

Facing facts: Neuronal mechanisms of face perception

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The face is one of the most important stimuli carrying social meaning. Thanks to the fast analysis of faces, we are able to judge physical attractiveness and features of their owners' personality, intentions, and mood. From one's facial expression we can gain information about danger present in the environment. It is obvious that the ability to process efficiently one's face is crucial for survival. Therefore, it seems natural that in the human brain there exist structures specialized for face processing. In this article, we present recent findings from studies on the neuronal mechanisms of face perception and recognition in the light of current theoretical models. Results from brain imaging (fMRI, PET) and electrophysiology (ERP, MEG) show that in face perception particular regions (i.e. FFA, STS, IOA, AMTG, prefrontal and orbitofrontal cortex) are involved. These results are confirmed by behavioral data and clinical observations as well as by animal studies. The developmental findings reviewed in this article lead us to suppose that the ability to analyze face-like stimuli is hard-wired and improves during development. Still, experience with faces is not sufficient for an individual to become an expert in face perception. This thesis is supported by the investigation of individuals with developmental disabilities, especially with autistic spectrum disorders (ASD).

Key words: face perception, emotion perception

INTRODUCTION

It is commonly accepted that the ability of fast and accurate face analysis plays a crucial role in the evolution and survival of mankind (see Ellis and Young 1989, 1998). Faces are the unique source of information concerning human beings. Merely looking at somebody's face enables us to determine sex, age, race and attractiveness, and what is even more important, tentatively estimate mood, intelligence and honesty, and also friendly and hostile attitudes in its owner (see Bruce and Young 1986). If the person whom we observe suddenly averts his/her eyes and looks in a different direction, we will follow his/her gaze expecting that there is something worth our attention (Friesen and Kingstone 1998).

Although each human face consists of the same components: eyes, nose, mouth, cheeks, chins, etc.,

most of us have the unique maximal capacity for memorizing examples of these social stimuli (Hochberg and Galper 1967, Yin 1969, Galper 1970, Yarmey 1971, Bower and Karlin 1974, Bahrick et al. 1975). This fact is confirmed by longitudinal studies of adults, who can recognize up to 90% photographs of their classmates even after 35 years after graduation from the secondary school independently of class size (Bahrick et al. 1975).

Nowadays the scientific interest focuses on neuronal mechanisms responsible for visual face processing. Unfortunately, the results of these studies seem to be rather inconclusive. The crucial issue pertains to the specificity of face perception, that is, whether the face is an extraordinary stimulus (Kanwisher et al. 1997, 1999, Farah et al. 1998, Eimer 2000c, Iidaka et al. 2006, Palermo and Rhodes 2007, Rolls 2007) or if the brain processes faces in the same manner as any other category of objects, like animals or buildings (Diamond and Carey 1986, Chao et al. 1999b, Ishai et al. 1999, Iidaka et al. 2006). Another issue reviewed in the present paper concerns the underlying mechanism

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of this extraordinary human competence. Some authors argue that these skills are inborn predispositions (Johnson and Morton 1991, Morton and Johnson 1991, Farah et al. 1998, 2000, Johnson and de Haan 2001, Johnson 2005, McKone et al. 2007). Advocates of this approach cite arguments coming from behavioral data, clinical observations, results of the examination of human and monkey brains as well as investigations of the development of face perception in healthy children and patients with developmental disorders such as autism.

Other authors emphasize the role of learning processes, claiming that we become experts in face recognition just by interacting with other people (Diamond and Carey 1986, Ellis and Young 1989, Gauthier and Tarr 1997, Gauthier and Logothetis 2000).

The main scope of this article is to present current state of the art concerning each of these issues and to attempt to integrate different lines of enquiries.

HOW THE HUMAN BRAIN PROCESSES THE FACE – THEORETICAL MODELS

The primary question concerning the face perception is: what stages visual information about faces has to undergo to be transformed into a neuronal representation? Bruce and Young (1986) give one of the answers.. They created a functional model which predicts that there are several modules in the brain which independently process information about human faces. According to these authors each face is represented mentally by means of seven codes (dimensions): (1) the simple pictorial code keeps detailed information about static picture of face (e.g. grain, illumination and flaws of the photograph as well as the captured pose and expression of portrayed person); (2) the structural code encodes data about the face structure regardless of the context of a picture, facial expression and spatial frequency (enable us among other things to identify a face from a caricature); (3) the facial speech code related to lips and tongue movements during speech and (4) the expression code encodes information about facial expression. The model's proponents mentioned two more semantic codes. One is related to visually derived data (Pascalis et al. 2001) (visually-derived semantic code), for example information about sex and estimated level of intelligence, the other (identity specific semantic code) encodes additional information related to the seen face (e.g. information

about the owner's occupation, friends and his/her living place, etc.) helping to establish the identity of the person to whom the face belongs. The last code (name code) stores information related to the name of the recognized person.

Currently, Bruce and Young's model is often used as a first step to more contemporary theoretical considerations (Williams and Hollan 1981, Read and Bruce 1982, Breen et al. 2000, Palermo and Rhodes 2007, Vuilleumier and Pourtois 2007). One example of such a model was proposed by Haxby and coauthors (Haxby et al. 2000, 2002, see also Gobbini and Haxby 2007). These researchers argued that to recognize a face, the brain has to process information related to the changeable face aspects such as facial expression eye gaze direction or head position separately from features which are invariant allowing identification of the face's owner. Otherwise any small modification of the face could be misinterpreted as a change in face identity (Haxby et al. 2000). According to authors these processes are controlled by "the core system". The system is located in three functionally distinct regions of extrastriate cortex in both hemispheres. One of the regions is located in the inferior occipital gyrus and contributes to early stage of face perception. The data are further transferred to the remaining two regions located in the posterior part of the superior temporal sulcus and in the lateral part of the fusiform gyrus (Sergent et al. 1992, George et al. 1999, Hoffman and Haxby 2000). In accordance with Haxby and others (Puce et al. 1998, Hoffman and Haxby 2000, Haxby et al. 2002, Gobbini and Haxby 2007), the region of superior temporal sulcus is responsible for analysis of the changeable aspects of faces while the fusiform gyrus is responsible for the analysis of invariant elements related to the identity (Hoffman and Haxby 2000, Haxby et al. 2002, Gobbini and Haxby 2007).

Haxby and colleagues (Haxby et al. 2000) emphasized that the full analysis of information regarding a face requires strict cooperation of the core system with brain structures responsible for other cognitive functions such as spatial attention (located in interparietal sulcus and frontal eye fields), emotional processes (amygdala, insula and other structures of limbic system), auditory verbal comprehension (superior temporal gyrus). Cooperation of the core system with anterior part of temporal lobe, responsible for holding biographical information about the face owner, is

also required by the model. Functioning of those systems as well as their cooperation are controlled by “the extended system” (see Gobbini and Haxby 2007).

