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Human face and gaze perception is highly context specific and involves bottom-up and top-down neural processing

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ABSTRACT

This review summarizes human perception and processing of face and gaze signals. Face and gaze signals are important means of non-verbal social communication. The review highlights that: (1) some evidence is available suggesting that the perception and processing of facial information starts in the prenatal period; (2) the perception and processing of face identity, expression and gaze direction is highly context specific, the effect of race and culture being a case in point. Culture affects by means of experiential shaping and social categorization the way in which information on face and gaze is collected and perceived; (3) face and gaze processing occurs in the so-called ‘social brain’. Accumulating evidence suggests that the processing of facial identity, facial emotional expression and gaze involves two parallel and interacting pathways: a fast and crude subcortical route and a slower cortical pathway. The flow of information is bi-directional and includes bottom-up and top-down processing. The cortical networks particularly include the fusiform gyrus, superior temporal sulcus (STS), intraparietal sulcus, temporoparietal junction and medial prefrontal cortex.

1. Introduction

Humans are social beings. They thrive through interaction with other persons. This interaction is based on verbal and non-verbal communication. In non-verbal communication the face plays a major role (Barclough and Perrett., 2011). Other people’s faces easily attract attention; they are faster detected than other visual stimuli (Palermo and Rhodes, 2007). Also the saccades of the eyes move quicker to faces than to animals or vehicles (Crouzet et al., 2010). This quick orienting underlines the importance of the face - and especially the eyes - in social interaction (Leopold and Rhodes, 2010; Schilbach, 2015). Actually, the eyes serve a double function in social interaction: they are not only used to perceive the identity, emotions and intentions of others, they also signal to others intentions and future actions (Gobel et al., 2015; Klein et al., 2009; Schilbach, 2015).

The face provides information on identity (including race, age and gender), emotional state and – especially via gaze - direction of attention and intention (Haxby et al., 2000; Leopold and Rhodes, 2010). During the last ten years the complex processes involved in the perception and

processing of face and gaze have been reviewed in papers addressing specific topics, e.g., face recognition (Johnson et al., 2015), facial expression (Hinojosa et al. 2015; Jack, 2013; Liu et al., 2021; Spunt and Adolphs, 2019), gaze (Burra et al., 2019b; Carlin and Calder, 2013; Dalmaso et al., 2020; Northover et al., 2017; Schilbach, 2015) and developmental aspects including differences between face and object processing (Hoechl and Peykarjou, 2012), the other-race effect (Anzures et al., 2013), social categorization (Quinn et al., 2019), the face inversion effect (Cashon and Holt, 2015) and subliminal face processing (Jessen and Grossmann, 2020).

The recent Covid-19 pandemic heightened awareness on how much we rely on information of the whole face during social interaction (Pavlova and Sokolov, 2021; Pazhoohi et al., 2021). Therefore, the current paper aims to review the three facial aspects involved in social cognition: perception and processing of face identity, expression and gaze. This means that the paper may be regarded as an update of the review of Itier and Batty (2009). In addition to being an update, the present paper addresses three specific questions: (1) What is the evidence that the perception of facial information has a prenatal origin? (2)

Abbreviations: aSTS, anterior superior temporal sulcus; ERP, event related potential; FFA, fusiform face area; fMRI, functional magnetic resonance imaging; MEG, magnetoencephalography; OFA, occipital face area; PGO, ponto-geniculo-occipital; PMA, postmenstrual age; pSTS, posterior superior temporal sulcus; REM, rapid eye movement.

