LFP), and more importantly, what unique information each modality can provide.

Multimodal approaches, such as concurrent EEG-fMRI, have been used to study neural face processing.[173,174] Furthermore, a study using concurrent electrical stimulation of the amygdala with iEEG (electrical stimulation tract-tracing) or fMRI (electrical stimulation fMRI) has provided strong inferences about the effective connectivity of amygdala subdivisions with the rest of the brain.[175] However, an underexplored approach is to employ human single-neuron recordings to study the neural circuits for face processing, and few studies have combined microscopic data with macroscopic data. Human single-neuron recordings provide a very unique and valuable opportunity to directly study face processing at the neuronal and neural circuit levels in the human brain. Recording directly from neurons in the human brain will bridge the gap between standard neuroimaging techniques that lack this level of spatial and temporal resolution and neurophysiological studies of nonhuman animals (note that it is often very hard to probe emotion and social trait judgment in nonhuman animals). With the highest possible spatial and temporal resolution currently available, human single-neuron recordings can have a significant impact on studying face processing. Notably, our publicly available datasets[160,161] can facilitate the research community to study face processing using human single-neuron recordings.

A network view of emotional face processing

The studies discussed in this review focus on a single brain area at a time. However, functional neural networks for emotional face processing are complex systems that involve multiple brain regions and processes. Although a large literature has documented the functional localization of emotional face processing, fewer studies have systematically investigated the functional neural network underlying emotional face processing, especially when the processing requires orchestration between multiple brain areas. It is, therefore, important to understand emotional face processing (as well as social trait judgment of faces) from a network view. For example, functional connectivity analyses can elucidate how the amygdala, dorsomedial prefrontal cortex (dmPFC), and ventromedial prefrontal cortex (vmPFC) collectively encode emotion ambiguity.[70]

Some studies have investigated effective connectivity and functional organization underlying emotional face processing, and the amygdala is a key node of the emotional face processing network. For example, emotional faces increased the coupling between the fusiform gyrus and the amygdala, whereas famous faces increased the coupling between the fusiform gyrus and the orbitofrontal cortex.[176] Using emotional faces, emotion-induced loss aversion increases amygdalastriatal functional connectivity in low-anxious individuals,[177] activation of the rostral cingulate is accompanied by a simultaneous and correlated reduction of amygdalar activity in an emotion Stroop task,[178] and acute tryptophan depletion significantly reverts the functional connectivity between the amygdala and vACC as

well as ventrolateral prefrontal cortex (vlPFC) while viewing facial signals of aggression (angry faces).[179] Beyond the amygdala, explicit processing of facial affect leads to a prominent increase in the effective connectivity from the inferior occipital gyrus to vlPFC.[180] Clinically, effective connectivity between the amygdala and orbitofrontal cortex is disrupted in patients with social anxiety disorder during facial emotion discrimination tasks,[181] abnormal amygdala-prefrontal effective connectivity to happy faces differentiates bipolar from major depression,[182] and increased connectivity between the amygdala, especially basolateral amygdala, and distributed brain systems involved in attention, emotion perception, and regulation is associated with high childhood anxiety.[183]

Again, multimodal approaches can be used to study functional connectivity at three scales: (1) at the *macroscopic* level, psychophysiological interaction and dynamic causal modeling analyses can be performed on fMRI data, and coherence and coupling analyses can be performed on EEG data; (2) at the *mesoscopic* level, cross-correlation, coherence, and Granger causality analyses can be performed on iEEG data; and (3) at the *microscopic* level, LFP phase shift, spike-LFP coherence, LFP-LFP coherence, Granger causality, and spike-train differential latency analyses can be performed on single-neuron recording (i.e., microwire recording) data. Functional connectivity analyses at multiple scales can enable us to systematically and comprehensively understand the neural processes underlying emotional face processing.

Practices to advance a generalizable understanding of emotional face processing and social trait judgment of faces

We recommend the following practices to advance a more generalizable understanding of emotional face processing and social trait judgment of faces. The first recommendation is to use multiple, diverse sets of participants and stimuli to improve the generalizability of the findings to different populations and situations. Preregistration of studies is also encouraged. The second recommendation is to use more naturalistic stimuli in order to better understand emotional face processing and social trait judgment of faces in real-world contexts. Prior studies have primarily used computer-generated or controlled photographs to study emotion and social trait judgments from faces, which may limit the generalizability of the conclusions. More naturalistic stimuli, such as photographs of individuals from diverse races with varied facial expressions and in complex contexts, should be used. Notably, deep neural networks can effectively analyze such naturalistic faces.[170] Specifically for studying social trait judgments, the third recommendation is to sample comprehensive sets of social traits and faces for collecting human judgments.[118] Prior research has examined a limited number of social traits, which may not be representative of the full range of trait judgments that people make from faces in a wide range of contexts. Understanding how individuals make judgments along all trait dimensions will allow for greater generalizability to diverse trait judgments of faces. Lastly, the use of complex and convergent analytic approaches as well as multimodal data fusion is recommended to allow for a multifaceted and comprehensive analysis of emotional face processing and social trait judgment of faces.