To summarize, both Bruce and Young (1986) and Haxby and colleagues (2000) postulate multistage processing of face information and separate means of analysis (Burton et al. 1991, Hancock et al. 2000, Gobbini and Haxby 2007). Both models however do not take into account (or at least underestimate) some factors which could strongly affect the quality of face specificity. Indeed, people seem to differ in perceptual sensitivity to particular face features, like the expression of negative emotions. For example persons with relatively high anxiety levels recognize threatening faces faster than others (Bruce 1982, Bradley et al. 1999). Moreover, these models take into account neither situational factors nor relations between face perception and attentional processes (Vuilleumier et al. 2001a, Pessoa et al. 2002, Holmes et al. 2003, for a review see Palermo and Rhodes 2007). Last but not least, these models do not specify which of stages of face processing reach the level of consciousness and which do not. (Bauer 1984, Tranel and Damasio 1985, Cauquil et al. 2000, McCarthy 2000, Downing et al. 2001, Carmel and Bentin 2002, Pessoa et al. 2002, Stone and Valentine 2004, Wiens 2006, Palermo and Rhodes 2007).

A solution to the last problem (i.e. contribution of conscious and unconscious processes to face percep-

tion) can be found in two-route model proposed by Bauer (1984, 1986) and later developed by Ellis and Young (1990). Bauer was the first who noticed that a patient with prosopagnosia (i.e. inability to recognize familiar faces due to damage of the inferior temporal lobes) exhibited an enhanced skin conductance response (SCR) to the presentation of familiar faces. Therefore, her brain partially processed visual information even though she could not consciously recognize the faces. Bauer concluded that healthy persons have two neural visual pathways for the analysis of face information, both being directly connected with the limbic system. The so-called ventral route is responsible for overt face recognition. It starts at the visual association cortex and, *via* the inferior temporal lobes, reaches the amygdala and hypothalamus. The dorsal route (thanks to which patients with prosopagnosia can react to familiar faces) is responsible for the covert analysis of face stimuli. This pathway starts also at the visual association cortex and comprises the superior temporal and inferior parietal lobes, the cingulate gyrus and hypothalamus. Bauer’s model may account for the face perception deficits accompanying some other disorders such as Capgras syndrome (Ellis and Young 1990, but see Ellis 2007), unilateral spatial neglect (Vuilleumier 2000, Vuilleumier and Sagiv 2001, Vuilleumier et al. 2001b, 2002) and the blindsight phenomenon (Morris et al. 1998, Palermo and Rhodes 2007).

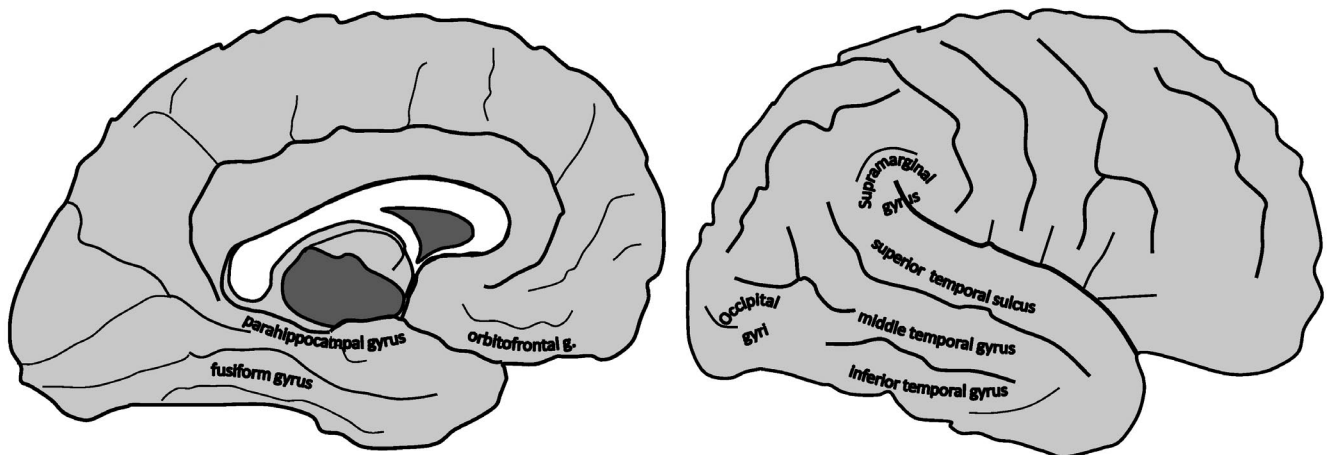


Fig. 1. Brain regions involved in face perception. The fusiform gyrus is responsible for seeing structural features of face, the superior temporal sulcus is responsible for processing dynamic features. The orbitofrontal cortex and anterior middle temporal gyrus are engaged when people see famous and familiar face.

UNIQUE PROCESSING OF FACE: BEHAVIORAL AND CLINICAL DATA

Experimental data

A majority of researchers believe that face perception differs qualitatively from the perception of other objects or words (see e.g. Bruce and Young 1986, Carey and Diamond 1994, Breen et al. 2000). Some authors (e.g. Farah et al. 1998, Farah 1991, Rhodes et al. 1993, Searcy and Barlett 1996, Freire et al. 2000, Leder and Bruce 2000, Moscovitch and Moscovitch 2000) claim that there are two functionally separated systems in the brain which differentially deal with incoming visual information. One system deals with particular parts of an image (i.e. part-based analysis) to create an integrated representation of a perceived object whereas the other system is active when perception occurs in a holistic manner. The authors assume that the human face belongs to objects, which, despite their complexity, are registered and processed as a whole and for that reason face perception engages mostly the second system. Some empirical evidence confirms this point of view.

Firstly, a phenomenon called the inversion effect occurs when participants have to recognize faces displayed either in upright or inverted (rotated by 180°) orientation. The results of many such experiments showed that participants made on average 30% more errors in recognition of inverted faces in respect to upright faces (Hochberg and Galper 1967, Yin 1969, Yarmey 1971, Scapinello and Yarmey 1970, Valentine 1991). Conversely, recognition of other objects like houses, planes, dogs etc, did not deteriorate that much after similar rotation (Hochberg and Galper 1967, Yin 1969, Scapinello and Yarmey 1970, Yarmey 1971, Valentine 1991). The inversion effect was especially remarkable with black-and-white, high-contrast images of faces deprived of grey tones (i.e. Mooney faces, Mooney 1957) which after inversion were virtually unrecognizable (George et al. 1997). This phenomenon leads to conclusion that there has to be a mechanism responsible specifically for face perception as a whole, not as a sum of its components (Yin 1969).

The claim that human faces are processed in a holistic manner is also confirmed by results of other experiments in which speed and accuracy for face recognition were compared with those for the recognition of other objects (e.g. houses). These stimuli were pre-

sented in an intact form or with displaced elements (e.g. a nose on the forehead, a door instead of a window etc.). Although recognition efficiency did not differ in case of intact objects, it was considerably worse in case of scrambled faces than in case of scrambled objects (Homa et al. 1976, Farah et al. 1998, Tanaka and Farah 1993).

