



Face perception in its neurobiological and social context

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Abstract

Significant advances in the understanding of processes involved in face perception have been achieved. This study aims to review the literature of face perception in neurobiological and social contexts. The review focused on the mechanisms of mediation of face perception by neural substrates, and discussed some of the social signals provided by faces. We showed that psychological, neurophysiological and neuroimaging studies have demonstrated that a dedicated neural system for face perception exists in primates, which includes the fusiform face area (FFA), anterior superior temporal sulcus (STS) and anterior inferior temporal gyrus (ITG). But it remains to be understood how the integration of face perception occurs in the neurobiological context and in the social context.

Keywords: face perception, neural substrates, social signals, prosopagnosia, face-responsive cells, face symmetry.

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Introduction

Face perception may be one of the most developed visual perceptual skills in humans. People probably spend more time looking at faces than at any other single stimulus (Morton & Johnson, 1991). The human face is important for the identification of individual members of the human species, a process that relies on the subtle differences and variations that make every face unique (Bruce, 1982). From an evolutionary view, the face has evolved in order to allow other organs to function (the mouth for eating, for instance); however, these organs are used for additional purposes, as the signaling of emotion by movements of the facial muscles (Darwin, 1872).

The early efforts at determining a clear theoretical basis for the understanding of face processing date from the 1970s and 1980s, through information-processing models (Hay & Young 1982; Bruce & Young, 1986; Ellis, 1986), a computer-recognition model (Kohonen, Oja, & Lehtio, 1981), a neurophysiological model (Baron, 1981), and neuropsychological models (Damasio, Damasio, &

Hoesen, 1982; Ellis, 1983; Rhodes, 1985). Since then, the increasing interest in the processes underlying the perception and recognition of faces has been demonstrated by the large number of studies in this field.

The purpose of this paper is to review the literature on face perception in neurobiological and social contexts. The review focuses on the mechanisms of mediation of face perception by neural substrates, and discusses some of the social signals provided by faces.

Prosopagnosia and the Early Studies on Neural Substrates for Face Perception

The existence of a specialized system for face perception in the human brain was first suggested by the observation of patients with focal brain damage who had a selectively unimpaired ability to recognize other objects. Most cases reported an upper left quadrantanopia, some with defects in the upper right quadrant as well. Therefore, critical substrates for face recognition were localized in the right temporal cortex or bilateral temporal cortices in most people (Meadows, 1974). This syndrome was called prosopagnosia (Hecaen & Angelergues, 1962; McNeil & Warrington, 1993). Prosopagnosia was further associated with lesions in other areas, such as the ventral occipitotemporal cortex (Damasio et al., 1982; Sergent & Signoret, 1992), and right unilateral lesions (De Renzi, 1986; Landis, Cummings, Christen, Bogen, & Imhof, 1986).

The contribution of prosopagnosia to the study of face perception is that prosopagnosia suggested the existence of separate systems for the recognition of faces and for the recognition of objects (McNeil & Warrington, 1993; Damasio et al., 1982). Evidence of the independence of face

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and object recognition has been shown. Farah, Levinston and Klein, (1995) demonstrated that face perception does not involve the same processes and representations as the perception of objects. Moreover, Feinberg, Schindler and Ochoa (1994) reported patients who showed dissociation between object and face recognition, suggesting that prosopagnosia is not simply a mild general visual agnosia, because such an interpretation is inconsistent with the possibility of relatively preserved face recognition in the presence of object agnosia.

Concerning the two subtypes of prosopagnosia, it has been suggested that associative prosopagnosia is caused by damage to bilateral anterior temporal areas, whereas apperceptive prosopagnosia is due to unilateral right lesions of the fusiform and lingual gyri (Damasio, Tranel, & Damasio, 1990; De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994; Barton et al., 2002). However, further extensive neurophysiological and/or functional imaging studies are required in order to clearly define the neural substrates for each subtype of prosopagnosia.