Barriers associated with conducting multimodal investigations

Last but not least, we would like to acknowledge that there are technical barriers to conducting multimodal investigations. These investigations can be complex and expensive processes, often necessitating expertise and collaborations across multiple laboratories or institutions. Researchers need to possess the necessary expertise in collecting and analyzing multimodal data, which may involve very different techniques (e.g., fMRI, EEG, and single-neuron recordings). Training the next generation of researchers with multimodal investigations in mind and providing them with opportunities to collaborate across laboratories could be a long-term solution to this challenge. Some successful multi-institutional collaborative data collection initiatives (e.g., Ref. 184) may help alleviate such difficulty.

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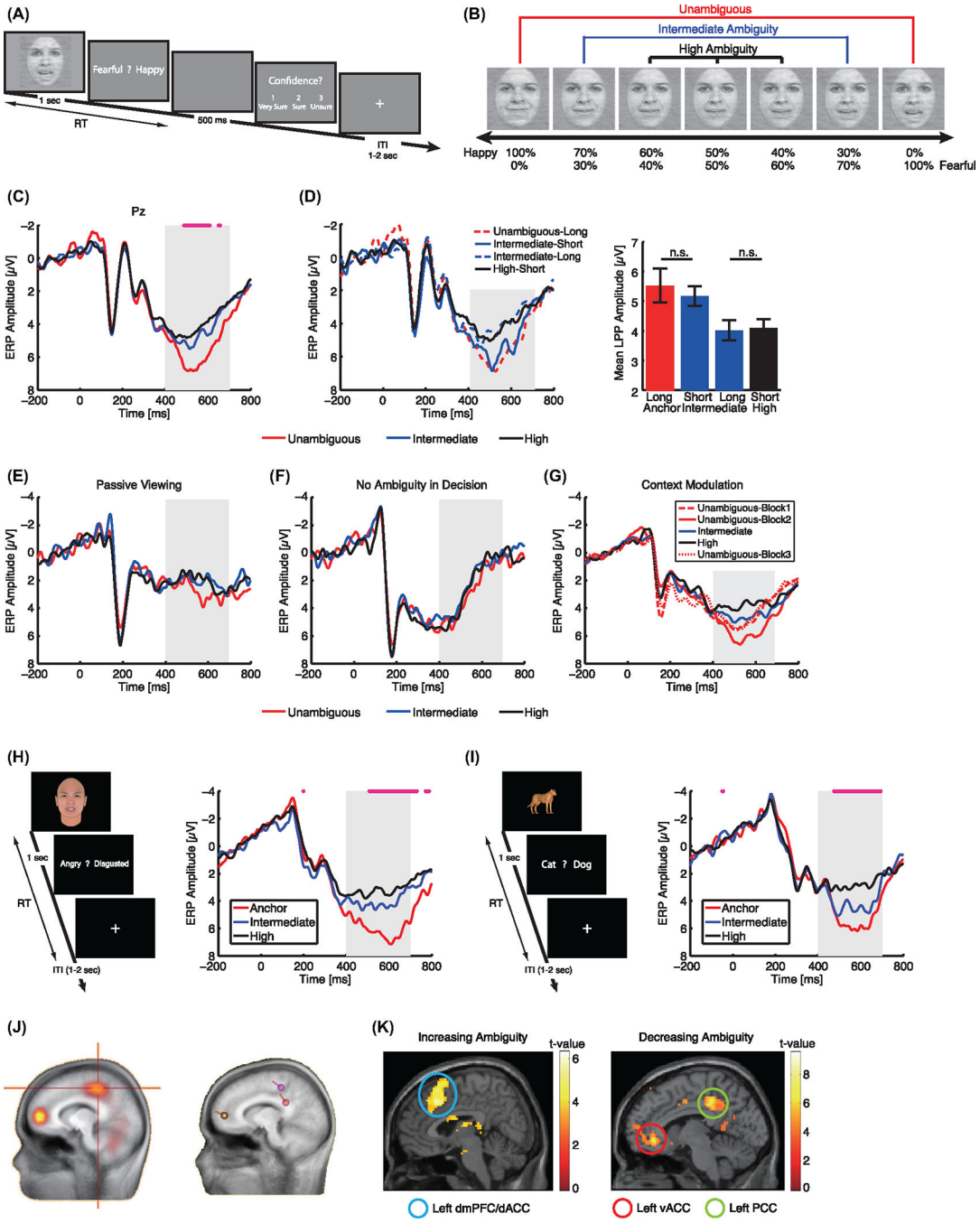

FIGURE 1.