A similar situation occurs either when spatial relationships between face components are distorted purposely (e.g. the distance between eyes and nose is increased unnaturally (Tanaka and Farah 1993, Leder and Bruce 1998) or when some components are shown upside down (Bruce 1982, Carbon et al. 2005). In both these cases, the participants have the impression that distorted faces assume a grotesque shape. However when photos are inverted 180° – this effect disappears and the observer is not able to detect any face modifications. It is noteworthy that in case of non-face objects, the detection of similar experimental changes remains relatively unaffected.

Effectiveness of face recognition decreases also in other conditions where the natural scheme of a face is broken; for example when face is represented as a photographic negative relative to photographic positive (Galper 1970) or when the face is represented by a line drawing picture relative to a standard photograph (Davies et al. 1978).

All these findings strongly suggest that face perception differs from the perception of other objects (but see Diamond and Carey 1986, Gauthier and Tarr 1997). A holistic analysis of the human face seems to play a crucial role in face perception. This is no longer true in situations when the configuration of facial components is disturbed (Freire et al. 2000), which forces the brain to perceive a face just like any other object that is relying on part-by-part analysis (Gauthier and Tarr 1997, Farah et al. 1998, Haxby et al. 2000).

Clinical data

Described theoretical models are supported by clinical investigations of subjects with brain damage. For example, Farah and others (data presented in Farah 1996, but see Gauthier and Tarr 1997) described a patient with prosopagnosia, who – as most people with this disorder – had difficulties with recognizing faces as a whole, but performed excellently when a picture of the presented face was cut into pieces. The control group on the other hand, showed just the opposite ten-

dency. A patient who suffered from object agnosia (Moscovitch et al. 1997) had opposite symptoms, that is, his ability to distinguish human faces was intact. However, once the faces were cut onto pieces he was not able to recognize them as faces and performed as poorly as with non-face objects. In addition, it was reported that people with prosopagnosia exhibit a phenomenon opposite to the inversion effect. It appears that, contrary to controls, they recognize inverted faces much better than upright faces (Yin 1970, Farah et al. 1995, de Gelder and Rouw 2000).

This observation favors the claim that the brain system responsible for face processing processes the face as whole rather than merely by analyzing its separate parts.

FACE-SELECTIVE NEURONS: PRIMATE STUDIES

Studies of brain-damaged patients – though spectacular – are not sufficient to generalize results to the healthy population. First, patients differ in depth, immensity and localization of damage to brain tissue. Second, the quality of their responses can be modified by medication (Krolak-Salmon et al. 2004). Thus the researchers found another indirect way to study brain structures specialized in face processing. An answer to this question may be provided by studies of the monkeys whose brains are most similar to ours.

Research indicated that regions of the superior temporal sulcus and the inferior temporal gyrus contain neurons which exhibit activity only when a monkey is shown a picture of human or monkey face (Hasselmo et al. 1989, Perrett and Mistlin 1990, Desimone 1991, Rolls 2005, for a review see Rolls 2007). It was determined that these cells can be divided into functionally specialized groups. The neurons of each group react to different information about faces. Neurons in the superior temporal sulcus analyze mainly the changeable aspects of the face like emotional expression (Perrett et al. 1984, Hasselmo et al. 1989), eye gaze, head position relative to the viewer's line of sight (Perrett et al. 1985, 1992, Perrett and Mistlin 1990), and mimicry (Perrett et al. 1985, Oram and Perrett 1996). Among them one can also find neurons reacting to the faces of particular monkeys and neurons responding simultaneously to both face and its expression (Hasselmo et al. 1989). Second group of neurons, located in the inferior temporal gyrus, seem to register the invariant features

of faces (Perrett et al. 1984, 1985, 1990, Hasselmo et al. 1989, Perrett and Mistlin 1990).

The neural specialization of primate face processing does not end at the temporal lobe. It was shown that cells specifically reacting to faces can also be found in the region of the orbital cortex and in its vicinity (Thorpe et al. 1983, Wilson et al. 1993, O'Scalaidhe et al. 1997, Rolls 1999, Rolls et al. 2006). They react with longer latencies and lower intensity than those from the temporal regions. However, they seem to be more effective in distinguishing particular faces, face gestures or movement (Rolls et al. 2006). Of interest is that many of these neurons respond much more intensively to the real 3D faces than to 2D photographic images (Rolls and Baylis 1986). The researchers suggested that these neurons take part in generating an appropriate reaction (e.g. fight or flight) to the monkey face in real social situations. For example when the monkey must recognize a threatening rival in its herd or estimate danger on the basis of the frightened facial expression of another monkey (Hasselmo et al. 1989, Rolls et al. 2006).

Therefore, one can infer that if the primate brain delegates the perception of the face to specialized groups of neurons, it should also be possible in humans. However, it is not clear to what extent the face-specific brain regions in monkeys are functionally similar to those in humans (Gauthier and Logothetis 2000, Haxby et al. 2000, Kanwisher and Moscovitch 2000, Rolls 2007).

HUMAN FACE PERCEPTION

Neuroimaging techniques: PET and fMRI

Neuroimaging techniques have been used in attempts to resolve these doubts (Sergent et al. 1992, Kanwisher et al. 1997, Haxby et al. 2000, Haxby et al. 2002, Spiridon and Kanwisher 2002, Grill-Spector and Malach 2004, O'Toole et al. 2005, Spiridon et al. 2006).

The region of the fusiform gyrus

One face-specific region is in the fusiform gyrus (i.e. FFA¹) in both brain hemispheres (Sergent et al. 1992, Kanwisher et al. 1997, Halgren et al. 1999,

¹ FFA – fusiform face area occupies the region of lateral fusiform gyrus and areas adjacent to it and is thought by some authors to be a main module specialized in face perception (Kanwisher et al. 1997, but see Gauthier et al. 1999, Tarr and Gauthier 2000).

Haxby et al. 1999, Rossion et al. 2000a). Its activation reaches highest levels (especially in the right hemisphere) when participants are looking at faces while activation in relation to faces decreases remarkably when participants are looking at non-face stimuli such as houses (Aguirre et al. 1998, Haxby et al. 1999, Ishai et al. 1999), chairs (Ishai et al. 1999), tools (Chao et al. 1999a), landscapes (Epstein and Kanwisher 1998) or nonsense stimuli (Haxby et al. 1994, Clark et al. 1996, Epstein and Kanwisher 1998). Additionally, the FFA was claimed to be intensively active when the face was presented in front or in profile, whereas its activity decreased significantly when people had to recognize a person by viewing his or her head from the back (Tong et al. 2000). This implies that the FFA does not just analyze features of the top part of the body generally, but rather features of the face. Moreover, an increase in FFA activation can also be observed when the subject is shown animal faces (Chao et al. 1999b, Tong et al. 2000) and even faces of cartoon characters (Tong et al. 2000). In a task where participants were required to recognize whether a viewed person was a man or a woman, an actor or a non-actor (Sergent et al. 1992) or to decide if two portraits are the same or not (Hoffman and Haxby 2000), FFA activity increased if invariant features of human faces were analyzed. However, in the opposite situation (i.e. during analysis of changeable elements of the face) the FFA activity dramatically decreased, especially if the task required processing of eye-gaze direction (Hoffman and Haxby 2000).