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Are face and gaze perception and processing context specific? Specific attention is paid to the effect of race and/or culture and the potential interactive effects of face identity recognition, facial expression and gaze direction; (3) Does experience and context only result in changes in the bottom-up processing of face and gaze information, or is evidence available on a contribution of top-down processing? Accumulating evidence indicates that sensory perception is not only a matter of bottom-up processing but also involves anticipatory processes predicting the nature of the perceived stimulus (Bar et al., 2006; O'Callaghan et al., 2016). The paper is structured in the following way. Section 2 addresses face recognition, Section 3 discusses the perception of facial expressions of emotion, and Section 4 reviews the perception of gaze. Each section includes the following subsections (a) the capacities of the human newborn addressing the question of prenatal origin; (b) the context dependency – this section pays special attention to the effect of culture and/or race as a specific example of the role of context and experience; and (c) the neural substrate including the contribution of top-down processing. The term ‘race’ is used to refer to a social group whose members descended from a common ancestor and who share a subset of physical attributes (e.g., skin tone, facial and body shape; Chiao et al., 2008). The term ‘culture’ means, according to the *Oxford English Dictionary*, “a society or group characterized by distinctive ideas, customs, social behaviour, products”. In fact, culture is the net result of interactions between genotype and behaviour over centuries resulting in a set of norms, value systems and practices that imposes behavioural rules or strategies on individuals (Pilgrim and Pretty, 2010; Richerson and Boyd, 2006). In this way the cultural context may induce changes in behaviour and cognition. Section 5 contains the concluding remarks and suggestions for future research. It reveals that: (1) Some evidence is available suggesting that the perception and processing of facial information starts in the prenatal period, so that at birth the infant has a preference to look at faces with direct gaze. The newborn brain recruits during face and gaze perception both subcortical and cortical networks; (2) The perception and processing of face identity, facial expression and gaze direction strongly depends on experience and is highly context specific. The context involves the interdependency of face identity, emotional expression and gaze direction, and it includes aspects of the expresser, the observer and the external condition. This is exemplified by the modulating effect of race and culture on face and gaze processing; (3) in the processing of face and gaze signals two neural pathways may be distinguished: a subcortical and a cortical one. The cortical networks involved in the processing of face and gaze signals form part of the so-called ‘social brain’. Which parts of the face and gaze networks are primarily recruited depends on the task and its context. The network processing involves bi-directional streams of information, i.e., it involves both bottom-up and top-down processing, including for instance preparatory top-down processing associated with the social categorization of faces.

2. Face recognition

The fact that passports carry a photograph of their owner's face underscores how strongly the face is interwoven with identity. In identity recognition faces are processed holistically. This means that in the brain faces are represented in terms of global patterns or relations among parts, and that face recognition is not based on a piecemeal processing of the isolated features or parts (Freiwald et al., 2016). The latter, feature-based processing is used in the recognition of most common objects. The holistic processing of faces may be demonstrated by the so-called inversion effect: inversion of the face – turning the face upside down so that the chin points upwards – impairs recognition much stronger than the inversion of objects impairs their recognition (De Haan et al., 2003). The face inversion effect indicates that the holistic processing of faces is experience depended. This notion is supported by four findings. First, the face inversion effect disappears when the contrast polarity of a black-and-white picture of the face is reversed - the unusual

negative contrast polarity hampers the holistic processing of the face (Tomalski et al., 2009). Second, adult persons with severe hearing impairment from early life onwards strongly rely on visual facial information during communication. Hence, they can be considered as face experts and – indeed - their facial recognition is more hampered by face inversion than that of typical adults (De Heering et al., 2012). Third, in persons living in a racially relatively homogeneous environment the face inversion effect is stronger for the recognition of own-race faces than for the recognition of other-race faces (Sangrigoli and de Schonen, 2004). Fourth, experts of dogs or landscapes also show an inversion effect in the recognition of dogs and landscapes, respectively, whereas this inversion effect is absent in non-experts (Diamond and Carey, 1986).

When adults learn to recognize specific faces, they scan the observed face with varied eye movements. Limiting the scanning eye movements impairs this learning process (Henderson et al., 2005). Which parts of the face are scanned preferentially, depends on the scanner's culture, the emotional expression displayed by the face (see Sections 2.2.1, 3.2.2 and 3.2.2.1) and whether the face belongs to a talking person or not. During scanning of faces of talking persons both the mouth and eye region are fixated, but most scanning movements dwell in the mouth region (Rennig and Beauchamp, 2018). In non-talking faces the eye region is more fixated than the mouth region; this is true for memory and recognition tasks (McKelvie, 1976; Vinette et al., 2004). The human preference for the eye region is specific for human faces and does not hold true for faces of macaques (Dahl et al., 2009). Likewise macaques have a preference to scan the eye region of faces of conspecifics, while lacking a similar preference for human faces (Dahl et al., 2009; Gothard et al., 2009). Humans and macaques lose the preference for the eye region when the faces are inverted or blurred (Dahl et al., 2009). The leading role of the eye region in the human recognition of non-talking faces was demonstrated elegantly with the use of the Bubbles technique. The latter means, that faces had to be recognized while a large part of the face was hidden, except for a peephole revealing a small part of the face. Faces were most quickly recognized (within 47–94 ms) when the Bubble peephole revealed the left eye. The finding that it was the left eye and not the right, most likely reflects the dominance of the right cortical hemisphere in face processing (Vinette et al., 2004). The human's preference for the eyes in the face may also be illustrated by the finding that all over the world selfies centre on the eyes, in particular on the left eye (Bruno et al., 2019). In addition, faces with larger eyes are perceived as more attractive (Geldart et al., 1999; Hugenberg and Wilson, 2013).