The late positive potential (LPP) is a physiological signature for perceptual ambiguity. (A, B) Sample task and stimuli to study facial emotion ambiguity. (A) A face is presented for 1 s followed by a question asking participants to identify the facial emotion (fearful or happy). After a blank screen of 500 ms, participants are then asked to indicate their confidence in their decision ("1" for "very sure," "2" for "sure," "3" for "unsure"). (B) Sample stimuli of one female identity ranging from 100% happy/0% fearful to 0% happy/100% fearful are shown on the right. Three ambiguity levels (unambiguous, intermediate,

and high) are grouped as shown above the stimuli. (C) The LPP at the electrode Pz differentiates ambiguity levels. Gray shaded area denotes the LPP interval. The top magenta bars illustrate the points with significant difference across three ambiguity levels (one-way repeated-measure ANOVA, $p < 0.05$, corrected by FDR for $Q < 0.05$[185]). (D) LPPs from trials with similar RTs are similar even for different ambiguity levels. Mean LPP amplitude for each condition is shown on the right (averaged across the entire LPP interval). Error bars denote one SEM across participants. n.s., not significant. (E) The LPP is abolished when participants freely view the faces without judging emotions (passive viewing). (F) The LPP is abolished when participants judge whether the stimulus is a human face or an animal, an unambiguous aspect of the stimuli. (G) The LPP is not only modulated by ambiguity levels, but also by the context of ambiguous stimuli. Specifically, the LPP for the same anchor (unambiguous) stimuli is enhanced when there are ambiguous stimuli presented in the same block (Block 2). Only unambiguous stimuli are shown in Block 1 and Block 3. (H) Face judgment task with anger-disgust morphed emotions. (I) Animal judgment task with cat-dog morphs. (J) Source localization of the LPP. Mean differential ERPs (unambiguous minus high ambiguity) are used to obtain the sources. Source locations are in standard Talairach space. *Left*: Sources estimated using a distributed model. The locations and intensities (color coding) of the regional sources are shown for a 40-ms time interval within the LPP time window (560–600 ms) for illustration. *Right*: Sources estimated using a discrete model. Five dipoles (four fixed and one free) were fitted for the time interval of 400–700 ms after stimulus onset. (K) fMRI results. *Left*: Increasing ambiguity is correlated with increasing BOLD activity in the bilateral IFG/anterior insula and dmPFC/dACC. *Right*: Decreasing ambiguity is correlated with increasing BOLD activity in the left vACC, PCC, dlPFC, IPL, and right postcentral gyrus. The generated statistical parametric map is superimposed on anatomical sections of the standardized MNI T1-weighted brain template. Figure adapted from Refs. 68 and 69.