Superior temporal sulcus

It was found that these changeable elements (like the emotional expression and lip movements) were processed by a second face-specific processor which is located in the posterior part of the superior temporal sulcus (STS) (Kanwisher et al. 1997, Puce et al. 1998, Chao et al. 1999a, Halgren et al. 1999, Haxby et al. 1999, Allison et al. 2000, Hoffman and Haxby 2000, Puce et al. 2007, see also Gauthier and Logothetis 2000). For example, Hoffman and Haxby (2000) showed that STS activity depended on the aspects of the face upon which attention was focused. In their ingenious experiment, two faces with different eye gazes (a changeable aspect) or identity (an invariant aspect) were presented in each consecutive trial. Two groups of participants were asked to indicate whether

presented faces have the same eye gaze or the same identity. In such the task, subjects focus their attention on either dynamic or static features of the presented human face. Activity in the STS region was significantly higher when subjects were paying attention to the changeable aspects of the face than in the other condition.

Although the STS is generally known to respond to biological motion (of a hand or a whole body) (Bonda et al. 1996, Decety and Grezes 1999), in case of the face, the STS reacts similarly both to changes of mimics (natural motion) and to dynamic aspects provided by static pictures (e.g. photos) (Kanwisher et al. 1997, Chao et al. 1999a, Halgren et al. 1999, Haxby et al. 1999, Hoffman and Haxby 2000).

It should be noted that besides the STS numerous other highly specialized structures participate in the processing of dynamic aspects of the face: for example, estimation of gaze direction is analyzed by the intraparietal sulcus (which plays an important role in attention) (Puce et al. 1998, Hoffman and Haxby 2000), speech-related lip movements activate the auditory cortex (Calvert et al. 1997), and the amygdala and other structures of the limbic system and the right part of the somatosensory cortex and the anterior part of the frontal cortex analyze the emotional expression (Breiter et al. 1996, Haxby et al. 2000, Adolphs 2003, Palermo and Rhodes 2007, Vuilleumier and Pourtois 2007).

Occipital, temporal, and frontal regions

Imaging techniques have allowed researchers to pinpoint some more areas engaged in face perception, namely the inferior occipital gyrus (Occipital Face Area, OFA) (Kanwisher et al. 1997, Chao et al. 1999a, Halgren et al. 1999, Haxby et al. 1999, Adolphs 2003), the anterior part of the middle temporal gyrus (AMTG), the orbitofrontal cortex (Sergent et al. 1992, Nakamura et al. 2000, Gorno-Tempini and Price 2001) and the right ventrolateral prefrontal cortex (Marinkovic et al. 2000). The first of these regions is responsible for preliminary face analysis and, according to the model proposed by Haxby and coauthors, it projects to FFA and STS (Haxby et al. 1999, 2000). However, it appears that increased activation of this gyrus in tasks in which FFA is activated, suggests that the OFA is also involved in processing the identity of faces (Hoffman and Haxby 2000, Haxby et al. 2000). Two more struc-

tures, that is, the AMTG and the orbitofrontal cortex² show high activity when faces of famous or familiar persons are viewed (Sergent et al. 1992, Gorno-Tempini et al. 1998, Nakamura et al. 2000, Gorno-Tempini and Price 2001).

Interesting studies of patients with epilepsy who had electrodes surgically implanted directly into the brain have provided insights into the role of the right ventrolateral prefrontal cortex (Marinkovic et al. 2000, Vignal et al. 2000). It was found that this region is populated with very little clusters of neurons which responded extremely vigorously to human faces (Marinkovic et al. 2000). Moreover, when these neurons were electrically stimulated, the patients had hallucinations of a series of faces (Vignal et al. 2000). Marinkovitch and colleagues (2000) point out that, because volume of discovered structures is small, techniques like PET or fMRI can “loose” the signal from those structures during the recording of the whole range of brain activity from prefrontal and frontal regions. (Sprengelmeyer et al. 1998, Nakamura et al. 1999, Adolphs 2003). As one can see, it is extremely difficult to determine the function of the frontal lobes in processing of the human face. A hint can be provided by the fact that activation of the frontal regions (especially their medial parts) increases significantly when a face image is degraded. Thus, the above-mentioned areas probably play fundamental role in establishing whether a given object is a face or not, especially under perceptually ambiguous circumstances (Grady et al. 2000).

Event related brain potentials (ERP) and magnetoencephalography (MEG)

Neuroimaging techniques allow one to localize structures involved in the analysis of the viewed face but due to their poor temporal resolution these methods provide little information about dynamic aspects of the processes involved. This gap can be filled by results coming from event related potentials (ERP) and event related fields (ERF). Studies using such methods have shown that a stimulus is classified in the extrastriate cortex as a face as soon as 100 ms after its presentation what is indicated by evoked potential peak denoted as P1 (Linkenkaer-Hansen et al. 1998, Halit et al. 2000,

Taylor et al. 2001a, Itier and Taylor 2002, Liu et al. 2002, Herrmann et al. 2004, 2005a,b, Pegna et al. 2004). It means that the face is classified about 10 ms earlier than images of animals (Rousselet et al. 2003) and about 100 ms earlier than other objects or words (Taylor et al. 2001a, Pegna et al. 2004). A positive face-specific wave with the same frontal topography and a latency of 135 ms was observed with both intact and scattered faces; however, its amplitude was larger for intact than scattered faces (Yamamoto and Kashikura 1999). This result strongly suggests that the human face is detected faster than other complex objects.

Furthermore, presentation of a face usually evokes a negative wave with an average latency of 170 ms (N170 or M170³) distributed bilaterally over the occipito-temporal cortex (Bötzel et al. 1995, Bentin et al. 1996, George et al. 1996, Eimer and McCarthy 1999, Eimer 2000b,c,d, Rossion et al. 2000b, Sagiv and Bentin 2001, Liu et al. 2002, Itier et al. 2006, Heisz et al. 2006). It is commonly believed that N170 is specific only for human and monkey faces (Bötzel et al. 1995, Bentin et al. 1996, Rossion et al. 2000b, Carmel and Bentin 2002, de Haan et al. 2002, Itier et al. 2006). The N170 does not occur when participants are presented with different categories of objects⁴ like houses, hands, cars, furniture, animals and scrambled faces (Bentin et al. 1996, George et al. 1996, Eimer 1998, Eimer and McCarthy 1999, Jemel et al. 1999, Bentin and Deouell 2000, Eimer 2000a,c, Halgren et al. 2000, Sagiv and Bentin 2001, Iidaka et al. 2006, Itier et al. 2006). Moreover, the face-specificity of the N170 is further supported by clinical studies, as this component is absent in patients with prosopagnosia (Bentin et al. 1999, Eimer and McCarthy 1999).

