

# The Social Perception of Faces

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Faces are one of the most potent social stimuli conveying information about social categories (e.g., sex, age, race), mental states (e.g., puzzled), emotional states (e.g., angry), attractiveness, and identity. People also infer a host of personality characteristics from facial appearance such as trustworthiness and competence (Todorov, Said, & Verosky, 2011), although these inferences are not necessarily accurate (Olivola & Todorov, 2010a). People can rapidly extract information from faces about:

- identity (Grill-Spector & Kanwisher, 2005; Yip & Sinha, 2002)
- race and gender (Cloutier, Mason, & Macrae, 2005; Martin & Macrae, 2007; Ito & Urland, 2003, 2005)
- emotional expressions (Esteves & Öhman, 1993; Whalen et al., 1998)
- attractiveness (Locher, Unger, Sociedade, & Wahl, 1993; Olson & Marshuetz, 2005)
- a variety of social trait inferences (Bar, Neta, & Linz, 2006; Rudoy & Paller, 2009; Rule & Ambady, 2008a; Rule, Ambady, & Adams, 2009; Todorov, Pakrashi, & Oosterhof, 2009; Willis & Todorov, 2006)
- and can recognize familiar faces after more than 50 years (Bahrick, Bahrick, & Wittlinger, 1975).

These are amazing cognitive feats. In fact, decades of computer science research have not been able to produce computer models that match human performance (Bowyer et al., 2006; Sinha et al., 2006).

Not only are social inferences from faces rapidly formed but also they are consequential.

Such inferences predict a range of social outcomes, including economic decisions (Scharlemann, Eckel, Kacelnik, & Wilson, 2001; Van't Wout & Sanfey, 2008), sentencing decisions (Blair, Judd, & Chapleau, 2004; Eberhardt, Davies, Purdie-Vaughns, & Johnson, 2006; Porter, ten Brinke, & Gustaw, 2010; Zebrowitz & McDonald, 1991), occupational success (Hamermesh & Biddle, 1994; Langlois et al., 2000; Mazur, Mazur, & Keating, 1984; Montepare & Zebrowitz, 1998; Mueller & Mazur, 1996; Rule & Ambady, 2008b), and electoral success (Antonakis & Delgas, 2009; Ballew & Todorov, 2007; Little, Burris, Jones, & Roberts, 2007; Olivola & Todorov, 2010b; Todorov, Mandisodza, Goren, & Hall, 2005).

This chapter is organized in five sections. The first two sections review evidence about the “special” status of faces. Section I reviews the major behavioral findings suggesting that perception of faces is different from perception of objects. Section II reviews the major neuropsychology, neurophysiology, and functional neuroimaging findings suggesting that there are neural circuits dedicated to perceptual analysis of faces. The next three sections review research on social perception of faces. Section III reviews research on social inferences from faces. Section IV describes computational models of social perception of faces. Finally, based on a recent meta-analysis of functional magnetic resonance imaging (fMRI) studies (Mende-Siedlecki, Said, & Todorov, in press), section V describes the potential brain network dedicated to social perception of faces. This network comprises not only regions involved in the perceptual analysis of faces (section II) but also a number of subcortical and prefrontal regions.

## SECTION I: THE SPECIAL STATUS OF FACES – PERCEPTUAL AND COGNITIVE PROCESSES

Several early studies have shown that newborns with minimal visual experience preferentially orient to face-like stimuli than to equally complex stimuli (Fantz, 1963; Johnson et al., 1991; Valenza et al., 1996). These findings have been challenged on the grounds that newborns visual preferences are tuned to general geometric configurations (e.g., top-heavy patterns with more elements on the top than on the bottom) rather than to faces (Turati, 2004). However, it is not clear why such general perceptual biases should be present at birth. In contrast, an innate preference for faces (in the form of sensitivity to face-like templates) provides a parsimonious explanation of the findings. In a recent, extensive replication of the earlier studies, newborns with postnatal age from 13 to 168 hours were exposed to a number of different stimulus configurations (Farroni et al., 2005). The key property of stimuli that biased infants' visual preferences was contrast polarity (darker areas around the eyes and the mouth) in an upright face configuration. Moreover, infants preferred faces lit from above (i.e., the natural lighting conditions) than faces lit from below. These findings strongly suggest an innately specified bias to faces in their natural lighting conditions. Importantly, infant monkeys reared without exposure to faces for 6 to 24 months still show preference for faces over other objects (Sugita, 2008). Studies with human newborns also show that they prefer faces with open eyes (Batki et al., 2000) and direct gaze (Farroni et al., 2002), suggesting an early bias to communicative cues in the face. Such early biases can facilitate learning about faces, individuals, and social relations. Undoubtedly, face perception abilities undergo important developmental changes, and experience is critical for tuning these abilities (Pascalis & Kelly, 2009), a topic that is revisited in section III.

In addition to developmental evidence for the special status of faces, there is rich evidence for differences in processing of faces and objects (Farah, Wilson, Drain, & Tanaka, 1998; McKone, Kanwisher, & Duchaine, 2007; Sinha et al., 2006; Yue, Tjan, & Biederman, 2006). Some of the best documented phenomena include the inversion effect, the part-whole effect, and the composite face effect. For example, face recognition is much more dependent on orientation – with dramatic reduction in performance for inverted faces – than object recognition. Similarly, recognition of facial parts (e.g., a mouth) is more accurate when these parts are embedded in the face rather than

presented in isolation and this effect is more pronounced for faces than objects (e.g., a door and a house). Both of these phenomena can be explained by the hypothesis that faces are processed holistically in an upright orientation (Maurer, Le Grand, & Mondloch, 2002): processed as *gestalts* so that the perception of individual features changes when integrated with other features.