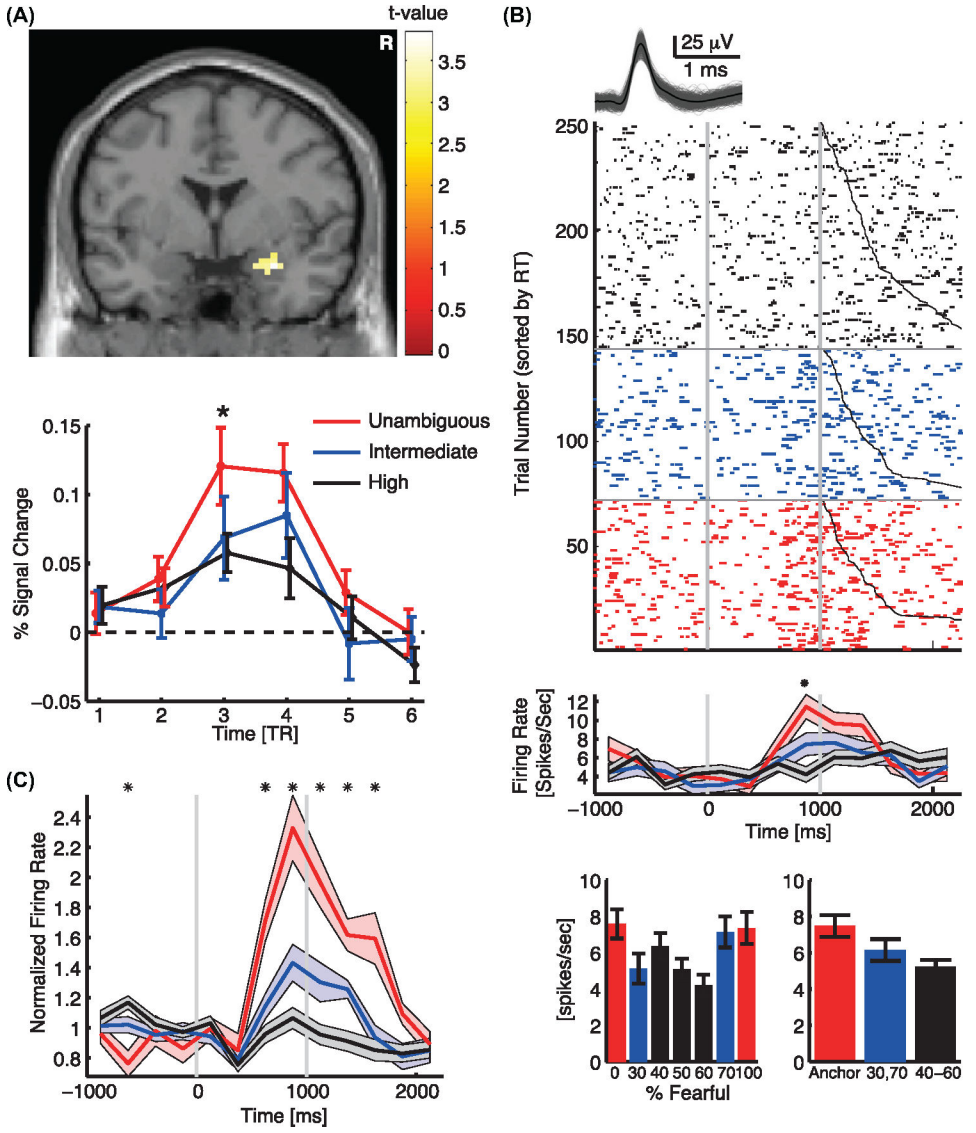

FIGURE 2.

The human amygdala encodes facial emotion ambiguity. (A) fMRI result. *Upper*: Ambiguity levels were correlated with the BOLD activity in the right amygdala (functional ROI defined by localizer task). *Lower*: Time course of the BOLD response in the right amygdala (averaged across all voxels in the cluster) in units of TR (TR = 2 s) relative to face onset. Error bars denote one SEM across participants. One-way repeated ANOVA at each TR: *$p < 0.05$. (B) An example neuron that fires most to the anchors and least to the most ambiguous stimuli (linear regression: $p < 0.05$). Each raster (top), PSTH (middle), and average firing rate (bottom) is color coded according to ambiguity levels as indicated. Trials are aligned to face stimulus onset (left gray bar, fixed 1-s duration) and sorted by reaction time (black line). PSTH bin size is 250 ms. Shaded area and error bars denote ±SEM across trials. Asterisk indicates a significant difference between the conditions in that bin ($p <$ 0.05, one-way ANOVA, Bonferroni-corrected). Bottom left shows the average firing rate for each morph level 250- to 1750-ms post-stimulus-onset. Bottom right shows the average

firing rate for each ambiguity level 250- to 1750-ms post-stimulus-onset. Waveform for this unit is shown at the top of the raster plot. (C) Group average normalized firing rate of ambiguity-coding neurons that increased ($n = 29$) firing rate for the least ambiguous faces. Asterisk indicates a significant difference between the conditions in that bin ($p < 0.05$, one-way ANOVA, Bonferroni-corrected). Figure adapted from Ref. 42.

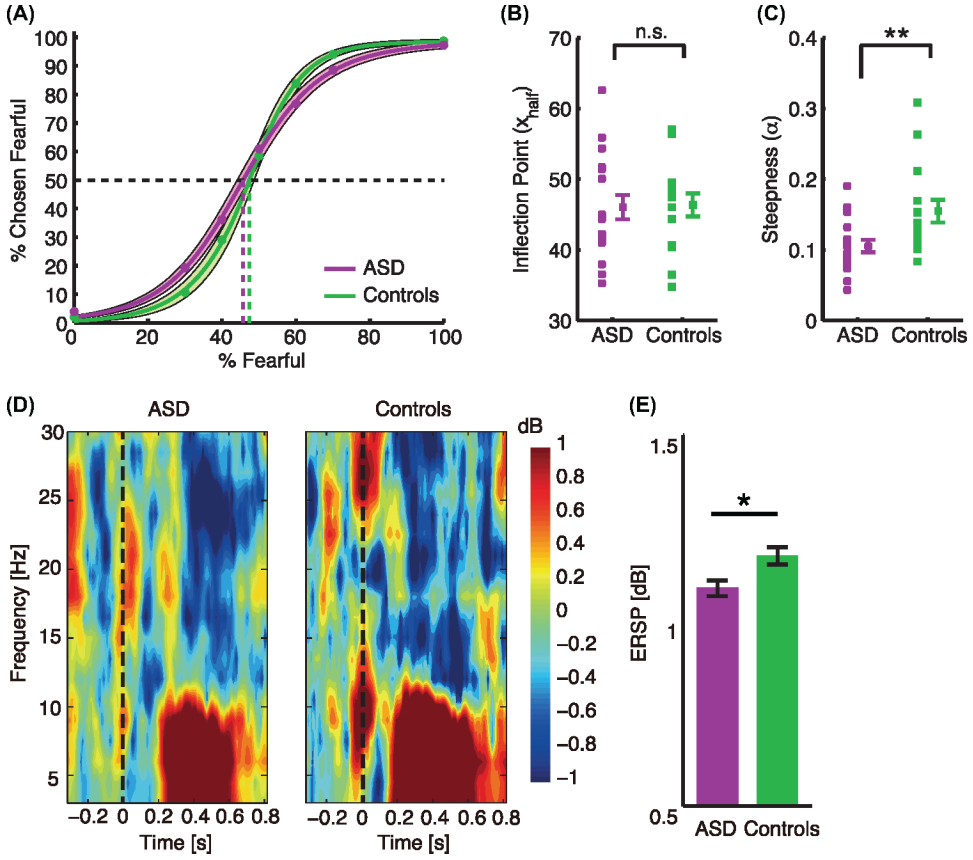

FIGURE 3.