Humans share the preference for looking at the eye region with the bonobos (*Pan paniscus*), but not with the other *Pan* species, the chimpanzees (*Pan troglodytes*; Kano et al., 2015, 2018). Chimpanzees, who are less socially gifted than bonobos (De Waal, 2009; Hare, 2017), look significantly less to the eye region than bonobos do (Kano et al., 2015, 2018).

2.1. Face recognition capacities in the human newborn

The study of Reid et al. (2017) suggested that the postnatal learning process to recognize faces starts from an innate preference for face-like stimuli: foetuses of 33–36 weeks postmenstrual age move their head significantly more often towards a face-like stimulus (a configuration of three lights, with two in the upper row and one below) than towards a non-face stimulus with similar contrasts. The findings of Reid's challenging but also debated study (Scheel et al., 2018; Reid et al., 2018) correspond to the multiple reports of the newborn's preference to look at human faces and face-like stimuli (Cashon and Holt, 2015; Macchi Cassia et al., 2004; Grossmann and Johnson, 2007; Hoehl and Peykarjou, 2012; Johnson, 2005; Johnson et al., 2015; Simion and Giorgio, 2015), a preference that is present as early as ten minutes after birth (Goren et al., 1975). Thus, it is conceivable that the newborn's preference for face-like stimuli has a prenatal origin. Yet, this does not imply that the preference is based solely on reading of the genetic script; most

likely also prenatal experience is involved (see Section 2.3). The ability to recognize faces rapidly improves with increasing infant age (Hoehl and Peykarjou, 2012; Quinn et al., 2019). This improvement is largely facilitated by the infant's frequent exposure to faces in daily life (Fausey et al., 2016; Jayaraman and Smith, 2019).

2.2. Context dependency of face recognition

How easily people recall and recognize faces does not only depend on experience but also on social category formation (Bernstein et al., 2007). It is well known that human beings rapidly categorize other persons as belonging to a specific social group, such as gender, race and age (Hugenberg et al., 2012). Face recognition is – also independent of experience – easier for in-group members than for out-group members (Anastasi and Rhodes, 2006; Bernstein et al., 2007; Herlitz and Lovén, 2013; Hugenberg et al., 2012; Meissner and Brigham, 2001).

Human beings more easily learn to recognize faces on the basis of dynamic faces moving at natural speed, for instance during speech or emotional expression, than on the basis of static faces (O'Toole et al., 2002). But also the emotional expression of still faces affects identity recognition: in particular happy expressions facilitate face recognition, an effect due to a better encoding and recall (Chen et al., 2015; D'Argebeau and Van der Linden, 2007; Liu et al., 2014). Other studies have indicated that also fearful expressions may facilitate face recognition (Righi et al., 2012; Sergerie et al., 2004). In addition, it has been shown that gaze direction affects face identity recognition: it is easier to learn to recognize faces exhibiting direct gaze than faces with averted gaze; again the effect is attributed to better encoding and better recall (Hood et al., 2003; Mason et al., 2004).

2.2.1. Face recognition: the other-race effect

The other-race effect refers to the phenomenon that same-race faces are more easily recognized than other-race faces among individuals living primarily in mono-racial societies (Hugenberg et al., 2010). The effect has been demonstrated across races (Meissner and Brigham, 2001). Also recognition memory for same-race faces is better than that for other-race faces (Golby et al., 2001). Levin (2000) found evidence that the difference in the recognition of own- and other-race faces was based on different visual coding strategies for social categories: in own-race faces cognitive focus is on the in-group individual, in other-race faces on the out-group social category. As a result an other-race face is more easily detected among own-race faces than an own-race face among other-race faces (Levin, 2000).

Interestingly, Caharel et al. (2011) demonstrated that reaction time to recognize same-race faces was longer than that to other-race faces. As this face-race difference was absent when the faces were inverted, the authors concluded that the longer reaction time for the processing of same-race faces was caused by the more time consuming holistic processing of same-race faces. The finding that infants aged 3 months recognize same-race faces equally easy as other-race faces and that the other-race effect emerges at the age of 5–7.5 months and becomes stronger during the rest of the first year suggests that the other-race effect is not innate but experience dependent (Kelly et al., 2007, 2009; Sugden and Marquis, 2017). The development of the other-race effect is accompanied by the formation of social categories: 6-month-old Western Caucasian infants are able to distinguish Western Caucasian, African and East Asian faces, whereas 9-month-old Caucasian infants lump African and Asian faces into one other-race category (Quinn et al., 2021). The process underlying the development of the other-race effect has been labelled perceptual narrowing (Kelly et al. 2007) or rather perceptual attunement (Maurer and Werker, 2014). It is important to realize that the development of perceptual attunement in face recognition is not an irreversible process. For instance, 9-month-old infants still could recognize other-race faces when parents had regularly exposed them in the preceding three months to booklets with pictures of other-race faces, that had been labelled with the individual's name