Perhaps, the best paradigm illustrating holistic processing is the composite face paradigm (Young, Hellawell, & Hay, 1987). In the original demonstration of the composite face effect, the alignment of the top half of a familiar face with the bottom half of another face interfered with the recognition of the identity of the original face (e.g., top half). Since this demonstration, similar effects have been demonstrated for perception of gender (Baudouin & Humphreys, 2006), race (Michel, Corneille, & Rossion, 2007), attractiveness (Abbas & Duchaine, 2008), trustworthiness (Todorov, Loehr, & Oosterhof, 2010), and emotional expressions (Calder, Young, Keane, & Dean, 2000). In the case of social judgments, facial halves of “positive” faces (attractive and trustworthy) are judged more negatively when aligned with facial halves of “negative” faces (less attractive and less trustworthy looking), although participants are instructed to ignore the irrelevant halves (Abbas & Duchaine, 2008; Todorov et al., 2010). That is, participants are unable to ignore the “irrelevant” face information. Importantly, this effect is substantially reduced or eliminated when the faces are inverted or the facial halves misaligned, demonstrating the nature of holistic processing. The two facial halves fuse to form a new face.

In addition to holistic processing, another distinctive feature of face processing is the extremely high tolerance for perceptual degradation of familiar faces (Sinha et al., 2006). People can recognize familiar faces under a number of suboptimal conditions: blurring of the face images (leaving primarily low spatial frequency information in the face) and perceptual distortions such as compression of the face and caricatures of the face: i.e., people maintain highly robust representations of familiar faces.

Finally, face perception depends on both shape and reflectance (surface) information (O'Toole, Vetter, & Banz, 1999; Sinha et al., 2006; Todorov & Oosterhof, 2011). Dependence on surface information accounts for findings that contrast polarity inversion (e.g., as if looking at the negative of a picture) interferes with face recognition and sex identification (Bruce & Langton, 1994; Russell et al., 2006), as well as social judgments from faces (Santos & Young, 2008). Studies that model separately shape and surface information (see section IV) also show that these types of

information have relatively equal effects on face recognition (O'Toole et al., 1999) and social judgments from faces (Todorov & Oosterhof, 2011).

## SECTION II: THE SPECIAL STATUS OF FACES – NEURAL BASIS

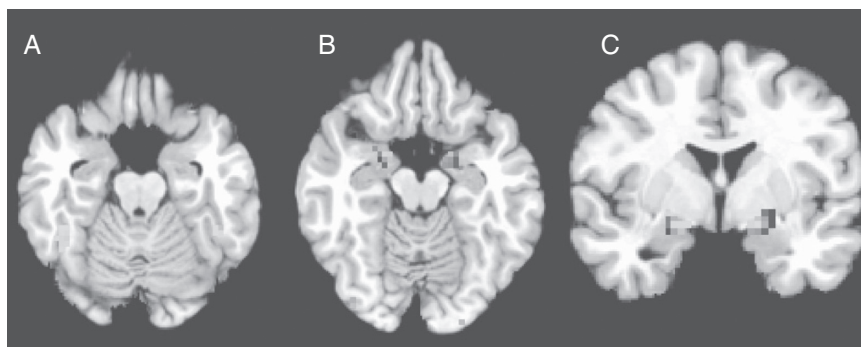
Given the developmental and behavioral data described in the previous section, it should not be surprising that there are brain regions dedicated to face processing. Cases of prosopagnosia – an inability to recognize familiar faces while being able to recognize people by using other cues such as voice, gait, or clothing – have been described as early as the 19th century (Mayer & Rossion, 2005). This perceptual impairment is most frequently caused by bilateral or right lateralized lesions in the inferior part of temporo-occipital regions (fusiform and lingual gyrus). While cases of acquired prosopagnosia are extremely rare, there have been many recent documented cases of developmental prosopagnosia (Duchaine, 2011), and there is evidence that this impairment has a genetic component (Duchaine & Nakayama, 2006).

The data from lesions are largely consistent with neurophysiology and neuroimaging studies. Face-selective neurons were discovered in the inferior temporal (IT) cortex of the macaque brain in the 1970s (Bruce, Desimone, & Gross, 1981; Desimone, 1991; Perrett, Rolls, & Caan, 1982). A number of subsequent studies also recorded from face-selective neurons in the superior temporal sulcus (STS) (Allison, Puce, & McCarthy, 2000; Perrett, Hietanen, Oram, & Benson, 1992).

Consistent with these findings, positron emission tomography (PET) studies of humans in the early 1990s reported face responsive regions in fusiform and inferior temporal regions (Haxby et al., 1993; Sergent, Ohta, & MacDonald, 1992).

Subsequent fMRI studies used a functional localizer approach in which the brain response to faces is contrasted to a number of other categories such as houses, hands, chairs, flowers, etc. Such studies identified several face-selective regions: a region in the fusiform gyrus – labeled the fusiform face area (FFA; see Fig. 6.1A) – (Kanwisher et al., 1997; McCarthy et al., 1997; Tong et al., 2000) a region in the occipital gyrus – labeled the occipital face area (OFA) – (Gauthier et al., 2000; Puce et al., 1996) and a face-selective region in the posterior STS (pSTS, Allison, Puce, & McCarthy, 2000; Puce et al., 1996). These three regions are usually considered the regions comprising the core system for perceptual analysis of faces (Haxby et al., 2000; Said, Haxby, & Todorov, 2011). These regions can be reliably identified in most individual subjects and, at least in the case of FFA, the results are robust with respect to task demands and control categories (Berman et al., 2010).

Two of the most exciting recent developments in the field are the combination of fMRI and single cell recordings in macaques (Tsao et al., 2008) and the use of transcranial magnetic stimulation (TMS) in humans (Pitcher et al., 2007). Tsao and her colleagues used fMRI to identify face-selective patches in the macaque brain and then recorded from these patches. In contrast to previous studies, which have rarely reported more than 20% of face-selective neurons from the sample of recorded neurons, Tsao and her



**Figure 6.1** An example of fMRI research using a functional localizer. Brain regions respond more strongly to faces than to chairs: bilateral fusiform gyri (A) and bilateral amygdala (B & C). The regions were identified in a group analysis ( $n = 37$ ),  $p < 0.001$  (uncorrected). Face-selective voxels can also be identified at the level of individual brains.

colleagues reported more than 90% of face-selective neurons in some of the patches. Pitcher and his colleagues used TMS to transiently disrupt the activity of the right OFA (it is not possible to target the FFA) and found that this affected performance on face perception tasks, providing evidence for the causal significance of the OFA in face processing.