It is generally assumed that the N170 reflects early stages of information processing about the face, including the analysis of its structure and the configuration of its elements (Bentin et al. 1999, Rossion et al. 1999, Eimer 2000b,c,d, Heisz et al. 2006, Itier et al. 2006, Vuilleumier and Pourtois 2007). This is supported by following facts. First, the N170 is sensitive to face orientation. Indeed, the amplitude of this component increases when the head is presented in front and in profile, and decreases dramatically when it is viewed

² One can find more information about the role of the orbitofrontal cortex in the face perception, especially its participation in emotional expression analysis, in studies by Damasio and others (1994), Hornak and others (1996), and Morris and others (1998).

³ M170 refers to component registered using MEG (Liu et al. 2002) whereas N170 was isolated by EEG (Bentin et al. 1996, Eimer 2000c).

⁴ Some of researchers state that the N170 appears as a response to stimuli others than faces, including words, but usually in these cases the N170 has a significantly lower amplitude and longer latency (Bentin et al. 1996, Carmel and Bentin 2002, Itier and Taylor 2004b).

from the back or when only small part of the face is visible (Eimer 2000d). Secondly, the N170 (though with smaller amplitude and longer latency) appears in response to both faces lacking some internal elements like eyes, noses or mouths, or external elements like foreheads, cheeks, or hair (Eimer 1998, Eimer 2000a). In addition, the N170 appears in response to an isolated mouth and nose (Bentin et al. 1996) or eyes. In the latter case, the N170 amplitude is even higher than when the intact face is displayed (Bentin et al. 1996, Eimer 1998, Jemel et al. 1999, Taylor et al. 2001a,b, Shibata et al. 2002). Delayed and higher N170s were evoked by inverted images of faces (see above on inversion effect) (Bentin et al. 1996, Rossion et al. 2000b, Sagiv and Bentin 2001, Itier et al. 2006.). These data strongly suggest that the N170 reflects wide range of nonspecific processes involved in the recognition of the human face.

It is worth pointing out that properties of the N170 are independent of whether a face is familiar to the subject or not. This suggests that the N170 is not related to determination of face identity (Bentin and Deouell 2000, Eimer 2000a,b, Heisz et al. 2006)

Most authors also believe that the N170 is evoked by both neutral and emotional⁵ faces (Munte et al. 1998, Bobes et al. 2000, Halgren et al. 2000, Krolak-Salmon et al. 2001, Herrmann et al. 2002, Eimer and Holmes 2002, 2007). Although the most recent studies suggest that the N170 amplitude depends on emotional expression (Pizzagalli et al. 2002, Campanella et al. 2002, Eger et al. 2003, Batty and Taylor 2003, Ashley et al. 2004, Miyoshi et al. 2004, Pourtois et al. 2004), there is no clear pattern of N170 features for each separate emotion (Campanella et al. 2002, Ashley et al. 2004). Perhaps, this pattern would become clearer if origin of this component is considered. The discrete dipole methods (Shibata et al. 2002), LORETA analysis (Pascual-Marqui et al. 2002, Pizzagalli et al. 2002), as well as studies of patients with implanted electrodes, has revealed that the N170 is generated in the region of the fusiform gyrus which, as already mentioned, is insensitive to emotional expression (Bentin et al. 1996, Allison et al. 1999, McCarthy et al. 1999, Pascual-Marqui et al. 2002, Pizzagalli et al. 2002, Shibata et al. 2002) but see also (Itier and Taylor 2004a who point to the role of STS in creating N170).

Studies of patients with implanted electrodes has led to the discovery and localization of another face-specific potential – the N200 – which, similarly to the N170, is generated by a region of the fusiform gyrus and the posterior-inferior temporal gyrus (Allison et al. 1994). This peak, similarly to the N170, seems to be a correlate of early stages of structural face encoding and it is also subject to the face inversion effect (Allison et al. 1994, 1999, McCarthy et al. 1999, Puce et al. 1999).

Further stages of the brain's analysis of information about the human face are represented by a positive wave with average latency of 344 ms (P350), which can be recorded bilaterally from the posterior and right anterior ventral temporal cortices (Sergent et al. 1992, Puce et al. 1996, Gorno-Tempini et al. 1998, Allison et al. 1999, Eimer 2000b, Leveroni et al. 2000). Some studies showed that the P350 can be regarded as a correlate of the retrieval of biographical information associated with face identification (Sergent et al. 1992, Allison et al. 1994, Gorno-Tempini et al. 1998, Puce et al. 1999, Leveroni et al. 2000).

To summarize, both EEG/ERP and MEG/ERF show face-specific patterns of human brain activity. Authors are not sure about which structures are true generators of the ERP and ERF peaks and how they are related to the face-specific regions discovered by neuroimaging techniques (Eimer 1998, 2000b,c, Allison et al. 1999, McCarthy et al. 1999, Puce et al. 1999, Herrmann et al. 2005b, Palermo and Rhodes 2007, Vuilleumier and Pourtois 2007).

Note that waves with similar topographies as the face-specific potentials, but with longer latencies and lower amplitudes, are also generated by other objects (McCarthy et al. 1999, Puce et al. 1999, Carmel and Bentin 2002, Itier and Taylor 2004c, Palermo and Rhodes 2007, Vuilleumier and Pourtois 2007). This is consistent with the finding that the FFA and STS also show residual activity when non-face stimuli are presented (Chao et al. 1999b, Gauthier et al. 1999, Ishai et al. 1999, Gauthier and Logothetis 2000, Gauthier et al. 2000).

These findings show that it is still uncertain to what degree the aforementioned structures involved in face perception are specialized in the processing of this particular stimulus, and to what degree they participate in the visual analysis of other objects (Gauthier and Logothetis 2000, Haxby et al. 2000).

⁵ For detailed information about emotional face expression using ERP (see Eimer and Holmes 2007, Palermo and Rhodes 2007, Vuilleumier and Pourtois 2007).

THE DEVELOPMENT OF FACE PERCEPTION IN CHILDREN

Face uniqueness is also supported by some of developmental studies

If we assume that detection and an effective analysis of the face play a crucial role in our survival (Darwin 1872, Ellis and Young 1989, 1998), then this capacity should appear at early stages of ontogenetic development. Observational and experimental data suggest that it is indeed the case (see e.g. Macchi Cassia et al. 2001, Farroni et al. 2002, Turati et al. 2002, Simion et al. 2002a, Johnson 2005).

