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Social judgments from faces

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People make rapid and consequential social judgments from minimal (non-emotional) facial cues. There has been rapid progress in identifying the perceptual basis of these judgments using data-driven, computational models. In contrast, our understanding of the neural underpinnings of these judgments is rather limited. Meta-analyses of neuroimaging studies find a wide range of seemingly inconsistent responses in the amygdala that co-vary with social judgments from faces. Guided by computational models of social judgments, these responses can be accounted by positing that the amygdala (and posterior face selective regions) tracks face typicality. Atypical faces, whether positively or negatively evaluated, elicit stronger responses in the amygdala. We conclude with the promise of data-driven methods for modeling neural responses to social judgments from faces.

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Introduction

There is a vast amount of research on the cognitive and neural basis of face perception [1]. In fact, there is probably no other category of stimuli that has been studied as extensively. There are good reasons for this obsessive focus on the face. Besides being one of the most important stimuli in the social environment conveying information about person identity, mental, and emotional states, the face is often at the center of key debates in cognitive neuroscience about the functional organization of the brain [2,3]. Yet, face perception research has been almost exclusively focused on two areas: face recognition and recognition of emotional expressions, with occasional forays into the role of eye gaze in social cognition. This leaves out a large part of what other information people extract from faces. After all, we interact with many strangers and most expressions are neutral.

Yet, the human face is anything but affectively neutral. It is inherently imbued with affect and perceivers draw multiple social inferences from minimal (non-emotional) facial cues about the person [4,5]. The idea that the face reflects one's personality could be found in every ancient culture, and reached its prime in 19th century physiognomy — the pseudo-science of reading personality from faces. Physiognomy has been long discredited as a science for good reasons, but physiognomists got a few things right. Firstly, people make all kinds of social judgments from faces of strangers; secondly, there is consensus in these judgments; and thirdly, these judgments matter for social interaction.

Efficiency and consequences of judgments from faces

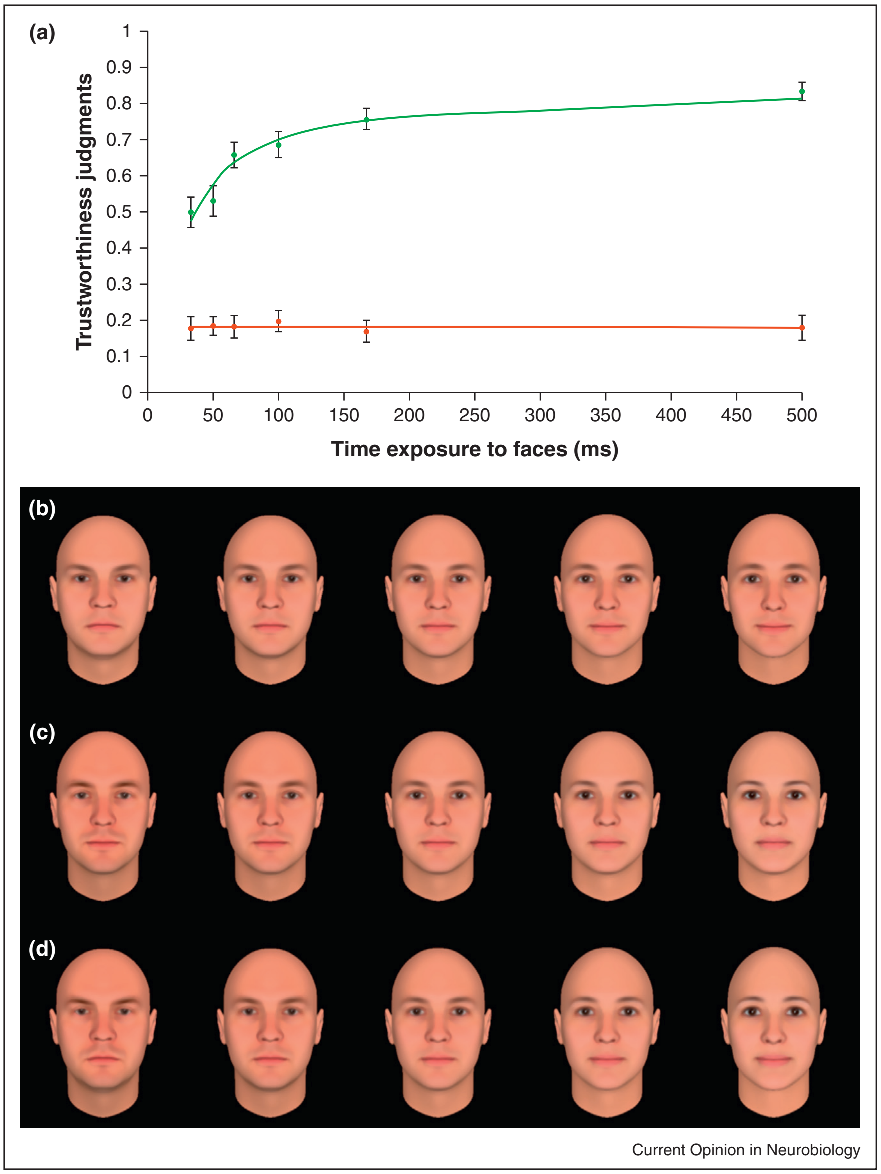
Extremely brief exposures to unfamiliar faces are sufficient for people to make social judgments like trustworthiness and aggressiveness [6–9]. Typically, these effects are measured by correlating judgments made after limited time exposure with judgments made after unlimited time. This correlation, indicating consensus, rapidly increases as time exposure increases and reaches a plateau at exposures of about 200 milliseconds. It is also possible to measure these effects with faces generated by computational models of social judgments [10–12]. As shown in Figure 1a, even after 34 milliseconds masked exposure to faces, people judge 'trustworthy' faces generated by a model of trustworthiness as more trustworthy than 'untrustworthy' faces. We revisit these models and their promise for neuroscience research in the last section.