In addition to functional neuroimaging and single unit recording studies, electrophysiological studies have also identified face-selective responses. Studies recording directly from the fusiform gyrus in epileptic patients found negative potentials (N200) evoked by faces (Allison et al., 1994; Allison, Puce, Spencer, & McCarthy, 1999). Studies recording from the skull also consistently identify a negative potential selective for faces: the N170 (for an excellent review, see Rossion & Jacques, 2008). This potential emerges between 130 and 200 ms from stimulus onset and peaks at about 170 ms at occipito-temporal sites of recording. A similar response, traceable to the fusiform gyrus, has been observed in magnetoencephalography (MEG) studies (Halgren, Raji, Marinkovic, Jousmaki, & Hari, 2000).

It is likely that faces automatically evoke responses not only in the posterior face-selective network (FFA, OFA, and pSTS) but also in regions in the medial temporal lobe (MTL; see Fig. 6.1B and C) (Todorov, 2011). Recent studies have also shown face selectivity in the lateral orbitofrontal cortex of the macaque's brain (Rolls et al., 2006; Tsao et al., 2008). This is not surprising given the affective and social significance of faces. At about the time of the discovery of face-selective neurons in IT cortex, a number of neurophysiology studies reported face responsive neurons in the macaque's amygdala (Leonard et al., 1985; Perrett et al., 1982; Rolls, 1984; Wilson & Rolls, 1993; for a review see Rolls, 2000). Recent studies have confirmed these findings (Gothard et al., 2007; Kuraoka & Nakamura, 2007; Nakamura et al., 1992). Importantly, the monkey neurophysiology findings have been replicated in human studies (Fried, MacDonald, Wilson, 1997; Kreiman, Koch, & Fried, 2000). Fried and his colleagues recorded from neurons in the MTL of patients undergoing treatment for epilepsy. They found face-selective neurons in the amygdala, hippocampus, and entorhinal cortex. Subsequent studies have shown that the responses of some of these neurons are modulated by face familiarity (Quiroga et al., 2005; Viskontas, Quiroga, & Fried, 2009).

In addition to data from single unit recordings, data from meta-analyses of functional neuroimaging studies also support a general role of the amygdala in face processing. Two large meta-analyses of PET and fMRI studies on emotional

processing showed that faces are one class of stimuli that most consistently elicit responses in the amygdala (Costafreda, Brammer, David, & Fu, 2008; Sergerie, Chochol, & Armony, 2008) and that these responses do not depend on the valence of the faces (e.g., positive vs negative expressions). Two recent meta-analysis of studies on social perception of mostly emotionally neutral faces have also shown that the amygdala is consistently activated across these studies (Bzdok et al., 2011; Mende-Siedlecki et al., in press). These findings are revisited in section V.

### SECTION III: SOCIAL PERCEPTION OF FACES – EMPIRICAL FINDINGS

Most of the research reviewed in sections I and II has been the exclusive purview of cognitive psychologists and vision scientists. But the study of face perception is at the intersection of cognition, affect, and motivation. As noted in the introduction, people make a variety of social inferences from faces and often act on these inferences: i.e., perceptual information extracted from facial appearance brings to mind relevant social knowledge that can provide a basis for multiple social attributions. For example, attractiveness is associated with a number of social attributions, including social and intellectual competence, concern for others, integrity, and adjustment (Eagly, Makhijani, Ashmore, & Longo, 1991). So is facial maturity (Montepare & Zebrowitz, 1998) and group categorization (Fiske, Cuddy, & Glick, 2007), although they are associated with different sets of social attributions. In a particularly disturbing example, people with more stereotypical African-American appearance are likely to receive harsher legal sentences (Blair et al., 2004; Eberhardt et al., 2006; for a general review of how stereotypical appearance within the same social category affects perception, see Maddox, 2004).

Models of person perception make a fundamental distinction between social category and individuating information and assume that category information is more accessible (Bodenhausen & Macrae, 1998; Brewer, 1988; Fiske & Neuberg, 1990). In fact, there is a lot of evidence that basic categorizations such as age, gender, and race are rapidly extracted from facial appearance (e.g., Cloutier, Mason, & Macrae, 2005; Ito, Thompson, & Cacioppo, 2004; Ito & Urland, 2003; Mason, Cloutier, & Macrae, 2006). However, there is also a lot of evidence that information that could be considered “individuating” is rapidly extracted. This includes information about identity (Jacques & Rossion, 2006; Ramon,

Caharel, & Rossion, 2011; Macrae et al., 2005); attractiveness (Locher et al., 1993; Olson & Marshuetz, 2005; van Leeuwen & Macrae, 2004); facial maturity, masculinity, and threat (Bar et al., 2006; Rule et al., 2009; Willis & Todorov, 2006); general valence of the face often measured with trustworthiness judgments (Todorov et al., 2009); emotional states (Esteves & Öhman, 1993; Whalen et al., 1998); and current focus of attention (e.g., eye gaze, see Frischen, Bayliss, & Tipper, 2007).

For example, people can extract information from subliminal presentation of faces about emotional states (Whalen et al., 2004), attractiveness (Olson & Marshuetz, 2005), and face valence (Todorov et al., 2009). Event-related potential (ERP) studies are particularly informative about the speed of these processes. As noted in section II, the first face-specific ERP responses emerge around 130 ms and peak around 170 ms (Rossion & Jacques, 2008). Within the same time window, people can discriminate between different facial identities (Jacques & Rossion, 2006), and differences between responses to trustworthy- and untrustworthy-looking faces emerge between 200 and 400 ms after the stimulus onset of the faces (Rudoy & Paller, 2009).