(Heron-Delaney et al., 2011). Moreover, when infants have developed the other-race effect, experience may induce its reversal. For instance, three weeks of daily exposure to short videos of other-race faces that sang or produced infant-directed speech was able to reverse the inability of 8–10 months old infants to recognize other-race faces (Anzures et al., 2012). Perceptual attunement in face recognition can also be reversed at later age: individuals born in East Asia, who had been adopted during childhood by families living in rather homogeneous Caucasian communities did not show the other-race effect (De Heering et al., 2010) or showed the reverse of the original other-race effect (Sangrigoli et al., 2005) – the difference in outcome between the two studies being related to the duration of the exposure to the novel racial environment. The above data suggest that face perception develops in an experience-dependent way from a broadly tuned capacity to a more focused ability (Hoehl and Peykarjou, 2012).

Studies that evaluated the other-race effect by comparing face recognition in Western Caucasian and East Asian individuals did not only confirm the other-race effect, but also indicated that the two groups scan non-talking faces differently. Western Caucasian persons fixate more on the eyes and mouth with a preference for the eyes when they scan own-race and other-race faces, whereas East Asian individuals focus more on the nose, i.e., the central region of the face, when they scan own-race faces, but use an eye-centric strategy when scanning Western Caucasian faces (Blais et al., 2008; Hu et al., 2014; Lee et al., 2017). Most likely, these differences in the scanning of static faces can be attributed to cultural differences (Blais et al., 2008). For instance, Akechi et al. (2013) reported that East Asian individuals exhibit less eye contact than Western Caucasian persons. More importantly, accumulating evidence suggests that Asians process the environment more holistically, whereas Westerners use a more analytic strategy (Nisbett and Miyamoto, 2005; Rule et al., 2013). The study of Caldera et al. (2010) indicated that the differences in the scanning of static faces between Western Caucasian and East Asian individuals indeed are culturally driven. Caldera and colleagues used a so-called Spotlight technique, implying that the subjects viewed Western Caucasian and East Asian faces through peepholes of various sizes that moved gaze-contingent. When the peepholes were small, i.e., had Gaussian apertures of 2° or 5° and fixation of the nose did not allow the observation of eyes and mouth, both Western Caucasian and East Asian individuals mainly fixated the eyes. Only when the largest peephole was used, the 8° aperture that allowed for seeing eyes and mouth when fixating the nose, the previously described cultural difference in face scanning emerged. Caldera's study indicated that persons from both cultures use similar information to recognize faces, but that the strategies to collect this information is culture dependent. Interestingly, Kelly et al. (2011) reported that the culture-specific facial scanning strategy of East Asian people persisted in a substantial proportion of the second generation of Chinese adults living in the United Kingdom.

It should be realized that the described cultural differences in facial scanning hold only true for the viewing of still faces. Various studies indicated that the cultural diversity in facial scanning is different for dynamic faces and depends on the context. For instance, when faces sequentially moved mouth and shifted gaze both Western Caucasian and East Asian individuals mostly fixated the eyes, with the East Asian viewers exhibiting an even larger eye preference than the Western Caucasian viewers (Senju et al., 2012). Yet, during the observation of a video of a talking person exhibiting mutual gaze, the cultural difference known from the scanning of static faces occurred: East Asian persons especially scanned the nose region, whereas Western Caucasian individuals mostly scanned the eye region. However, when the talking person exhibited averted gaze the cultural difference disappeared: persons of both cultures mostly scanned the nose region (Gobel et al., 2017). When the situation consisted of a live dyadic social interaction, including some social smiling, about three quarters of the scanning movements of East Asian individuals dwelt on the upper half of the face, whereas those of Western Caucasian persons were more evenly