Mediation of Face Perception by Neural Substrates

A large number of studies have discussed distinct physiological processing systems enrolled in face perception, supporting the evidence for the existence of neural substrates for face perception. These include evidence of innate attentiveness to faces in newborn infants (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991), specialization of the right cerebral hemisphere for face recognition (De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994; Ellis, 1983), and neurophysiological evidence of face-responsive cells in the temporal lobes of monkeys (Desimone, 1991; Gross, 1992; Perrett, Rolls, & Caan, 1982; Perrett, Hietanen, Oram, & Benson, 1992; Eifuku, De Souza, Tamura, Nishijo, & Ono, 2004; De Souza, Eifuku, Tamura, Nishijo, & Ono 2005).

It is known that cells in two distinct regions of the temporal lobe are preferentially activated by faces in monkeys: one is located in the anterior superior temporal sulcus (STS), and the other in the anterior inferior temporal gyrus (ITG) (Rolls, 1992). Our group has recorded neuronal activity from the temporal lobe of Japanese monkeys (*Macaca fuscata*) to investigate whether cells in this region respond specifically to faces. Our results indicated that the anterior STS and the anterior ITG play different roles in the process of identifying familiar faces (Eifuku et al., 2004, De Souza et al., 2005). The population of neurons in the anterior STS responded to faces with selectivity for viewing angle, and these neurons are thought to be closely associated with the analysis of incoming perceptual information from faces, whereas the population of neurons in the anterior ITG was essentially involved in the recognition of facial identity. It appears, thus, that the functional roles of the anterior STS and the anterior ITG differ, although these roles might be complementary (Eifuku et al., 2004, De Souza et al., 2005).

More recently, the technology of functional magnetic resonance imaging (fMRI) has enabled considerable advances in the understanding of face perception in humans, partly because the spatial resolution of fMRI can yield a much more precise picture of face-specific areas compared to lesion studies. The fMRI studies indicate that there are multiple neural systems responsible for face perception distributed in both hemispheres (Haxby, 2000). Imaging studies have also identified the importance of the fusiform face area (FFA) during face perception tasks and the apparent nonexclusive activation of this area by faces (Gauthier, Skudlarski, Gore, & Anderson, 2000). The FFA was reported to be engaged both in detecting faces and in extracting the necessary perceptual information to recognize them. It has also been demonstrated that the FFA shows not only functional, but also structural specificity (Kanwisher & Yovel, 2006). Furthermore, three bilateral regions in the occipitotemporal visual extrastriate cortex were found to compose the human neural system for face perception: the region in the fusiform gyrus appears to be more involved in the representation of identity (Hoffman & Haxby, 2000; George, Dolan, Fink, Baylis, Russell, & Driver, 1999), whereas the region in the superior temporal sulcus appears to be more involved in the representation of changeable aspects of faces (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998). The region in the inferior occipital gyri may provide input to the other two regions.

These results are consistent with the studies performed with monkeys, which identified face-selective neurons in the anterior STS and ITG (Perrett et al., 1992; Desimone, 1991; Eifuku et al., 2004; De Souza et al., 2005). These results suggest that similar clusters of face-selective neurons may exist in homologous regions in the human brain. The exact location of these homologous regions in the human brain, however, is not obvious.

Social Cognition Involving Face and Gaze

Recognition of faces, facial expressions and gaze direction are important components of the non-verbal human social behavior (Argyle & Cook, 1976; Grusser, 1984). The face provides important social information related to sexual attraction, emotional state, and individual identity. Animal-based studies of specialized skills and neural systems for processing these social signals were recently reviewed by Tate, Fischer, Leigh, & Kendrick (2006), and have shown that these skills and systems evolved in a number of mammals and are not exclusive to humans. Much of the cognitive and neuroscience research in face perception has focused on people's ability to recognize individuals. The recognition of identity is based on the perception of aspects of the facial structure that are invariant across changes in expression and other movements of the eye and mouth (Bruce, Burton, Doyle, & Dench, 1989). According to Haxby (2000), however, social communication that is facilitated by the face may represent a more highly developed visual perceptual skill than the recognition of identity.