In general, these findings suggest that in addition to basic social categories (e.g., age, sex, and race), people extract information from faces relevant to several other basic dimensions. At a minimum, these include familiarity, attractiveness, valence, dominance, and emotional states. Furthermore, inferences about social, personality characteristics are most likely in the service of inferring intentions (Ames, Fiske, & Todorov, 2011) and can be derived from similarity to various cues with adaptive significance (Todorov, Said, Engell, & Oosterhof, 2008; Zebrowitz & Montepare, 2008), including self-resemblance (DeBruine, 2002; Krupp et al., 2008; Verosky & Todorov, 2010a), resemblance to familiar people (Kraus & Chen, 2010; Verosky & Todorov, 2010b) and familiar groups (Zebrowitz, Bronstad, & Lee, 2007; Zebrowitz, Wieneke, & White, 2008), and resemblance to emotional expressions (Montepare & Dobish, 2003; Neth & Martinez, 2009; Oosterhof & Todorov, 2009; Said, Sebe, & Todorov, 2009; Zebrowitz, Kikuchi, & Fellous, 2010). For example, structural similarity of emotionally neutral faces to expressions of anger leads to attributions of aggressiveness and dominance (Said, Sebe, et al., 2009).

As noted in section I, social perception of faces is holistic (Santos & Young, 2008, 2010; Todorov et al., 2010), and one of the important questions is how multiple cues (e.g., sex, race, eye gaze) are integrated. A holistic account would predict that this integration is rapid and that changing a single cue can easily change the resulting categorizations

and downstream consequences. A good example is research by MacLin and Malpass (2001, 2003), who showed that imposing an African or Latino hairstyle on the same racially ambiguous face changes the categorization of the face and leads to memory advantage for faces categorized as own race. Interestingly, the original interpretation of these findings was that a single feature changes face perception and that this featural processing is inconsistent with holistic accounts. However, the holistic account posits that the perception of individual features changes when integrated with other features, whether a single feature or multiple features (Maurer et al., 2002). In fact, face identification is impaired when one creates a composite of a familiar face and a familiar hairstyle of another person (picture Bill Clinton's face with Al Gore's hairstyle; Sinha & Poggio, 1996).

More importantly, people integrate multiple facial cues that include identity, gender, age, race, attractiveness, emotional states, eye gaze, and cues indicating membership in social groups with respect to the self. There have been many research demonstrations of "compound" effects, where one cue changes the effects of another cue (Hess, Adams, Grammer, & Kleck, 2009). These include race cues and emotional expressions (Bijlstra, Holland, & Wigboldus, 2010; Hugenberg & Bodenhausen, 2004; Hutchings & Haddock, 2008), gender cues and emotional expressions (Hess, Adams, Grammer, & Kleck, 2009), trustworthiness cues and emotional expressions (Oosterhof & Todorov, 2009), eye gaze and emotional expressions (Adams & Franklin, 2009; Adams & Kleck, 2003), race cues and eye gaze (Adams et al., 2010), and race cues and personality trait cues (Dotsch, Wigboldus, & van Knippenberg, 2011). These findings await a common account.

A question that has received substantial attention and is of both theoretical and practical significance is how people get attuned to specific category distinctions (Bukach, Gauthier, & Tarr, 2006). For example, one of the well-documented effects in face recognition is the own-race bias effect in memory for faces (Meissner & Brigham, 2001; Sporer, 2001). People are much better at recognizing faces of their own race than faces of other races. This finding has been of tremendous importance for understanding eyewitness errors in cross-race identifications. What leads to such biases in perception and memory? The best-supported hypothesis is that prolonged visual experience with members of a specific social category leads to better perceptual discrimination and memory for members of this category as opposed to members of less familiar categories.

Developmental evidence strongly supports the "expertise" hypothesis. In section I, I mentioned a study that showed that infant monkeys reared

without exposure to faces retain their preference for faces (Sugita, 2008). However, their first (1-month) exposure to specific types of faces – human vs monkey – was critical for the development of their perceptual expertise. For example, monkeys only exposed to human faces for a month easily discriminated different human faces but had difficulties discriminating monkey faces afterwards. In a similar vein, human studies show that whereas 6-month-old infants can recognize both human and monkey faces, 9-month-old infants recognize only human faces, showing evidence for perceptual narrowing (Pascalis, de Haan, & Nelson, 2002). Importantly, showing monkey faces to 6-month-old infants on a consistent basis preserves their ability to recognize these faces when they are 9 months old (Pascalis et al., 2005). Finally, whereas newborns do not show a preference for own-race faces, 3-month-old infants do (Kelly et al., 2005). And this preference can be reversed as a result of one's visual experience. Adults who were born in Korea but adopted as children by French parents show better recognition of Caucasian than Asian faces (Sangrigoli et al., 2005).

Adult studies are largely consistent with the expertise hypothesis. This includes evidence for more holistic processing of own- than other-race faces (Michel, Caldara, & Rossion, 2006; Tanaka, Kiefer, & Bukach, 2004), enhanced neural responses in the FFA to own-race faces (Golby et al., 2001), and better recognition of own-race faces (Meissner & Brigham, 2001). Both responses in the FFA and holistic processing have been shown to predict face recognition (Richler, Cheung, & Gauthier, 2011; Golarai et al., 2007). The evidence also includes better recognition of emotional expressions of own-culture faces (Elfenbein & Ambady, 2002, 2003). The expertise hypothesis also fits computational models of face perception that posit that faces are represented in a multi-dimensional face space (see section IV; Caldara & Abdi, 2006).

However, at least in the case of adult studies, the expertise hypothesis is not sufficient to account for a number of recent findings. Specifically, social categorization models posit that the mere categorization of faces as in-group or out-group produces a number of downstream consequences, including those mimicking the impaired recognition of other-race faces (Hugenberg et al., 2010; Hugenberg & Sacco, 2008; but see Rhodes et al., 2010). For example, Bernstein, Young, and Hugenberg (2007) showed that Caucasian subjects had a better memory for Caucasian faces that were categorized as in-group than for Caucasian faces categorized as out-group. Similar effects have been observed for the identification of emotional expressions (Young & Hugenberg, 2010). Other research has shown that categorizing other-race

faces as members of an in-group reduces implicit race biases (Van Bavel & Cunningham, 2009) and enhances neural responses in both the amygdala and fusiform gyrus to in-group faces (Van Bavel, Packer, & Cunningham, 2008).