People with autism spectrum disorder (ASD) show a deficit when judging ambiguous facial expressions. (A) Group average of psychometric curves. The psychometric curves show the proportion of trials judged as fearful as a function of morph levels (ranging from 0% fearful [100% happy; on the left] to 100% fearful [0% happy; on the right]). Shaded area denotes ±SEM across participants. (B) Inflection point of the logistic function (x_{half}). (C) Steepness of the psychometric curve (α). Error bars denote one SEM across participants. Asterisks indicate a significant difference using two-tailed two-sample *t*-test. **: $p < 0.01$. n.s., not significant ($p > 0.05$). (D) Time-frequency plots depicting the power of pupil oscillations for each group of participants. Black dashed line denotes stimulus onset (time = 0). (E) Mean power of pupil oscillation in the 3–12 Hz frequency range between 200 and 600 ms after stimulus onset. Error bars denote ±SEM across participants. Asterisk indicates a significant difference using two-tailed two-sample *t*-test. *: $p < 0.05$. Figure adapted from Refs. 59 and 108.

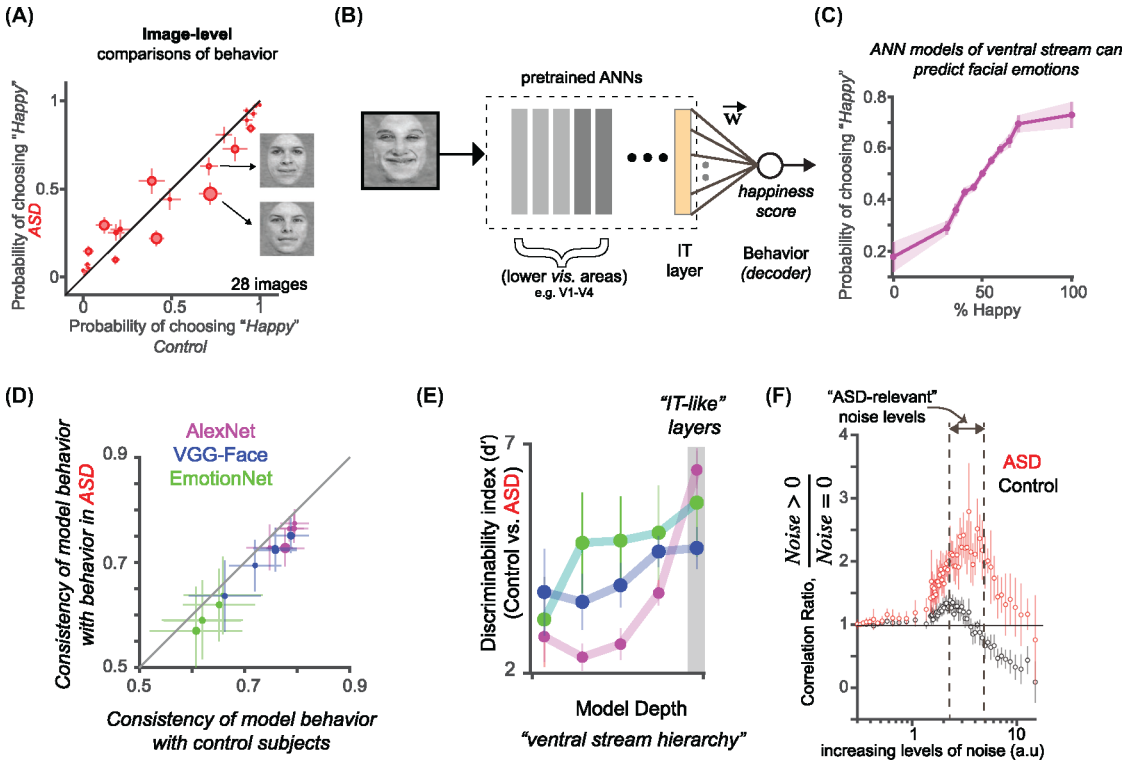

FIGURE 4.

Leveraging computational models to probe the neurobehavioral markers of face emotion recognition differences observed in ASD. (A) Quantification of image-by-image differences in behavior between ASD and neurotypicals. (B) ANN models of the primate ventral stream (typically comprising V1, V2, V4, and IT-like layers) can be trained to predict human facial emotion judgments. This involves building a regression model, that is, determining the weights $\vec{w}$ based on the model layer activations (as the predictor) to predict the image ground truth ("level of happiness") on a set of training images, and then testing the predictions of this model on held-out images. (C). An ANN model's predicted psychometric curves (e.g., AlexNet, shown here) show the proportion of trials judged as "happy" as a function of facial emotion morph levels ranging from 0% happy (100% fearful; left) to 100% happy (0% fearful; right). This curve demonstrates that activations of ANN layers (layer "fc7," which corresponds to the "model-IT" layer) can be successfully trained to predict facial emotions. (D) ANN behavior better matches the behavior measured in neurotypicals compared to ASD. (E) IT-like layers of ANN best discriminate between behaviors of ASD and neurotypicals. (F) Ratio of ANN behavioral predictivity of noisy versus noise-free ANNs. At specific levels of noise, referred to as the "ASD-relevant noise levels," the ANNs trained with noise show much higher predictivity for behavior measured in ASD while suffering a reduction in predictivity of the neurotypicals. Error bars denote bootstrapped confidence intervals (CIs). Figure adapted from Ref. 72.