The amygdala has been described as a critical component of the neural network underlying social cognition (Rosvold, Mirsky, & Pibram, 1954). This structure might play a role in guiding social behaviors on the basis of socioenvironmental context, possibly by modulating several areas of the visual and somatosensory cortices that have been implicated in social cognition. This structure might also help to direct overt visuospatial attention to face gaze (Adolphs & Spezio, 2006). The relation of the amygdala and the anterior STS with gaze recognition may explain why a patient with bilateral amygdala damage fails to recognize expressions of fear. In fact, the amygdala seems to be extensively involved in the recognition of facial expressions of fear (Nagai, 2007). Similarly, impairment in the ability to direct gaze towards, and to use information from, the eyes in the face of others, may explain the deficient recognition of basic emotions and deficient social judgment seen in patients with damage to the amygdala (Adolphs, 2007).

We have recently studied the modulation of face neuron responses in the anterior STS of monkeys, according to the direction of gaze in the observed face, since direction of gaze is an important determinant of the biological significance of an observed face. It should also be noted that in monkeys, the anterior STS has abundant neural connections with the amygdala (Amaral & Price, 1984). We found that modulation was more evident in the rostral region of the anterior STS. Some of the face neuron responses were specific to the combination of a particular facial view and a particular gaze direction, whereas others were associated with the relative spatial relationship between facial view and gaze direction (De Souza et al., 2005).

Researchers have hypothesized that the social dysfunctions in social developmental disorders, such as autism, impair the acquisition of normal face-processing skills (Heffer, Manoach, & Barton, 2005). Indeed, Dawson, Webb and McPartland (2005) have demonstrated that individuals with autism have impaired face discrimination and recognition, and use atypical strategies for processing faces characterized by reduced attention to the eyes and piecemeal rather than configural strategies. Face perception in autistic persons was studied by Schultz et al. (2000), who found a significantly smaller activation of the middle aspect of the right fusiform gyrus (FG) in 14 high functioning individuals with autism or Asperger syndrome, compared to controls. More recently, a study with individuals with autism spectrum disorder (ASD) concerning the activation of face identity-processing areas in the so-called social brain found a widely distributed network of brain areas related to face identity-processing, which included the right amygdala, the inferior frontal cortex (IFC), STS, and the face-related somatosensory and premotor cortex (Hadjikhani, Joseph, Snyder, & Tager-Flusberg, 2007). Furthermore, Kylliäinen, Braeutigam, Hietanen, Swithenby and Bailey, (2006) found subtle differences in face and gaze processing among autistic children as compared to children with normal development. Averted eyes evoked a strong right lateralized component

in the normally developing children, but a weak response in autistic children. By contrast, direct gaze evoked a left lateralized component only in children with autism.

Face Symmetry/Asymmetry and its Positive Relation to Attractiveness

In their analyses of the origins and nature of facial expressions, Darwin (1872) and Ekman (1993) suggested that facial expressiveness may be an important element related to social interactions and sexual reproduction. In this context, a general attractiveness for face symmetry, among animals, would represent an important feature for their survival (Kenrick, Montello, Gutierrez, & Trost 1993). Evolutionary theorists have argued that symmetry is a marker of good genes and resistance to disease that can cause asymmetrical development (Riggio & Woll, 1984). Moreover, asymmetry may be a more salient determinant of attractiveness in younger faces because it is rarer (Walster, Aronson, Abrahams, & Rottman, 1966). Bashour (2006) has identified symmetry as the most important factor of attractiveness when compared to typicality, sexual dimorphism and youthfulness. In contrast, Swaddle and Cuthill (1995) described a positive relationship between asymmetry and facial attractiveness, showing that it may be due to the fact that certain facial features (including those contributing to attractiveness) in fact show directional asymmetry or antisymmetry. Little and Jones (2006) have suggested symmetry preferences are driven by a mechanism that is independent of conscious detection, and which may be the result of specific pressures faced by human ancestors to select high-quality mates and could support a modular view of mate choice. They showed that symmetry preferences are influenced by inversion, whereas symmetry detection is not, and that the ability to detect facial symmetry is not related to preferences for facial symmetry.