These findings are very interesting because cues exogenous to facial appearance *per se* (e.g., a color background of the face) signaling in-group/out-group status can dramatically change how faces are processed. In fact, it appears that the mere categorization of faces as out-group reduces holistic processing (Hugenberg & Corneille, 2009; Michel, Corneille, & Rossion, 2007, 2010). One interesting implication of social categorization models is that inducing individuating learning of other-race faces may enhance memory for these faces (Hugenberg, Miller, & Claypool, 2007), as well as reduce negative implicit biases against members of other races (Lebrecht et al., 2009; Van Bavel & Cunningham, 2009).

Often, the expertise and social categorization hypotheses are contrasted, but this need not be the case. First, these hypotheses are not mutually exclusive. Second, some empirical findings are best explained by both hypotheses. When no specific individuation learning is induced, in-group categorizations seem to enhance memory for in-group own-race faces but not for in-group other-race faces. For example, learning White and Black faces in the context of rich and poor environments enhanced memory for White but not Black faces in rich environments (Shriver et al., 2008). Thus, the advantage for White faces was preserved but only when these faces were motivationally significant. Similar considerations apply to studies where the motivational significance of faces is manipulated by eye gaze (Adams, Pauker, & Weisbuch, 2010). More troubling for the expertise hypothesis are findings showing that individuating learning can eliminate memory advantages for own-race faces (Hugenberg et al., 2007; Lebrecht et al., 2009). However, most adults with normal face perception ability have sufficiently rich face representations that can accommodate perception of “other” yet familiar race faces. The interesting practical question is to what extent learning to individuate other-race faces would generalize to settings outside the specific experiments.

One of the important questions for future research is how learning shapes face perception and to what extent different types of perceptual learning can explain different biases (Lebrecht et al., 2009). For example, in a recent paper, Halberstadt, Sherman, and Sherman (2011) provided a simple learning/attentional account of hypodescent, the tendency to classify mixed-race faces as minority faces. Specifically, they argued that because one first learns faces of majority members, learning of minority members requires

attention to distinctive features. This specific strategy leads to minority categorization of mixed-race faces. In fact, whereas Caucasian subjects tended to categorize morphs of Chinese and Caucasian faces as Chinese, Chinese subjects tended to categorize the morphs as Caucasian. Experimentally inducing this learning strategy led to similar effects. Assuming that majority faces are perceived as more typical than minority faces, it should be noted that the hypodescent effect is also predicted by the attractor field model (Tanaka & Corneille, 2007; Tanaka, Giles, Kremen, & Simon, 1998) – a computation model within the face space framework (see section IV).

Learning specific person information, especially when this information has affective value, is also inextricably linked to face perception. For example, there are many behavioral studies showing that people spontaneously infer evaluations and traits from behaviors and that such inferences are associated with the faces that accompanied the behaviors (Bliss-Moreau, Barrett, & Wright, 2008; Carlston & Skowronski, 1994; Goren & Todorov, 2009; Todorov & Uleman, 2002, 2003, 2004). Such learning occurs after minimal time exposure to faces and behaviors, is relatively independent of availability of cognitive resources and explicit goals to form impressions, and subsequent effects on perception and judgments are independent of explicit memory for the behaviors (Bliss-Moreau et al., 2008; Todorov & Uleman, 2003). Several studies on patients with brain lesions provide evidence consistent with the idea of robust person learning mechanisms and their effects on face perception (Croft et al., 2010; Johnson et al., 1985; Todorov & Olson, 2008; Tranel & Damasio, 1993). For example, patients with amnesia due to hippocampal lesions are nevertheless able to preserve affective responses to faces that were acquired by learning person information about the faces (Croft et al., 2010; Todorov & Olson, 2008). Finally, intensive learning (“day in the life” stories) about unfamiliar people over a 5-day period can modulate early N170 responses to faces (Heisz & Shedden, 2009). The N170 response is attenuated when unfamiliar faces are repeated, but not when famous faces are repeated. Heisz and Shedden (2009) showed that, as in the case of famous faces, the N170 response was not attenuated after repetition of faces associated with rich behavioral, social information. This was not the case for faces associated with non-social information (e.g., stories about volcanoes).

As people learn over time more and more about their social environment, social face perception and social knowledge begin to mesh together. Beliefs about a person’s character influence the expected facial appearance of the person (Hassin & Trope, 2000) and evaluation of novel faces is

influenced by their similarity to known faces (Kraus & Chen, 2010; Verosky & Todorov, 2010b). Likewise, beliefs and attitudes about a group influence the expected facial appearance of group members (Dotsch, Wigboldus, Langner, & van Knippenberg, 2008; Dotsch, Wigboldus, & van Knippenberg, 2011) and greater familiarity with in-group (within-race) faces relative to out-group faces can partially explain in-group face preferences (Zebrowitz et al., 2007, 2008). Individual differences in these expectations have been shown to drive face categorization as a function of prejudice (Hugenberg & Bodenhausen, 2004), although this relationship is complex (Dotsch, Wigboldus & van Knippenberg, 2011).

#### SECTION IV: SOCIAL PERCEPTION OF FACES – COMPUTATIONAL MODELS

Models of representation of faces can be used as tools for modeling social perception (e.g., Oosterhof & Todorov, 2008; Todorov & Oosterhof, 2011; Walker & Vetter, 2009) or as testable hypotheses of how faces are represented in the brain (e.g., Leopold, Bondar, & Giese, 2006; Löffler, Yourganov, Wilkinson, & Wilson, 2005; Rhodes & Jeffery, 2006; Said, Dotsch, & Todorov, 2010). Both uses are invaluable. Models are (a) explicit in specifying the parameters important for face perception, (b) testable because of their explicitness, and (c) an excellent tool for generation of novel faces and for parametric manipulation of faces on parameters of experimental interest. As a general rule, statistical approaches for characterizing the commonalities and differences among individual faces attempt to reduce high-dimensional face representations (e.g., pixel values of photographs or three-dimensional (3D) points that define the skin surface) to a lower-dimensional “face space”. The dimensions of the face space define abstract, global properties of faces that are not reducible to single features.<sup>1</sup> Within this space, faces are represented as points, where each dimension is a property of the face.