Not only are social judgments from faces made from extremely limited information, but also they influence important social outcomes [13–15]. For example, judgments of competence predict the outcomes of important political elections [14] and judgments of criminality predict choices in lineup identification of suspects [16]. Recently, several research groups have used faces generated from the computational models mentioned above (Figure 1) and have demonstrated systematic effects of facial appearance on social interactions [17,18,19•]. Despite these effects on social interactions, the evidence for accuracy of social judgments from faces is slim [20–22], and there are good reasons to be skeptical. For example, different images of the same individual can lead to very different impressions [23••], and impressions from faces are overweighed in decisions [21].

Early neuroscience research

Adolphs *et al.* were the first to explore the neural basis of social judgments from faces [24]. They showed that

Figure 1



Social judgments of trustworthiness from faces. **(a)** Differences between judgments of trustworthy-looking (green line) and untrustworthy-looking (red line) faces are apparent after 34 ms masked exposure to the faces and reach a plateau around 200 ms exposure (data from [9]). The faces were generated by a computational model of trustworthiness [11]. Examples of faces that vary in **(b)** shape trustworthiness; **(c)** reflectance trustworthiness; and **(d)** shape and reflectance trustworthiness. The variations range from −3 SD to 3 SD with steps of 1.5 SD. The data from panel A are based on judgments of faces with −3 SD and 3 SD values on shape trustworthiness.

patients with bilateral lesions in the amygdala judge untrustworthy-looking faces as more trustworthy than normal and brain lesion controls. Interestingly, some developmental and acquired prosopagnosics are able to make typical trustworthiness judgments despite difficulties with face recognition [25,26]. Subsequent functional magnetic resonance imaging (fMRI) studies confirmed the involvement of the amygdala in trustworthiness judgments [27,28], observing increased amygdala activation to faces perceived as untrustworthy. With hindsight, the choice of trustworthiness judgments in these studies was fortuitous. Social judgments from faces are highly inter-correlated with each other. Principal component analyses of such judgments show that the first component, which accounts for about 60% of the variance and is interpreted as valence evaluation, is practically indistinguishable from trustworthiness judgments [10]. In fact, a re-analysis of fMRI data showed that the amygdala's response to the perceived trustworthiness of faces is entirely accounted for by the valence content of trustworthiness judgments [29].

These findings have a straightforward interpretation. Valence evaluation of faces is related to approach/avoidance responses, with the amygdala responding more strongly to stimuli-to-be-avoided [30]. This is consistent with findings that bilateral amygdala lesions may impair avoidance responses [31]. However, several subsequent studies have shown nonlinear responses to valence/trustworthiness with stronger responses to positive-looking and negative-looking faces than faces in the middle of the continuum [32,33]. These findings suggest that the simple approach/avoidance explanation needs to be revised.