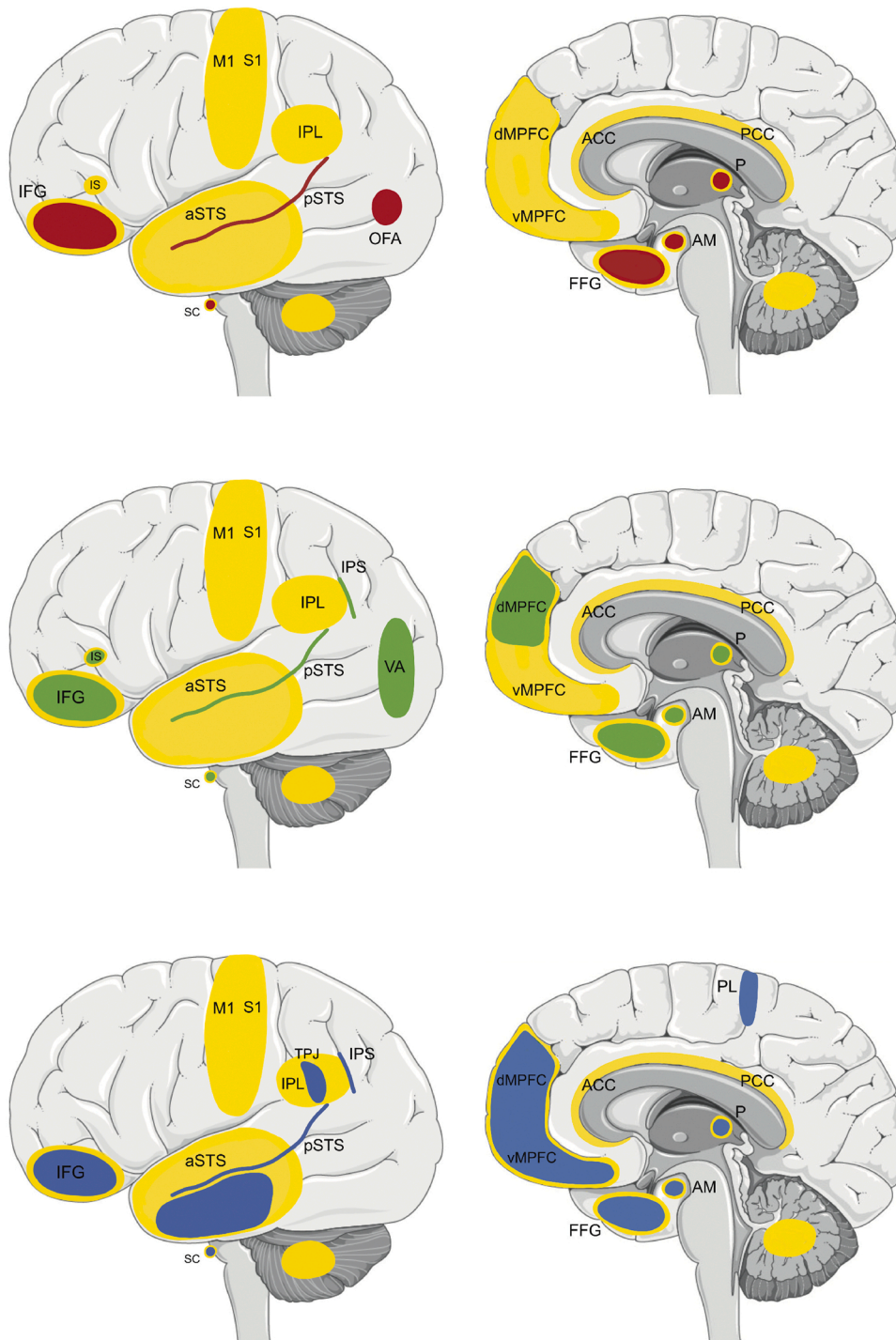


Fig. 1. Schematic diagrams of the networks involved in the processing of face and gaze signals.

Schematic diagrams of the networks involved in face and gaze processing; in the left column lateral views of the brain, in the right column medial views. The yellow areas indicate the parts of the brain most often reported to be involved in social cognition (the ‘social brain’ networks; Adolphs, 2009; Schurz et al., 2021; Van Overwalle et al., 2015). It is task and context dependent which parts are involved. The extensive neuro-imaging meta-analysis of Schurz et al. (2021) indicated that three groups of neuro-cognitive processes can be distinguished: (a) predominantly cognitive (mentalizing) processes that in particular are associated with activation of the medial prefrontal cortex (MPFC), the anterior cingulate cortex (ACC) and temporoparietal areas; (b) predominantly affective processes that especially recruit the inferior frontal gyrus (IFG), the right insula (IS), the temporal pole, the pre- and postcentral gyri, and the parietal supramarginal gyrus; (c) processes that combined cognitive and affective processes that activated in particular the temporal lobes and the temporoparietal cortex. Note that the IS, aSTS, pSTS, amygdala and SC are actually lying deeper than the figure suggests.