The conceptual idea of face space was proposed by Valentine (1991), who used this idea to account for a number of face recognition findings, including effects of distinctiveness (recognition advantage for distinctive faces and high false recognition of typical faces) and race (recognition advantage for own-race faces). For example, to explain the first phenomenon, one needs to assume that distinctive faces are located in less dense regions of the face space. Subsequently, statistical face models were defined using a principal components analysis of either the pixel intensities

of two-dimensional (2D) facial images (Turk & Pentland, 1991) or points on the face surface extracted from 3D laser scans of faces (Banz & Vetter, 1999, 2003). These multidimensional models provide a powerful representational framework that can account for variations in face identity and facial expressions (Calder & Young, 2005; Neth & Martinez, 2009), race (Caldara & Abdi, 2006; Furl, Jonathon, & O'Toole, 2002; O'Toole, Abdi, Deffenbacher, & Valentin, 1995), attractiveness (Potter & Corneille, 2008; Potter, Corneille, Ruys, & Rhodes, 2007; Said & Todorov, 2011), and social perceptions of various personality characteristics (Oosterhof & Todorov, 2008; Todorov & Oosterhof, 2011; Walker & Vetter, 2009).

As described in section I, perception of faces is holistic. This poses serious problems for modeling social perception: i.e. deriving the facial features that lead to specific social perceptions such as trustworthiness and dominance. Changes in any facial feature (e.g., the shape of the eyebrows) could lead to changes in social judgments, and the same feature would be perceived differently in the context of other features. Furthermore, it is not even clear what constitutes a proper feature (e.g., mouth vs upper lip vs segment of the face). Finally, the various feature combinations rapidly proliferate even for a relatively small number of features (10 binary features result in 1024 feature combinations, and 20 binary features result in 1,048,576 combinations).

Data-driven approaches based on face space models are particularly well suited for modeling the complexity of social perception (Todorov, Dotsch, Wigboldus, & Said, 2011). These approaches allow for the stimuli to vary across the whole face (and therefore all possible features) without limiting the search to specific features. This makes it possible for solutions to emerge that not only show effects of specific features but also effects of interacting features on social perception. For example, using a statistical face model, it is possible to uncover the variations in the structure of faces that lead to any social judgment whether on personality characteristics (e.g., trustworthiness, extroversion; see Fig. 6.2) or on social categories (e.g., the typical face for a particular group). Generally, the statistical model is used to randomly generate faces that are precisely characterized on the face dimensions. Subsequently, social judgments of these faces are analyzed as a function of the position of the faces in the multidimensional space. This analysis allows for the construction of new dimensions in the face space that account for the maximum variability in the judgments and, importantly, can be used to visualize the differences in facial structure that lead to specific judgments, as well as manipulate faces along these dimensions (Todorov

et al., 2008). Using this approach, a number of social judgments have been successfully modeled (Oosterhof & Todorov, 2008; Todorov & Oosterhof, 2011; Walker & Vetter, 2009).

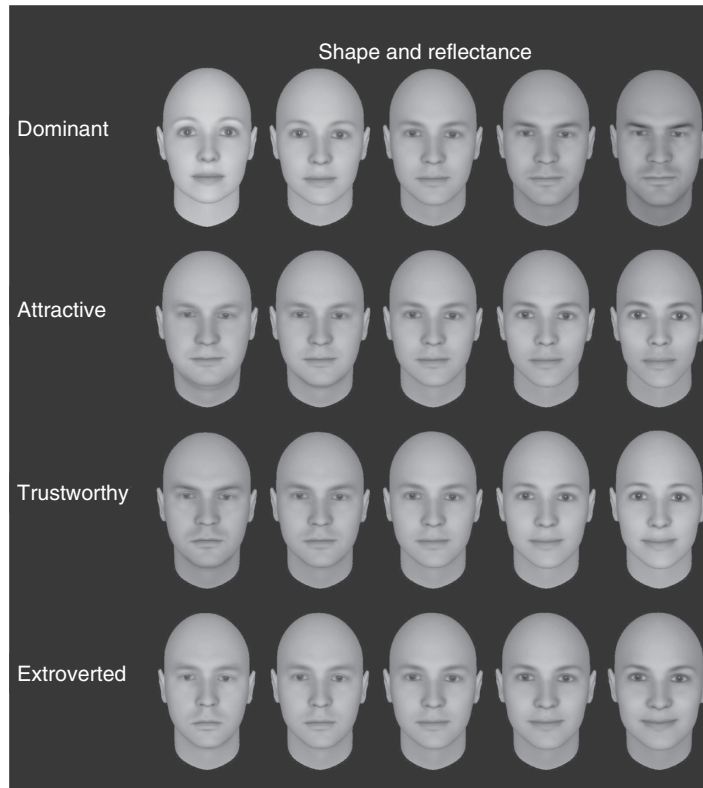
Whereas the above research uses face space models as tools for modeling social perception, these models were originally proposed as models of how faces are really represented in the brain. In principle, there are two versions of these models, according to which faces are either coded as exemplars or relative to a population norm – the average or prototypical face (Tsao & Freiwald, 2006; Valentine, 1991). The major difference between the exemplar and norm-based models is the importance of the average face. In the norm-based model, all faces are represented with respect to the average face. One way to think of the average face is as the prototype of faces extracted from one's experience and as the face at the origin of the multidimensional face space.<sup>2</sup> In fact, there is evidence that 3-month-old infants are capable of extracting face prototypes (de Haan, Johnson, Maurer, & Perrett, 2001).