There have been, so far, only a few neurophysiological studies regarding the neural substrates underlying the recognition of face symmetry and/or asymmetry. We have recently reported detailed characteristics of face-responsive cells in the anterior STS of macaque monkeys (De Souza et al., 2005). Interestingly, did not a small number of face neurons in the caudal region of the anterior STS responded equally to right- and left-angled faces, while on the other hand, face neurons in the rostral region of the anterior STS responded preferentially to faces in a unique (right or left) oblique view. In other words, face-responsive cells in the caudal region of the anterior STS tended to be insensitive to right-left symmetry on the face. On the other hand, face neurons in the rostral region of the anterior STS discriminated between right and left-angled faces. Therefore, the rostral region of the anterior STS may be important for the discrimination of right-left differences in faces, i.e. face asymmetry. Taken together, our results suggested a plausible functional hierarchy within the anterior STS along the rostro-caudal axis. (De Souza et al., 2005).

We have also reported an effect of familiarity on face symmetry/asymmetry in humans. In a previous report (Eifuku, De Souza, Tamura, Nishijo, & Ono, 2003), we investigated brain representations of familiar and unfamiliar faces during a reaction time (RT) task. This study used a pair association paradigm using facial stimuli. We found that RTs were influenced by previous learning in the case of both unfamiliar and familiar faces, but the shape of the RT curves differed markedly between cases involving familiar and unfamiliar faces. The RT curve for unfamiliar faces had two volleys, which were right-left symmetrical to the midline, whereas the RT curve for familiar faces had only a single volley, i.e., those showing right-left asymmetry. These results revealed a significant difference between the mental representations of familiar and unfamiliar faces. The results are also in agreement with those obtained in our previous study on responsiveness of face cells in the anterior STS of monkeys. The right-left symmetry reflected in the RT curves for unfamiliar faces might have been associated with the behavior of face neuron responses frequently observed in the caudal region of the anterior STS, where the majority of face neuron responses had two peaks that were right-left symmetrical to the midline (De Souza et al., 2005; Eifuku et al., 2003). Unfortunately, research has not yet linked symmetry or asymmetry in the human or monkey face to social meanings such as mating value, indicating that face symmetry (or asymmetry) might be an attractive matter of study for the near future.

Conclusion

The face is a very powerful image. It is one of our primary means of perception and communication as humans. From all possible objects, the face is what attracts us the most. For instance, when we meet someone, we usually look first at their face, and then to their body. We can recognize a familiar face, or distinguish one person from another as soon as we see her/him, because of abilities that are constructed in our brains.

The present review discussed important issues related to face perception such as whether face perception uses the same neural mechanisms as those used for the recognition of objects. Evolutionary arguments support the specialization for face processing and the existence of a neural mechanism for face perception.

Paul Ekman (1982) found that people from distinct cultures, even those from villages of New Guinea who had not been exposed to the western culture, can recognize certain emotional facial expressions. This indicates that face expressions of basic emotions can be universally recognized and, in a certain way that is biologically programmed (Ekman et al., 1987). Despite this, people often exert control on their facial expressions, adapting them according to each circumstance. In other words, the social context can influence the expression of emotions.

We showed in this article that a number of studies – psychological, neurophysiological and neuroimaging – have demonstrated one neural substrate, the FFA, which is specialized for face perception. But it remains unclear how the integration of face perception occurs in the neurobiological context and in the social context. For instance, how do brain structures involved in face perception and facial expression, such as the FFA and the amygdala, integrate to each other in the moment we look at one's face?

The understanding of the neural mechanisms in the recognition of facial expressions, gaze and face perception is important to demonstrate how special faces are in nonverbal communication. There is indeed no doubt about the importance of face perception for human communication but what still remains unclear is the whole system of information processing that can be provided by faces, such as age, emotional expression, and attractiveness.

An intriguing challenge for researchers in the future will be to link all of the information concerning neural mechanisms and social context, as well as to evaluate if or how these mechanisms change or influence face perception. Studies in this field are expected to bring a clearer comprehension of the interaction between neural structures and social signals provided by faces.

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