As early as 30 minutes after birth, infants more willingly and more often pay attention to stimuli resembling human faces⁶ than to any other objects (Goren et al. 1975, Johnson et al. 1991, Valenza et al. 1996, Macchi Cassia et al. 2004). Interestingly their reactions concern only upright and not inverted faces (Johnson and Morton 1991, Valenza et al. 1996, Mondloch et al. 1999, Mondloch et al. 2003, Macchi Cassia et al. 2004). Infants' preferences for viewing schematic faces prevail even when a high-contrast non-face object competes for their attention (Valenza et al. 1996, Umiltá et al. 1996). Studies by Bushnell and the others (1989) provide evidence that an infant can distinguish his or her mother's face from other faces just few days after birth. Other authors claim that infants are able to recognize a specific face independently of head position (Pascalis et al. 1998) and that they are also capable of distinguishing gaze direction (Vecera and Johnson 1995, Hains and Muir 1996, Hood et al. 1998, Mundy and Neal 2000). Of particular significance to an infant is the presence of eyes in the displayed face, a fact which is rather amazing since the visual system of infant is claimed not to be adapted to analysis of such complex stimuli (Batki et al. 2000, Farroni et al. 2002). It is supposed that those perception skills are possible given vivid contrast between the dark and light region of eye-socket and eye-white (Johnson 2005). This hypothesis is corroborated by the fact that infants prefer to look at scared faces with wide-open eyes than at happy faces (Nelson and Dolgin 1985).

⁶ In the majority of experiments the researchers have used an oval with three big dark blobs, which are distributed so as to look like two eyes and a mouth. These stimuli are of the high contrast, so they are suited to the limited abilities of immature visual system of child (see e.g. Johnson 2005).

It seems that the selective perceptual sensitivity of infants to the human face is adaptable in nature and facilitates the creation of an instant maternal relationship and relationships with other caregivers (Ellis and Young 1989, Johnson et al. 1991). Support for this opinion is provided in observations that infants attend more to those caregivers who keep eye-contact with the infants (i.e. when their eyes are open and gaze is straight) (Farroni et al. 2002) in comparison to those whose eyes are closed or whose faces are averted.

Recently, it was found that this preference in infants does not concern merely schematic faces but it extends to any object which contains more dark elements in the upper than lower part (Umiltá et al. 1996, Simion et al. 2002b, Turati et al. 2002, Simion et al. 2003, Macchi Cassia et al. 2004). For example, Macchi Cassia and coauthors (2004) show that infants younger than 12 weeks gaze equally attentively at faces with most of their components located in the upper part of the presented oval and at faces with the correct arrangement of elements. Turati and others (2002) achieved similar results with schematic faces and rectangles filled with dark squares composed in the shape of a T-letter (see also Umiltá et al. 1996).

The development of these structures seems to progress very fast. In 1- and 3-month-old infants one can observe a decrease in preferences for schematic faces in favor of realistic photos (Maurer and Barerra 1981, Morton and Johnson 1991, Macchi Cassia et al. 2006). A 6-month-old infant can distinguish between normal and schematic faces and no longer favors face schemes displayed upright over inverted schemes, suggesting that the young visual systems start to treat schematic faces as objects that are not connected with face representations (Johnson et al. 1991, Mondloch et al. 1999). On the other hand, infants up to three months can distinguish natural faces from schematic faces with T-shape elements (Macchi Cassia et al. 2006), and infants as young as five months exhibit Thatcher Illusion⁷ (Rose et al. 2002, Bertin and Bhatt 2004, Bhatt et al. 2005). These results clearly show a gradual increase of neuronal efficiency with age in the analysis of face information.

This early specialization in face processing is supported by studies employing neuroimaging techniques.

⁷ The Margaret Thatcher Illusion is a phenomenon where it becomes difficult to detect local feature changes (e.g. inversion of eyes or mouth) in an upside down face. The same changes appear obvious in an upright face (Thompson 1980). Susceptibility to this illusion highlights the sensitivity of the visual system to disturbances of the second-order relations of facial features, such as the spatial relations between eyes, nose and mouth (Rhodes 1988, Maurer et al. 2002, Bhatt et al. 2005).

The FFAs of children as young as two months old were clearly activated when the children looked at photos depicting women's faces (Tzourio-Mazoyer et al. 2002). In 3-months-old infants the activity of other face-specific regions of the neocortex was observed (Halit et al. 2004).

Similarly, two components (i.e. N300 and P400) were found in ERPs in 3-month-old infants, which appeared in response to faces but not to visual noise (Halit et al. 2004) as well as in response to human but not monkey faces (de Haan et al. 2003, Halit et al. 2003). Similar results were obtained with 6-to-12-months-old children (de Haan et al. 2003). It is believed that both peaks are precursors of the N170 (de Haan et al. 2002, 2003, Halit et al. 2003).

In spite of this early skill in face processing, primary-school children's capacity for processing face information is still not as perfect as in adults. The children (6–8 years old) recognized famous or familiar persons (e.g. classmates), relying mainly on external elements of their faces (presence of moustache, hat, glasses or hairstyle) while ignoring the composition of the internal elements (mouth, eyes, nose, cheeks) (Carey and Diamond 1977, Campbell and Tuck 1995, Campbell et al. 1995, 1999, Freire and Lee 2001, Want et al. 2003)⁸. The predominance of this specific strategy decreases in the period from 7 to 11 years and at this time children start to recognize better the composition of internal and not external elements of the human face (Campbell et al. 1995, 1999, Campbell and Tuck 1995, Want et al. 2003). This tendency is confirmed by the lack of a clear face inversion effect for children younger than 10 years (Brace et al. 2001, Pascalis et al. 2001, Pellicano and Rhodes 2003), though some authors claim that this effect can be observed already in 4–5-years-old children (Goldstein 1965, Carey and Diamond 1977, 1994, Diamond and Carey 1986, Carey 1996). The development of face-specific information interpretation skills is completed in adolescence (Ellis et al. 1979, Campbell et al. 1999, Mondloch et al. 2002), although, as some have pointed out, even 14-year-old children still made much more mistakes than adults in recognizing human faces (Carey et al. 1980).

To summarize, the findings presented above seem to support the hypothesis that the human system for face processing is innate and that it matures very fast and partially independently of experience.

⁸ This can explain why children of this age do not recognize familiar persons disguised as Santa Claus.

WHAT CAN WE LEARN ABOUT FACE PERCEPTION FROM PEOPLE WITH DEVELOPMENTAL DISORDERS?