Two types of behavioral evidence strongly support the norm-based model. First, people are faster recognized from caricatures of their faces, which have been obtained by exaggerating the difference between the faces and the average face, than from the original faces (Lee, Byatt, & Rhodes, 2000; Rhodes, Brennan, & Carey, 1987). Second, in norm-based models, each face has an anti-face (i.e., the opposite identity of the face) – the face across the origin (the average face) of the space (think of multiplying the face vector by  $-1$ ). Importantly, the face and its anti-face are very dissimilar (Rhodes & Jeffery, 2006). Yet, adaptation to the anti-face facilitates identification of its corresponding face (Leopold, O'Toole, Vetter, & Banz, 2001; Leopold, Rhodes, Müller, & Jeffery, 2005; Rhodes & Jeffery, 2006). Norm-based models easily accommodate these findings (Tsao & Freiwald, 2006). Neurophysiological and neuroimaging research also supports these models: both single unit recordings and fMRI studies have shown increased responses in face-selective regions as a function of the distance from the average face (Leopold et al., 2006; Löffler et al., 2005). Moreover, recent work shows that such models could also account for neural responses to the social value of faces (Said et al., 2010), a topic revisited at the end of section V.

## SECTION V: THE NEURAL BASIS OF SOCIAL PERCEPTION OF FACES

Section II outlined the regions involved in the perceptual analysis of faces. These include the





**Figure 6.2 Variations of face shape and face reflectance on four social dimensions derived from judgments of dominance, attractiveness, trustworthiness, and extroversion. The perceived value of the faces on the respective dimensions increases from left to right.**

FFA, the OFA, and face-selective regions in pSTS. But what are the regions involved in social perception of faces?<sup>23</sup> In the last decade, there has been a flurry of functional neuroimaging studies on social perception of faces (Todorov, Said, & Verosky, 2011). Most of these studies have focused either on perceived attractiveness or perceived trustworthiness. Importantly, about half of these studies used implicit paradigms, in which subjects are not instructed to explicitly evaluate the faces (Mende-Siedlecki et al., in press). Thus, one can draw conclusions that are not generally limited to specific evaluations of trustworthiness and attractiveness.

There have been a number of inconsistencies within attractiveness studies and within trustworthiness studies, as well as inconsistencies between these two types of studies. For example, the guiding assumption of attractiveness studies is that attractive faces should activate reward-related brain regions. Consistent with this assumption, many studies have observed increased activation

to attractive faces in medial orbitofrontal cortex (mOFC; e.g., Cloutier et al., 2008; Kranz & Ishai, 2006; O'Doherty et al., 2003; Winston et al., 2007) and some studies have observed similar responses in the nucleus accumbens (NAcc; e.g., Aharon et al., 2001; Cloutier et al., 2008). However, many other studies have not observed activations in NAcc (e.g., Kampe et al., 2001; O'Doherty et al., 2003; Kranz & Ishai, 2006; Winston et al., 2007).

Most neuroimaging studies on trustworthiness have focused on the role of the amygdala, following research with patients with bilateral amygdala lesions showing that they have a bias to perceive untrustworthy and unapproachable faces – as assessed by judgments of normal controls – as trustworthy and approachable (Adolphs, Tranel, & Damasio, 1998). Although subsequent fMRI studies with normal participants have confirmed the amygdala's involvement in perceptions of trustworthiness, there have been inconsistencies in the nature of the observed responses. Whereas

some studies have observed linear responses – the amygdala responded more strongly to untrustworthy-looking faces (Engell, Haxby & Todorov, 2007; Winston et al., 2002), other studies have observed non-linear responses – the amygdala responded more strongly to both trustworthy- and untrustworthy-looking faces than to faces in the middle of the continuum (Said, Baron, & Todorov, 2009; Said et al., 2010; Todorov, Said, Oosterhof, & Engell, 2011). Similar non-linear amygdala responses have also been observed in studies on attractiveness (Liang et al., 2010; Winston et al., 2007). Finally, it is puzzling that studies on attractiveness and trustworthiness emphasize different sets of regions (Todorov, Said, & Verosky, 2011), given that judgments of attractiveness and trustworthiness are highly correlated with each other (with correlations ranging from 0.60 to 0.80; see Oosterhof & Todorov, 2008; Todorov et al., 2008).

In addressing these issues, meta-analytic methods are especially helpful. These methods can be used to identify regions that are consistently activated across a large number of studies of the same psychological phenomenon. Recently, Mende-Siedlecki and colleagues (Mende-Siedlecki et al., in press) conducted a multi-level kernel density analysis (MKDA) of 28 studies on face evaluation. In contrast to standard approaches, the MKDA approach accounts for the fact that individual activation peaks are nested within contrast maps, making these maps the unit of analysis rather than individual peaks (Wager et al., 2008), and also weights contrasts so that studies with larger sample sizes and more statistically rigorous analyses contribute more to the results of the meta-analysis (Kober et al., 2008).

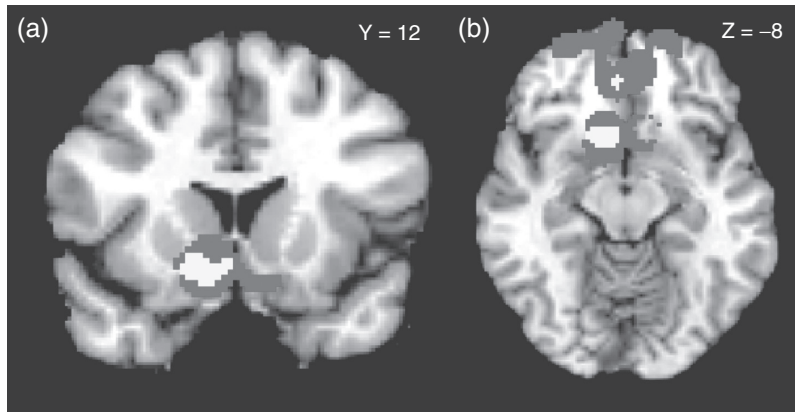
Across studies, Mende-Siedlecki and colleagues (in press) observed consistently stronger activations to negatively evaluated than to positively evaluated faces in right amygdala. Less consistent areas of activation were observed in left amygdala, right anterior insula, right inferior frontal gyrus, right ventrolateral prefrontal cortex, and right globus pallidus. Consistently stronger activations to positively evaluated than to negatively evaluated faces were observed in left caudate extending into NAcc/mOFC, vmPFC, dACC/pgACC, right thalamus, as well as less consistent activations in right amygdala, bilateral insula, IFG, and vIPFC. Interestingly, these patterns of activations in response to negative and positive faces parallel activations in response to angry and happy faces, respectively. These findings are consistent with the emotion overgeneralization hypothesis (see section III; Montepare & Dobish, 2003; Neth & Martinez, 2009; Oosterhof & Todorov, 2009; Said, Sebe, & Todorov, 2009; Zebrowitz, Kikuchi, & Fellous, 2010) and the

hypothesis that novel faces are automatically evaluated with respect to their approach/avoidance value (Todorov, 2008).