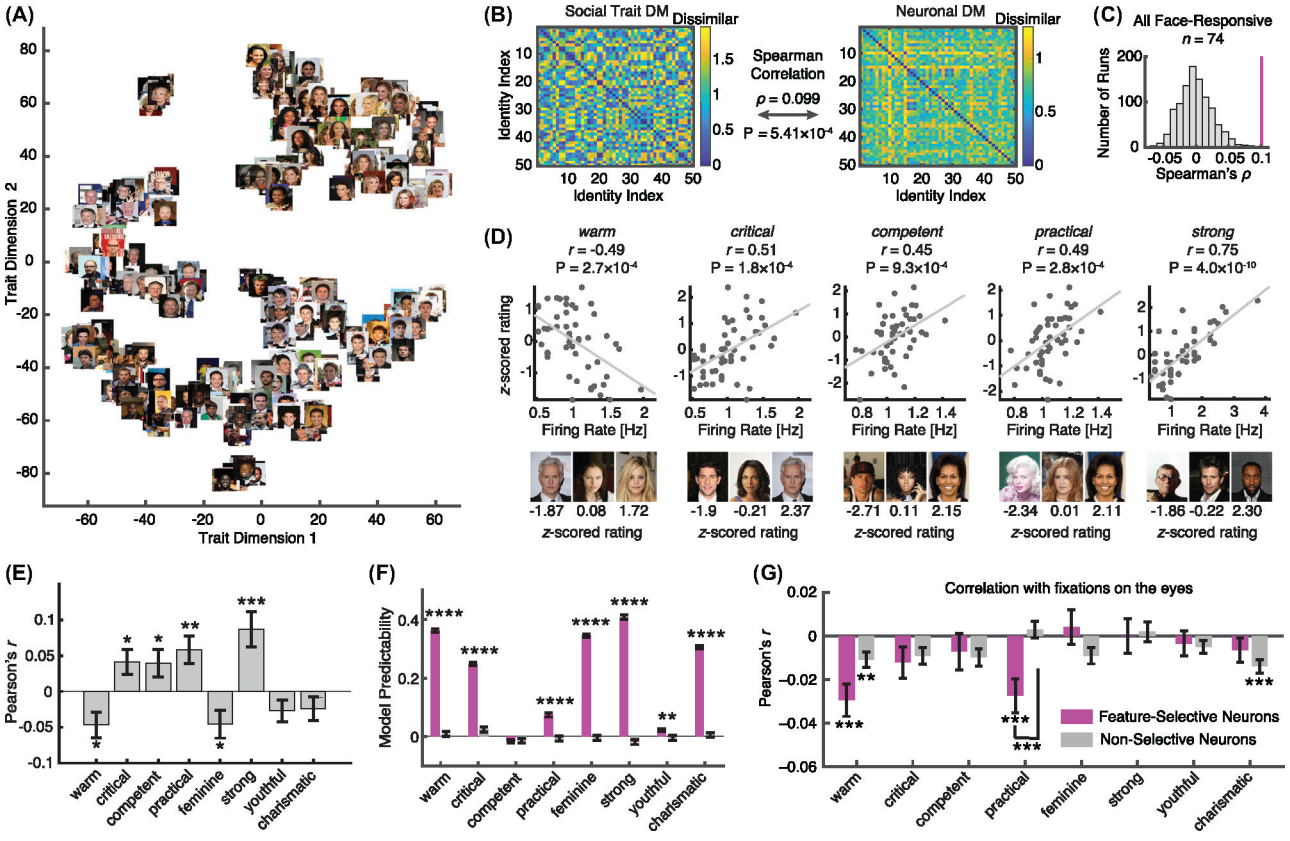

FIGURE 5.