There are situations in which the system responsible for human face analysis develops incorrectly (due to e.g. congenital cataract, Le Grand et al. 2001) or its development is disturbed resulting in difficulties in face processing and/or reading emotional expressions (Phillips et al. 2003, Green and Phillips 2004). These problems appear in people with Williams Syndrome (Wang et al. 1995, Karmiloff-Smith 1997, Deruelle et al. 1999, Karmiloff-Smith et al. 2003, Meyer-Lindenberg et al. 2005), Turner Syndrome (Reiss et al. 1993, Ross et al. 1995, 1997, Wang et al. 1995, Romans et al. 1998, Lawrence et al. 2003), Huntington disease (Phillips et al. 2003, Green and Phillips 2004) as well as in developmental prosopagnosia (Bentin et al. 1999, Eimer and McCarthy 1999, Jones and Tranel 2001, Nunn et al. 2001, Behrmann and Avidan 2005, Harris et al. 2005) and autism (Landgell 1978, Tantam et al. 1989, Klin et al. 1999, Elgar and Campbell 2001, Behrmann et al. 2006b, Jemel et al. 2006, Sasson 2006).

The last mentioned example – autism – deserves more attention mainly because of the expressiveness of its symptoms and the wide literature dedicated to this condition. In the following paragraph we will address this problem.

How do autistics see a face?

Although difficulties in the processing of the human face do not belong to autism's main symptoms as listed in the DSM-IV (Diagnostic and Statistical Manual of Mental Disorders – IV) (American Psychiatric Association 1994) classification, a series of clinical observations and experimental findings provide some evidence for the occurrence of such difficulties.

Experimental studies showed that persons with ASD⁹ performed worse than controls matched in sex, age and level of intelligence (Hobson 1986) in recogni-

⁹ ASD (Autistic Spectrum Disorders) defines group of Pervasive Developmental Disorders (PDD) in the DSM-IV classification, including five separated categories i.e. (1) autistic disorders, (2) Asperger Syndrome, (3) Rett Syndrome, (4) Childhood Disintegrative Disorder, and (5) Pervasive Developmental Disorder Not Otherwise Specified. The problems of ASD persons concern three main areas (1) social interactions, (2) verbal and nonverbal communication, and (3) presence of repetitive, restricted and stereotyped patterns of behavior or interests (see Department of Health and Human Services, National Institute of Health 2007) (Volkmar et al. 2004). Because most cited literature use the ASD definition, we also will use this term interchangeably with autism.

tion and remembering unfamiliar faces (Boucher and Lewis 1992, Ellis et al. 1994, Gepner et al. 1996, Hauck et al. 1998, Blair et al. 2002), identification of familiar faces (Boucher et al. 1998), as well as recognition of emotional expression (Hobson et al. 1988a, Celani et al. 1999, Howard et al. 2000, Njiokiktjien et al. 2001, Gross 2004). The difficulties in face recognition are especially serious when the face is displayed in a position other than in front view (e.g. in profile) (Davies et al. 1994, Klin et al. 1999). Moreover, autistics have problems with performing such simple tasks as determining the sex or age of the presented faces (Hobson 1987, Njiokiktjien et al. 2001). They have also difficulties in more complex tasks which require face recognition on the basis of the face's individual features. For example, Behrmann and colleagues (2006a) presented autistic adults pairs of faces of persons who differed in sex or in identity (while having the same sex). When participants were asked to indicate which pairs are the same (i.e. which one have the same sex or identity), ASD persons responded much slower than controls. This effect was especially prominent when participants were asked to identify faces on the basis of their individual features rather than gender.

Some authors argue that these difficulties of autistics do not concern only human faces but also non-social stimuli (Davies et al. 1994, Barton et al. 2004, Lopez et al. 2004, Behrmann et al. 2006a), which can only be explained successfully by a more global deficit (cf. e.g. Weak Central Coherence Theory; Frith 1989, Frith and Happé 1994, Happé 1994a,b).

However, most studies exploring the face-perception difficulties of autistics report that their ability to make similar operations on other objects is at least as good as it is in controls (Landgell 1978, Hobson et al. 1988b, Tantam et al. 1989, Boucher and Lewis 1992, Davies et al. 1994, Hauck et al. 1998, Klin et al. 1999, Blair et al. 2002). Moreover, as Klin and others (1999) conclude after examining large group of 120 children with ASD, and with other developmental disorders (not belonging to ASD), only autistic persons have problems with face perception, so this deficit cannot be a result of general mental retardation or visual memory deficits.

The most credible evidence of the existence of face specific deficit in ASD patients would be, according to double dissociation principle, the existence of another developmental disorder that allows face processing

expertise to develop normally but disrupts the development of other types of perceptual expertise. Unfortunately we are not aware of any case report describing such a disorder.

What is the nature of the difficulties in processing face information in autistics? A majority of researchers believe that autistics do not perceive the human face as a whole and use mainly a strategy based on the analysis of particular elements, as when perceiving other objects (Landgell 1978, Hobson et al. 1988b, Miyashita 1988, Schultz et al. 2000a,b, Klin et al. 2002, Joseph and Tanaka 2003). The evidence is based on the following findings. First, autistics have low sensitivity to face inversion (Landgell 1978, Hobson et al. 1988b, Tantam et al. 1989). Second, both children and young adults with ASD group photos of faces using the local-feature strategy (e.g. according to hats or hairstyle), while controls classify them on the basis of more holistic criteria (e.g. on the basis of expressed emotion) (Hobson 1987, Bormann-Kischkel et al. 1990, 1995, Teunisse and de Gelder 1994). To confirm these claims, experiments employing eye tracking technology were performed. Their results showed that unlike healthy participants, ASD persons directed their gaze mainly on non-essential, external components of faces, ignoring the internal features, especially eyes (Klin et al. 2002, Pelphrey et al. 2002, Dalton et al. 2005, but see, van der Geest et al. 2002, Bar-Haim et al. 2006). It seems that autistics also use specific strategy of mouth exploration when they are required to recognize a face or to define its emotional expression (Landgell 1978, Hobson et al. 1988b, Joseph and Tanaka 2003, Klin et al. 2002, Gross 2004). In one of the studies confirming this hypothesis Klin and coauthors (2002) measured the time of eye fixation in ASD participants when they viewed short video films presenting various situations with social meaning. The autistics focused mainly on the mouth while exploring the faces of actors, whereas the eyes seemed to carry unimportant information for them. Other researchers did not observe preferences for the mouth area in ASD participants, although they confirmed the tendency to ignore the eye region (van der Geest et al. 2002, Dalton et al. 2005, Bar-Haim et al. 2006).

These findings suggest that autistics analyze human face in an atypical manner and they are not able to treat them (or do so to a lesser extent) as a rich source of social information (Baron-Cohen et al. 1997, Hobson et al. 1988a, Klin et al. 2002).