A) The red areas are involved in face recognition; a yellow border indicates participation in the social brain network; the right hemisphere is dominant; B) the green areas are involved in the processing of emotional expressions; emotional expressions mostly involve areas in both hemispheres; C) the blue areas are mostly involved in specific forms of gaze perception, in general both hemispheres are involved in various left-right combinations.

Additional abbreviations: AM = amygdala; aSTS = anterior superior temporal sulcus; dMPFC = dorsal medial prefrontal cortex; FFG = fusiform gyrus with fusiform face area; IPL = intraparietal lobule; IPS = intraparietal sulcus; M1 = primary motor cortex in the precentral gyrus; OFA = occipital face area; P = pulvinar of the thalamus; PCC = posterior cingulate cortex; PL = paracentral lobule; pSTS = posterior superior temporal sulcus; S1 = primary somatosensory cortex in the postcentral gyrus; SC = superior colliculus; VA = visual association areas; vMPFC = ventral medial prefrontal cortex.

distributed between the upper and lower halves of the face (Haensel et al., 2020, 2021).

2.3. Neural substrate of face recognition

Face recognition depends on other neural processes than the recognition of other types of objects, suggesting that the primate brain is hard-wired to pay special attention to faces (Duchaine and Yovel, 2015; Hugenberg and Wilson, 2013). This may be illustrated by the presence of face-selective cells in the temporal and prefrontal cortex (Barracough and Perrett., 2011; Freiwald et al., 2009, 2016). Freiwald et al. (2009) showed that the face-selective neurons in the middle face patch of the

macaque temporal cortex were partially feature driven, but also clearly holistically engaged: they responded more than twice as often to a facial feature in the face context than to isolated face features. The neurons also responded considerably less to inverted faces than to upright faces. More cells responded to the eye region than to the mouth or nose.

The neural structures involved in face perception are part of the ‘social brain’, i.e., the brain networks involved in the perception and integration of social cues. The social brain comprises the medial prefrontal cortex, the inferior frontal gyrus, the insula, the pre- and postcentral gyri, the inferior parietal lobule, the superior temporal gyrus, the fusiform gyrus, the cingulate gyrus, amygdala and cerebellum (see Fig. 1; Adolphs, 2009; Schurz et al., 2021; Van Overwalle et al., 2015).

Most studies aiming to unravel the neural networks of face perception focus on the cerebral cortex. Yet, it should be realized, that also subcortical networks are involved (Johnson, 2005; Johnson et al., 2015). Johnson and colleagues argued, that in the processing of faces two parallel and interacting pathways can be distinguished: (1) a subcortical pathway involving the superior colliculus in the midbrain, the thalamic pulvinar and the amygdala and (2) a cortical pathway. The subcortical pathway responds to low spatial frequency information of the face, i.e., its general outlines and clear contrasts. It is a relatively fast system (responding within 100 ms) that reacts especially to stimuli in the temporal visual field. The slower cortical pathway can also deal with high spatial frequency information involved in the details of the face, such as the wrinkles around the eyes. The information of the subcortical pathway continuously modulates the activity in the cortical networks (Johnson, 2005; Johnson et al., 2015).

The cortical networks of face recognition involve both hemispheres, with the right hemisphere being dominant (Duchaine and Yovel, 2015; Freiwald et al., 2016). In the cortical processing of face recognition two pathways can be distinguished, a ventral and a dorsal stream (Bruce and Young, 1986; Duchaine and Yovel, 2015; Haxby et al., 2000). This corresponds to the way in which visual information is processed generally, i.e. via a so-called ventral and dorsal stream. The ventral stream consists of projections from the primary visual cortex to the inferior temporal cortex. It deals with the identification of objects or rather serves the provision of visual recognition routines for identifying goals and potential threats. The dorsal stream comprises projections from the primary visual cortex to the posterior parietal cortex. It handles the spatial characteristics of objects therewith serving the direct real-time guidance of movements (Goodale and Milner, 1992, 2018). In face recognition this means that the ventral stream comprises the occipital face area (OFA) located in the inferior occipital gyrus, the fusiform face area (FFA) in the posterior part of fusiform gyrus of the inferior temporal cortex, and the anterior temporal lobe (Duchaine and Yovel, 2015; Grill-Spector et al., 2017). The ventral stream face areas preferentially process the invariant features of the face involved in identity recognition. Nevertheless, they also contribute to the processing of emotion recognition (Duchaine and Yovel, 2015). The dorsal stream of face recognition areas comprises the posterior and anterior superior temporal sulcus (pSTS and aSTS) and the inferior frontal gyrus (of the prefrontal cortex; see also Fig. 1A). It is involved especially in the processing of dynamic faces, i.e., emotional expressions, gaze direction and mouth movements (Duchaine and Yovel, 2015; Haxby et al., 2000).