Current neuroscience research

In addition to evaluation of trustworthiness, neuroimaging research has also explored the neural bases of perceptions of facial attractiveness [34]. Given the high correlations between trustworthiness and attractiveness judgments [10], a recent meta-analysis was conducted to identify which regions most frequently display activity as a function of face valence [35]. Since the publication of that meta-analysis, additional relevant studies have been published. Here, we report an updated analysis including these new data. The current database contains 62 individual contrasts from 37 total studies (these are available on request from the authors). For purposes of the analyses reported here, we excluded any contrasts stemming from region-of-interest analyses, leaving 52 contrasts from 33 studies.

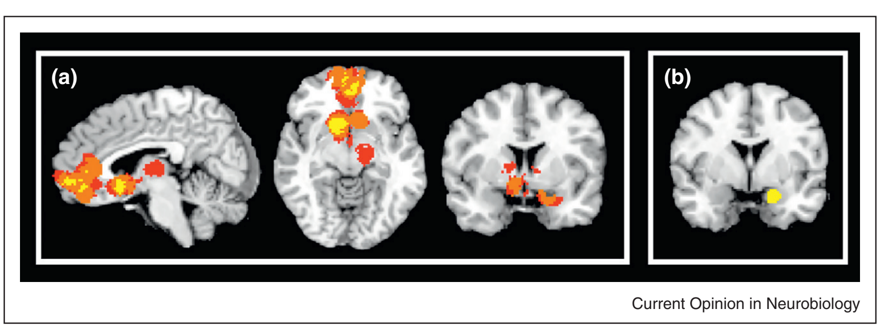
The results of these new analyses are consistent with the previous results [35]. An analysis of the contrasts showing stronger neural responses to *positive* (i.e. attractive or trustworthy) faces than to negative (i.e. unattractive or untrustworthy) faces showed consistent activations clustered around the nucleus accumbens (Nacc) and extending into medial orbitofrontal cortex (mOFC). There were also consistent activations in ventromedial prefrontal cortex (vmPFC), pregenual anterior cingulate cortex (pgACC), and right amygdala (Figure 2a). An analysis of the contrasts showing stronger responses to *negative* faces than to positive faces showed consistent activations in right amygdala only (Figure 2b).

However, as discussed elsewhere [35], these effects of positivity and negativity are driven primarily by contrasts isolating effects of attractiveness and untrustworthiness, respectively. Given that judgments of attractiveness and trustworthiness are so tightly correlated, it is puzzling that their neural signatures look so strikingly different. One difference between attractiveness and trustworthiness studies is that whereas the former tend to use extremely attractive faces (e.g. models), the latter tend to use more average looking faces. Controlling for these stimulus differences showed that the activations in Nacc/mOFC, as well as throughout the vmPFC, primarily originated from studies that used extremely attractive faces. This finding is consistent with the hypothesis that such faces activate reward-related circuits in the brain.

As noted above, previous work has identified nonlinear responses to face valence [32,33,36]. Unfortunately, very few published studies have tested for nonlinear effects. An analyses of the eight nonlinear contrasts, showing higher responses to both positive and negative faces than to neutral faces, revealed consistent activations in a dorsal portion of the right amygdala (Figure 3), as well as in medial PFC.

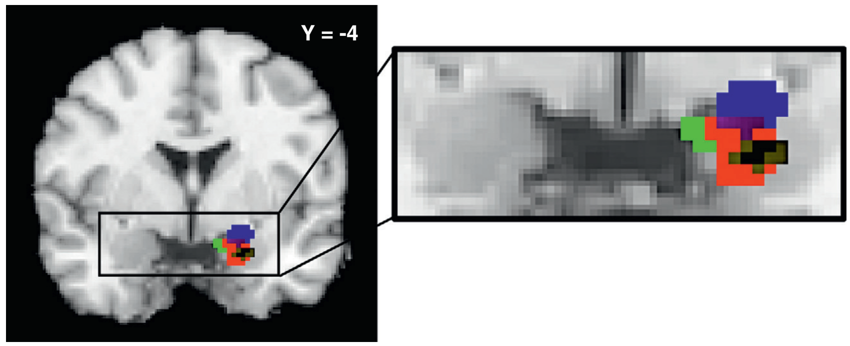
Recent work has gone beyond the identification of neural correlates of social judgments from faces and has explored how initial impressions shape subsequent interactions [37••,38•], and how these judgments may be shaped by hormonal [39•] and social influences [40•], as well as age differences [41].

Figure 2



Consistently activated regions that co-vary with social judgments from faces (data from a meta-analysis of fMRI studies [35]). **(a)** More positive judgments of faces are associated with increased activations in vmPFC, pgACC, Nacc/caudate extending into mOFC, and right amygdala (from right to left). **(b)** More negative judgments of faces are associated with increased activations in right amygdala. Details of the analyses are available in [35].