Separate analyses of trustworthiness and attractiveness studies showed that these studies were associated with different loci of activations: right amygdala in trustworthiness studies, and the NAcc/caudate and vmPFC/pgACC in attractiveness studies. However, most of these differences could be attributed to differences in the face stimuli used in the respective studies. Specifically, attractiveness studies that used extremely attractive faces were the ones leading to more consistent activations in the NAcc/caudate and vmPFC/pgACC (see Figure 6.3). These findings show that the type of face stimuli used in a particular study could determine the nature of the observed behavioral and neural responses, a topic that is revisited later.

Importantly, the MKDA analysis revealed several brain regions consistently activated across studies on face evaluation in implicit paradigms not requiring face evaluation. These included bilateral amygdala, vmPFC, bilateral caudate, and NAcc/mOFC. These regions seem to be automatically engaged upon the presentation of faces. Most likely, the region that is central for the face evaluation network is the amygdala (Todorov, 2011). This is consistent with both anatomical studies of the macaque's brain (Amaral et al., 1992) and neurophysiology findings of face-selective responses in the amygdala (Gothard et al., 2007; Nakamura et al., 1992; Rolls, 2000). The amygdala receives input from the inferior temporal (IT) cortex and projects back not only to IT cortex but also to extrastriate and striate visual areas. The amygdala also has strong interconnections with anterior cingulate cortex, orbitofrontal cortex, medial prefrontal cortex, basal ganglia, and anterior insula. This anatomical position of the amygdala allows for it to serve as an affective hub of information.

Future research needs to establish the functions of the regions involved in social perception of faces. Based on the literature, Mende-Siedlecki and colleagues (in press) have argued that highly processed face information in inferior temporal regions can be further processed in the amygdala for determining the affective significance of the faces. Faces that are deemed significant either by virtue of their atypicality (Said et al., 2010) or emotional expressions (Vuilleumier et al., 2004) can be more deeply processed in these regions via feedback projections from the amygdala. Faces that are tagged as affectively significant in the amygdala can be further processed in prefrontal regions. Prefrontal-amygdala connections have been explored in the vmPFC (Quirk et al., 2003; Heinz et al., 2004), as well as the pgACC



**Figure 6.3** More consistently activated areas in studies that used extremely attractive faces than in studies that used more typical faces a) NAcc extending into mOFC, b) pgACC and vmPFC. (The opposite contrast did not produce regions of consistent activation.) Brighter voxels withstood height-based thresholding and darker voxels withstood extent-based thresholding ( $p < .001$ ). The thresholding was based on Monte Carlo simulations (see Kober et al., 2008 and Mende-Siedlecki, in press, for technical details).

(Stein et al., 2007; Zink et al., 2010), both of which were observed as consistently activated to positively evaluated faces. Finally, the consistent activation in the left caudate nucleus, extending broadly into the NAcc, suggests that the impressions from faces may depend, in part, on the recruitment of structures implicated in reward-processing (Haruno et al., 2004; Knutson et al., 2001a, 2001b). However, as noted above, activations in these regions seem to be driven by extremely attractive faces.

One of the important and unresolved research questions is what properties of faces are coded in the different regions comprising the face evaluation network. The models reviewed in section IV could be particularly useful in guiding this research. In the context of face space models, Said and colleagues recently tested whether the FFA and the amygdala respond to general face properties characterized by the distance to the average face (i.e., face typicality) rather than to more specific “social” properties (Said et al., 2010). Specifically, they compared the responses to faces parametrically manipulated by a statistical model of face valence and faces that were matched on the distance from the average face but varied to a much lesser extent in their perceived valence. Both the amygdala and the FFA responded more strongly to faces distant from the average face irrespective of the valence of the faces.

This finding suggests that these regions are tracking face typicality. Importantly, this finding

accounts for previous inconsistencies in the literature. Studies that found a linear relationship between the amygdala response and face valence (e.g., Todorov & Engell, 2008) used faces for which there was a linear relationship between valence and typicality (with more positive faces perceived as more typical). Studies that found a non-linear relationship between the amygdala response and face valence (e.g., Todorov, Said et al., 2011) used faces for which there was a non-linear relationship between valence and typicality (with more positive and more negative faces perceived as less typical). Finally, although typicality and valence (and many specific social attributions) can be un-confounded in experimental contexts, they are highly correlated in real life. In fact, non-evaluative judgments of typicality correlated with 13 out of 14 evaluative social judgments (Said et al., 2010). In general, these findings suggest that brain regions involved in face evaluation may be coding general properties of faces that are extracted from statistical learning. Yet, these properties would be diagnostic for many social perceptions.

## CONCLUSION

Faces are special in many ways. Primates are born with perceptual biases to attend to faces.

Face perception involves processes that are distinct from processes in object perception. For example, perception of faces is holistic and not reducible to single features. There are neural circuits dedicated to face perception. But most importantly, from a social cognition point of view, people extract information from faces that is used for social category and personality judgments. Moreover, people act on these judgments and their effects could be consequential. The challenge for future research would be to provide a common computational account of the various facets of social perception of faces and to characterize the functions of the brain regions involved in this perception.

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## NOTES

1 Occasionally, the dimensions of face space can be interpreted as related to specific facial features such as mouth, eyes, etc. – e.g., Maclin and Malpass (2001) – but this is rarely the case in actual statistical models.

2 There is some work suggesting that people may hold different prototypes for distinctive groups of faces (Jaquet, Rhodes, & Hayward, 2008; Little, DeBruine, Jones, & Watt, 2008; Potter & Corneille, 2008).

3 A more detailed treatment of this topic can be found in Todorov and Mende-Siedlecki (in press).

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