The localization of the networks is mostly studied with functional magnetic resonance imaging (fMRI), but the timing of the neural processes is generally studied with electroencephalography (with or without fMRI), event related potentials (ERP) or transcranial magnetic stimulation. The latter technique allows a temporary inhibition of the neural tissue below the stimulator. Experiments using this technique revealed that the OFA responds after about 100 ms after the face stimulus. Next, the FFA and pSTS follow at a latency of about 170 ms and the inferior frontal gyrus around 250 ms (Duchaine and Yovel, 2015). The latency of 170 ms corresponds to the robust findings of ERP studies that presentation of faces results in a negative wave peaking at a latency of about 170 ms (the N170), that can be recorded from the lateral-posterior scalp (corresponding to the face areas in the temporal cortex; Bentin et al., 1996; Itier et al., 2007). The N170 is relatively specific for faces, i.e., its amplitude is considerably larger after presentation of a face than after presentation of common objects, such as cars or houses (Itier et al., 2011). This effect only occurs when high frequency spatial information of the face is available that provides information on facial details (Mares et al., 2018). The N170 amplitude is larger on the right side than on the left side (Bentin et al., 1996; Itier et al., 2007, 2011). Only a single glance to a face, i.e., one gaze fixation, is needed to elicit the N170 (Jacques et al., 2016). The N170 is substantially smaller when the eyes are removed from the face (Itier et al., 2007). In addition, a picture of the face that is limited to the eye region also elicits a clear N170; this

response is larger to human eyes than to eyes of apes, cats or dogs (Itier et al., 2011). It is rather the eye region with its two eyes that is responsible for the larger N170 than the presence of one eye in a face context (Parkington and Itier, 2018). Nonetheless, the N170 response to schematic eyes is larger when the observer has been primed with faces with similar eyes (Bentin et al., 2002). This suggests that eyes especially get their meaning in the facial context. Bentin et al. (2002) suggested that the priming by the facial context could be interpreted as sign of top-down processing in which the facial bias facilitates the interpretation of the eyes.

At the beginning of this section it was mentioned that face processing in the brain is hard-wired. Most likely, this hard-wiring is based on a continuous interaction between genetic information and experience (Arcaro et al., 2019), with the experience conceivably starting before birth. As a result, newborns respond to face-like stimuli by activation of major parts of the social brain network, i.e., they show activity in the bilateral occipital regions, the right occipitotemporal cortex, the medial posterior regions and the right superior frontal gyrus (Buiatti et al., 2019). The prenatal experience may be brought about by the intrinsically determined spontaneous patterned activity of neural tissue (Choi et al., 2021), which is a major driving force of neural development (Hadders-Algra, 2018). The spontaneous activity is reflected by the frequently occurring spontaneous movements of the foetus (Hadders-Algra, 2018) and the recurrent presence of so-called ponto-geniculo-occipital (PGO) waves during rapid eye movement (REM) sleep (Bednar and Miikkulainen, 2003). The spontaneous movements of the foetus include from 10 to 12 weeks PMA onwards hand movements directed to the face (De Vries et al., 1985). It may be hypothesized that this prenatal hand-face activity, presumably facilitated by the genetically determined anatomy of the foetal body and uterus, supports the development of face maps in the somatosensory cortex (Pitti et al., 2013). In turn, these maps may assist the newborn's emerging ability to recognize and imitate the facial movements of an adult (Marshall and Meltzoff, 2014). In addition, the PGO-waves may play a role in shaping the neural circuitry involved in face processing. This was indicated by the computer modelling experiments of Bednar and Miikkulainen (2003) suggesting that the spontaneously generated PGO-waves prepare the newborn's primary and higher-level visual cortical areas for the recognition of faces and face-like stimuli.