Neuroimaging studies provide some support for this opinion. It has been shown that ASD persons viewing photos of unfamiliar faces demonstrated significantly lowered activation of the FFA and increased activation (relative to controls) of the inferior temporal gyrus, which is responsible for processing objects other than faces (Schultz et al. 2000a, Pierce et al. 2001). One can observe weaker activity of the FFA in autistic persons in comparison to healthy participants in the recognition of familiar faces (Dalton et al. 2005), the determination of sex (Pierce et al. 2001, Hubl et al. 2003), emotional expression (Critchley et al. 2000, Hall et al. 2003, Hubl et al. 2003) and during identification of the same person in different presentations of his/her face (Pierce et al. 2001). These results seem to be inconsistent with more recent studies (Hadjikhani et al. 2004, Jemel et al. 2006). Some of them showed that FFA activation increased in the same way as in controls when a young person with ADS was especially interested in the presented stimuli, like characters of favorite cartoon (Grelotti et al. 2005). It is therefore hard to settle the issue of the role played by the FFA in the social functioning of autistics, as these data seem to suggest that the FFA is rather something like “a region of interest” than “face recognition area”¹⁰.

More consistent information about disturbed face processing in autistics comes from EEG and MEG studies. They showed the absence of differences in neuronal responses to exposure to the mother’s face versus to an unfamiliar person¹¹ in young (3–4 years old) children with ASD, whereas such a difference is clearly visible in normal children. In a control condition it was tested whether brain responses differed when the children viewed favorite and new toys. Differences were found in both groups, suggesting that autistics can easily differentiate familiar from unfamiliar non-face objects. (Dawson et al. 2002). Even more interesting is that these children did not distinguish neutral faces from those which expressed fear. This finding supports identical properties of negative slow wave (NSW) and of the above-mentioned N300, which is considered as a precursor to the N170 (Dawson et al. 2002). Additionally, in ASD persons differences were found neither when viewing faces from different view-

points (Grice et al. 2001, McPartland et al. 2004) nor when viewing familiar versus unfamiliar faces (Dawson et al. 2002) or when viewing faces expressing different emotions (Dawson et al. 2004). In healthy persons ERP properties depended on task conditions.

Generally, autistics show a deceleration in the neuronal processes responsible for face perception and an atypical specialization of cortical regions in which these processes take place (Dawson et al. 2005, Webb et al. 2006). In the former case, a prolonged latency (McPartland et al. 2004, O’Connor et al. 2005, Webb et al. 2006) and lower amplitude (Bailey et al. 2005, O’Connor et al. 2005) of face-specific potentials (mostly N170) were found. In the latter case, an atypical composition of active sources (Bailey et al. 2005, O’Connor et al. 2005) and the lack of the right hemisphere dominance (typically reported in healthy persons processing face stimuli) were reported (Dawson et al. 2004, McPartland et al. 2004, Senju et al. 2005, Webb et al. 2006).

In spite of a huge amount of experimental data, the question concerning whether ASD people process faces in the same manner as other objects is still unresolved. It can be argued that the autistic brain analyzes the human face using different strategies than the healthy brain. A reason for this could be congenital deficits of structures responsible for face and emotional analysis as well as structures responsible for social motivation. On the other hand the lack of expressing desire to initiate relationships with other people can subsequently limit the development of neuronal structures specific for faces (Dawson et al. 2002, 2005, Schultz 2005, Sasson 2006).

The studies described above indicate also that social experience with human faces both in autistics and healthy persons is not enough to achieve expertise in analysis of faces (Gauthier and Tarr 1997), although it is achievable in the case of other objects (Grelotti et al. 2005).

CONCLUSIONS

In the present article we try to characterize neuronal mechanisms responsible for perception of one of the most socially important stimulus – the human face. This issue is complex and its experimental verification is difficult. Researchers working on this topic are confronted by many methodological problems, for example, what kind of control stimulus is appropriate for the

¹⁰ For more information about function of neuronal structures involved in face perception at ASD persons see: (Baron-Cohen et al. 1999, Critchley et al. 2000, Schultz et al. 2000b, 2003, 2005, Grelotti et al. 2002, Pierce et al. 2004, Dalton et al. 2005, Schultz 2005).

¹¹ Potentials described are the posterior lateral P400 and the frontal Nc (Dawson et al. 2002).

task using face stimuli (Farah et al. 1998, McKone and Robbins 2007, Robbins and McKone 2007) or to what extent do the instruction given to participant and the experimental procedure affect the results (Hoffman and Haxby 2000). Separate problems are the individual differences between participants, especially if they suffer from Autistic Spectrum Disorders (Jemel et al. 2006).

Since a part of empirical data concerning face perception is not coherent, conclusions based on them cannot be decisive.

However, independently of the doubts mentioned above, the results described allow us to formulate some preliminary inferences. First, the face, although perceptually complex, is detected faster and it is analyzed in distinctly from other objects (Yin 1969, Herrmann et al. 2005b), rather as a whole than sum of consisted parts (Yin 1969, Farah 1991, Farah et al. 1998, Freire et al. 2000). This ability is probably a core of a inborn tendency to favor face-like stimuli. (Johnson et al. 1991, Umiltá et al. 1996, Turati et al. 2002). Thanks to it a special system for face perception can develop during the further ontogenesis (Farah 2000, Farah et al. 2000, Moscovitch and Moscovitch 2000, Johnson and de Haan 2001, Johnson 2005). The neuroimaging studies, and recording of electro-/magnetophysiological activity of neurons of those areas can provide some insight into how this system works (Kanwisher et al. 1997, Eimer 2000b,c, Hoffman and Haxby 2000, Tong et al. 2000). It appears that separate neuronal structures are responsible for the perception of particular aspects of the face (e.g. the definition of identity or eye gaze direction), and it seems that the activity is generally higher in the right hemisphere of the brain (Hoffman and Haxby 2000).

Some researchers have questioned the opinion that the face is a special stimulus for our brain, and point out that, the regions responsible for face perception are active also during the processing of different stimuli (Gauthier and Logothetis 2000, Gauthier et al. 2000). One should remember, however, that face-specific neurons in monkeys occupy only 20% of the surface of regions participating in analysis of this social stimulus while the remaining 80% of neurons respond to other categories of objects (Perrett et al. 1982, Baylis and Rolls 1987). It is possible that activity in analogical regions in humans, as described by Gauthier and her coworkers, is registered from these 80% of cells, but the neuroimaging techniques are not able to differenti-

ate between face- and non-face-evoked activity (cf. Haxby et al. 2000).

Moreover, damage or incorrect development of one of aforementioned structures automatically causes difficulties in face perception while analysis of other objects is usually intact (Eimer and McCarthy 1999, Bentin et al. 1999, Farah et al. 2000, Schultz 2005). The deficits can vary from total loss of the ability to recognize faces in prosopagnosia (Bentin et al. 1999, Eimer and McCarthy 1999, Farah et al. 2000) to more discrete symptoms indicating the usage of inadequate strategies in autistics (Landgell 1978, Hobson et al. 1988b, Klin et al. 2002, Joseph and Tanaka 2003, Schultz 2005). It is, however, unknown whether all these deficits are due to the dysfunction of a similar mechanism or whether all they have in common is that they are related to face perception because the underlying neuronal mechanisms are still debatable and the theoretical models still await final empirical verification.

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