A neuronal social trait space in the human brain. (A) Distribution of face images in the social trait space based on their consensus social trait ratings after dimension reduction using *t*-distributed stochastic neighbor embedding (t-SNE). (B) Correlation between dissimilarity matrices (DMs). The social trait DM (left matrix) was correlated with the neural response DM (right matrix). Color coding shows dissimilarity values ($1-r$). (C) Observed versus permuted correlation coefficient between DMs. The correspondence between DMs was assessed using permutation tests with 1000 runs. The magenta line indicates the observed correlation coefficient between DMs. The null distribution of correlation coefficients (shown in the gray histogram) was calculated by permutation tests of shuffling the face identities. (D) Example neurons that showed a significant correlation between the mean normalized firing rate and the mean *z*-scored rating for a social trait. Each dot represents a face identity, and the gray line denotes the linear fit. Sample face images with a range of consensus social trait ratings are illustrated below the correlation plots, and the corresponding consensus ratings (*z*-scored) are shown under each sample face image. (E) Encoding of each social trait. The bars show the average correlation coefficient across all face-responsive neurons for each social trait. Error bars denote ±SEM across neurons. Asterisks indicate a significant difference from 0 (two-tailed paired *t*-test). $*p < 0.05$; $**p < 0.01$; and $***p < 0.001$. (F) Decoding of each social trait using a linear decoding model on face identities. Model predictability was assessed using the Pearson correlation between the predicted and actual trait ratings in the test dataset. The magenta bars show the observed response and the gray bars show the permuted response. Error bars denote ±SEM across permutation runs.

Asterisks indicate a significant decoding performance (two-tailed two-sample *t*-test between observed vs. permuted). $^{**}p < 0.01$ and $^{****}p < 0.0001$. (G) Feature-selective neurons (i.e., neurons that differentiate fixations on the eyes vs. mouth) are related to social traits. Shown is the correlation between the firing rate for fixations on the eyes and perceived social traits. Similar analysis can be performed for fixations on the mouth. Error bars denote ±SEM across neurons. Asterisks indicate a significant difference above 0 (two-tailed paired *t*-test) or between feature-selective versus nonselective neurons (two-tailed two-sample *t*-test) after Bonferroni correction for multiple comparisons. $^{**}p < 0.01$ and $^{***}p < 0.001$. Figure adapted from Refs. 43 and 45.

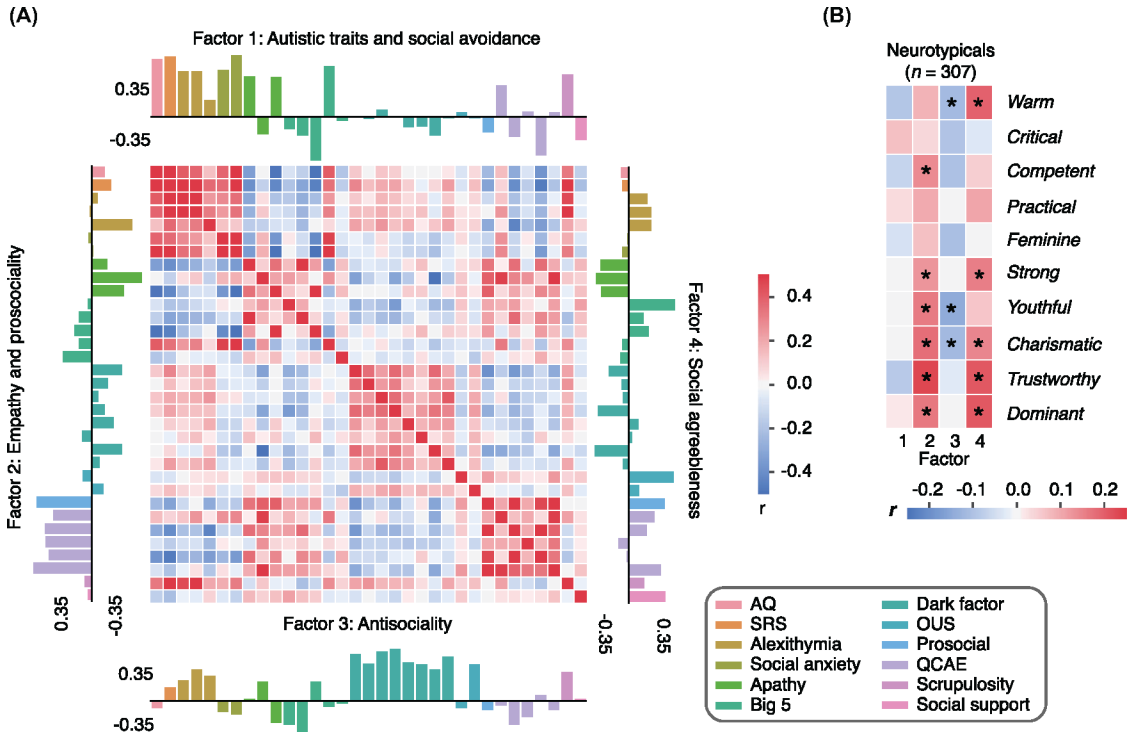

FIGURE 6.

Correlation between personality factors and social trait judgments. (A) The correlation matrix of 33 questionnaire subscales and loadings of each subscale for the four factors. (B) Correlations between factor scores and social trait judgments. Asterisks indicate a significant correlation. Figure adapted from Ref. 44.