Figure 3



Responses in right amygdala to social judgments from faces (data from a meta-analysis of fMRI studies [35]). Green and red colors denote consistent linear patterns of activation across positive and negative judgments, respectively. Blue color denotes a consistent nonlinear pattern of activation with stronger responses to both positively and negatively judged faces than faces in the middle of the continuum. Details of the analyses are available in [35].

The typicality hypothesis

Meta-analyses of fMRI studies consistently identify the amygdala as responsive to faces [35,42–44] and recent work suggests that it may contain face selective neurons [45,46]. Although the evidence for the importance of the amygdala in face evaluation is solid, there is no clear account of its role in this evaluation. Valence accounts are inconsistent with the observed nonlinear responses to faces at the extremes of the face valence continuum [32,33,35,36]. An alternative is that the amygdala tracks the affective salience of faces. However, recent work suggests that it may track even more general face properties [47••,48••].

Computational models of social judgments [10–12] treat faces as points in a multi-dimensional space centered on the average face. In these models, as faces are manipulated to look more positively or more negatively, they are moved away from the average face. If the manipulation is too extreme, the faces become grotesque. Generally, as the distance from the average face increases, the face typicality decreases. Two recent studies tested whether the amygdala and posterior face selective regions respond to face atypicality rather than to positivity and negativity of faces [47••,48••]. The studies compared responses to faces generated from a valence dimension and faces generated from a control dimension, matched on distance from the average face. Despite differences in experimental design and face stimuli, the findings were converging. The amygdala, as well as the fusiform face area (FFA), responded more strongly to atypical than typical faces (Figure 4), and these responses were not modulated by the valence content of the dimensions.

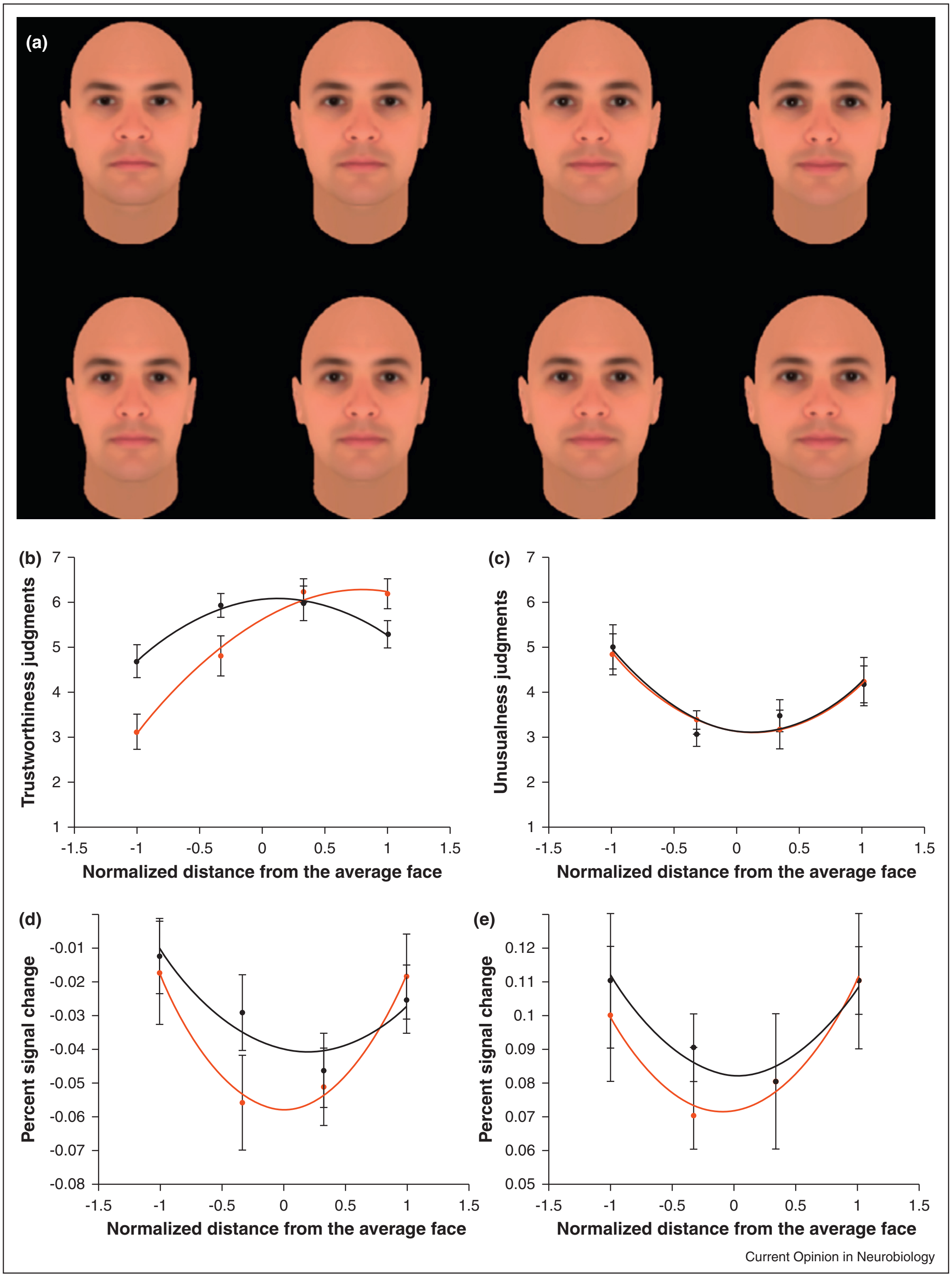
These findings show that face typicality is a key variable for understanding brain responses to face evaluation. The typicality framework parsimoniously explains both linear and nonlinear responses in the previous studies [47••]. Whereas studies that have primarily observed linear responses used faces whose valence was linearly related to typicality, studies that have observed nonlinear responses used faces whose valence was nonlinearly related to typicality. The typicality framework can also explain stronger responses to novel faces, bizarre faces, and emotional faces [46]. Finally, this framework provides a simple computational account of how faces are represented and evaluated in the brain. To extract face typicality, the brain only needs to learn the statistical properties of faces. Yet, these properties can carry information relevant for social attribution. Although we can experimentally un-confound typicality and evaluation of faces, these variables are correlated in real life [47••]. In sum, coding based on face typicality is computationally efficient and also provides information relevant to social perception.

The promise of data-driven methods

Data-driven methods have been very successful for modeling social perception of faces [49•]. For example, computational models of social judgments are a version of reverse correlation methods. These models can be used as tools for discovering the perceptual basis of social judgments from faces [4,49•]. Consistent with earlier work [50–53], these judgments originate in similarity to cues with adaptive significance. For example, trustworthy looking faces appear to express positive emotions and are more feminine (Figure 1b and c).

Data-driven, reverse correlation methods allow researchers to probe and visualize internal representations or social judgment strategies that guide face perception, without any *a priori* assumptions about diagnostic

Figure 4



A test of the hypothesis that the amygdala and the FFA track the typicality of faces (data from [47••]). **(a)** The faces on the first row are generated by a model of face valence (red line in subsequent panels). The faces on the second row are generated by an orthogonal control model (black line in subsequent panels). **(b)** Trustworthiness judgments of faces that vary on valence and control faces. **(c)** Unusualness judgments of faces that vary on valence and control faces. **(d)** Responses in the amygdala to faces that vary on valence and control faces. **(e)** Responses in the FFA to faces that vary on valence and control faces.

stimulus features [49•]. Originally developed in the domain of auditory perception [54], reverse correlation methods were successfully extended into visual perception [55,56]. Importantly, these methods have been recently applied to social face perception.

Two variants of reverse correlation methods have been particularly successful in modeling social perception: face space based reverse correlation [10–12,57] and noise based reverse correlation [58,59]. Both variants visualize internal representations on the basis of the covariation of randomly varied stimulus features and social judgments such as trustworthiness or dominance [10,60•], attractiveness [61,62], race [63,64], gender [58], and membership in social groups [65,66]. New advances in computing platforms allow the modeled judgments to be applied to pictures of real faces [12,67] and visualization of temporal dynamics using animated faces [68,69••].

Furthermore, the intriguing possibility to reverse correlate neural signals instead of behavioral responses (thus visualizing the stimulus features that covary with neural activity) is within reach. Reverse correlation has been applied to electroencephalography (EEG) components and oscillations [70–72]. The method has also been used in conjunction with fMRI BOLD response to visualize the representational basis of FFA and occipital face area (OFA) activity in a face detection task [73•]. Although most of these methodological advances have not yet been applied to the study of *social* judgments from faces, it is clear that exciting times are ahead of us.

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Despite the small sample of two participants, this study provides an important proof of concept about the feasibility of assessing the representational neural basis of face processing using reverse correlation methods on BOLD signals.