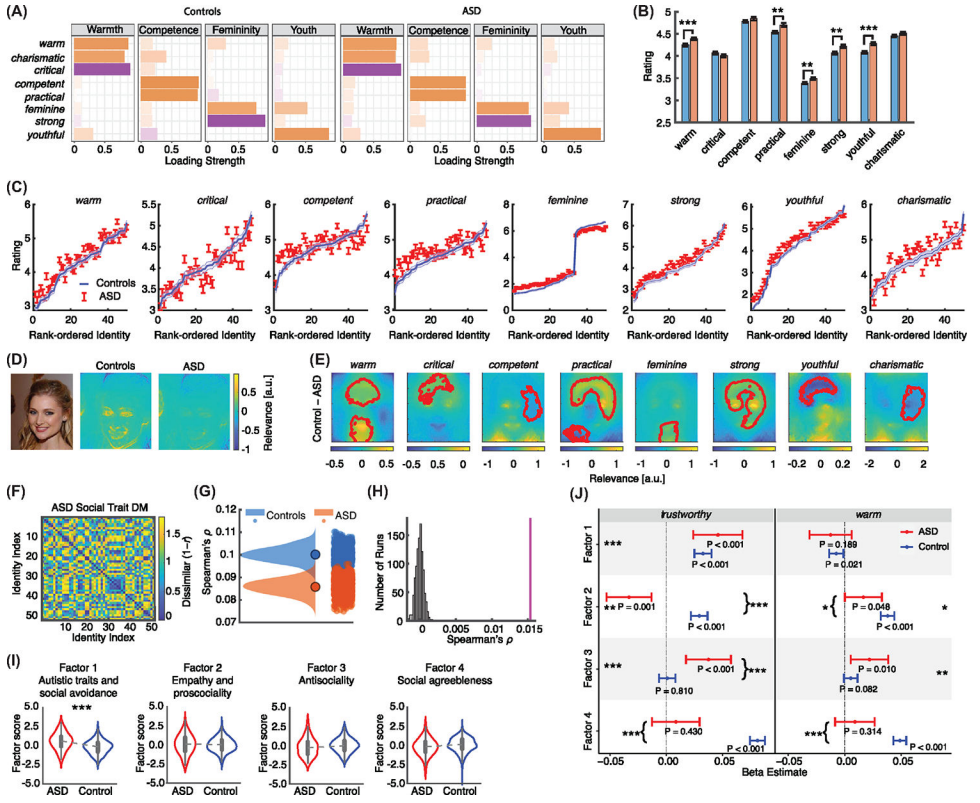

FIGURE 7.

Multifaceted investigation of atypical social trait judgment in ASD. (A) PCA loadings of social traits on the first four PCs. Each column plots the strength of the loadings (*x*-axis, absolute value) across traits (*y*-axis). Color coding indicates the sign of the loading (orange for positive and purple for negative). Saturated colors highlight each trait's most strongly correlated PC. (B) Aggregate ratings. Error bars denote ±SEM across rating modules. Asterisks indicate a significant difference between participants with ASD and neurotypicals using two-tailed two-sample *t*-test. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; and ****$p < 0.0001$. (C) Ratings for each face identity rank-ordered by mean ratings from neurotypicals. Red: ASD. Blue: neurotypicals. Error bars and error shades denote ±SEM across rating modules. (D, E) Features within faces that contribute to atypical trait ratings in ASD. Relevance of each pixel to classification was revealed using layer-wise relevance propagation (LRP). Color coding shows LRP values in arbitrary units (a.u.). Yellow pixels positively contributed to the classification, whereas blue pixels negatively contributed to the classification. (D) An example face and its corresponding LRP maps (trait *strong*). (E) Difference in LRP maps for each trait. Red contours show the regions with a significant difference between participants with ASD and neurotypicals. (F) The social trait dissimilarity matrix (DM) from participants with ASD. (G) Bootstrap distribution of DM correspondence for each participant group. Blue: neurotypicals. Red: ASD. The dots show the mean value of each distribution. Participants with ASD show a weaker correspondence with the neural response DM compared to neurotypicals. (H) Observed versus permuted difference in DM correspondence between participant groups. The magenta line indicates the observed difference in DM correspondence between participant groups.

The null distribution of difference in DM correspondence (shown in the gray histogram) is calculated by permutation tests of shuffling the participant labels (1000 runs). (I) Group differences in personality factor scores. As expected, the ASD group is significantly higher on Factor 1, which is primarily associated with standard autistic trait measures (i.e., AQ and SRS), social anxiety, and alexithymia. ***$p < 0.001$. (J) Relationship between social trait judgment and personality factors derived using representational-similarity analysis. The dissimilarity matrix structure of the social trait judgments (*trustworthy* and *warm*) is predicted by the dissimilarity matrices of the four personality dimensions or factors. Shown are regression coefficients of each personality dimension (factor) for *trustworthy* (left) and *warm* (right) judgments. The asterisks on the margins indicate a significant main effect of a personality dimension in predicting the social trait judgments, while the asterisks with curly brackets indicate a significant group-by-factor interaction, or in other words, a significant group difference in the predictive power of a given personality dimension. Figure adapted from Refs. 43, 44, and 121.