The human data mainly focused on an unidirectional, bottom-up flow of neuro-information, but animal studies indicated that information exchange between brain areas often occurs bidirectionally and in varied sequences. For example, STS cells may be activated before and after recruitment of cells in the amygdala or in the prefrontal cortex (Barraclough and Perrett, 2011). More recent data support the idea that also in the human top-down information affects the processing of faces (Freeman et al., 2020). The orbitofrontal cortex, including the medial prefrontal cortex, plays a significant role in the top-down processing, i.e., in the preparation of the higher visual areas for incoming information (Freeman et al., 2020). For instance, implicit racial bias, social stereotypes and in-group membership affect the processing of facial information by interaction between the orbitofrontal cortex and fusiform gyrus (Anzures and Mildort, 2021; Barnett et al., 2021; Herzmann and Curran, 2013). Activation of the orbitofrontal cortex may occur 30–50 ms earlier than that of the occipitotemporal cortex, including the FFA (Bar et al., 2006; Mattavelli et al., 2013). The functional connectivity between the orbitofrontal cortex and the fusiform regions is stronger when the facial images mainly contain low frequency spatial information (Bar et al., 2006). This coarse facial information is particularly mediated by the quick subcortical pathways. This indicates that the subcortical pathways may activate the orbitofrontal cortex, which in turn may assist the preparation of visual perception in the fusiform cortex. In addition, it could be hypothesized that the anticipatory circuitry involved in face processing, including the orbitofrontal cortex, starts its learning and development at early age, as we know that 1) in newborns the medial prefrontal cortex is already involved in the processing of facial

information (Buiatti et al., 2019; Farroni et al., 2013); 2) during human ontogeny the sensitivity to visual input is characterized by a coarse-to-fine development (Banks and Salapatek, 1978; Leat et al., 2009); 3) the subcortical pathways, that are particularly sensitive to low frequency spatial information, play a prominent role at early age (Johnson et al., 2015); and 4) neural network models indicated that the networks learned best to recognize visual input when during training the spatial frequency of the input gradually increased – similar to what happens during human ontogeny (Avberšek et al., 2021). In other words, it is suggested that the development of the visual and neural systems including the orbitofrontal cortex are shaped to learn from experience. It also allows for the building of social categories (Freeman et al., 2020), that facilitate the better recognition of familiar in-group faces.

2.4. Summary of face recognition

Recognition of faces is an experience driven ability based on a prenatally originating preference for face-like stimuli. The prenatal origin most likely is the result of experience brought about by the intrinsic property of neural tissue to generate spontaneous patterned activity. Postnatally, the ample experience due to daily facial exposure drives the development of holistic processing of faces by the cortex. The latter includes the presence of temporal neurons with a specific response to holistic face characteristics. A daily, clearly dominating exposure to own-race faces is the source of the other-race effect, i.e., having a lesser ability to recognize other-race faces than own-race faces. This other-race effect is also associated with the formation of social categories. Face recognition is not only affected by cultural context, but also by the context of the face's emotional expression and gaze direction.

Face recognition is an active process involving varied explorative scanning eye movements of the observed face. Most studies on face recognition used still, non-talking faces. In still faces, recognition is particularly based on information of the eye region. However, cultural background determines the strategy by which this information is collected: the scanning movements of East Asian people focus on the nose of faces of the own culture, those of Western Caucasian people on the eye region. The scanning of faces is not only culture specific but also depends on other aspects of the context. For instance, during dyadic conversation East Asian individuals mostly scan the upper half of the face, whereas Western Caucasian persons distribute scanning movements equally between the face's upper and the lower half.

The neural networks involved in face recognition form part of the social brain (Fig. 1A). They involve two pathways: (1) a fast and crude subcortical route, including the superior colliculus, pulvinar and amygdala, and (2) a slower and more precise cortical pathway that comprises the FFA in the fusiform gyrus and the pSTS and aSTS. The flow of information in the networks does not only include bottom-up processing, but also involves top-down modulation of incoming information, allowing for quick anticipation of the facial information, such as involved in social categorization. Information originating from the eye region especially contributes to the activation of the face processing networks.

3. Facial expressions of emotion

Facial expressions play an important role in social cognition (Ferretti and Papaleo, 2019). Indeed, faces with an emotional expression draw more attention than those without (Palermo and Rhodes, 2007). Interestingly, Susskind and colleagues suggested that facial expressions do not only serve social communication, but also play a role in the preparation of perception and action. For instance, the expression of fear with its widely opened eyes is associated with a subjectively larger visual field, faster eye movements during target localization, and a larger nasal volume and air velocity during inspiration (Susskind et al., 2008). Before discussing the details of the recognition and processing of facial expression, I first summarize the generation of facial expressions.

3.1. Generation of facial expressions

Humans and great apes have a large repertoire of facial expressions (De Waal, 2003; Ladygina-Kohts, 2002; Marler, 1976). In humans at least sixty expressions have been described (Jack et al., 2016). This varied repertoire emerges during prenatal life (Reissland et al., 2011, 2013). Humans and great apes also have the capacity to produce a blend of facial expressions (De Waal, 2003; Parr et al., 2005). The latter contrasts with the facial capacity of monkeys who – with their smaller repertoire – are only able to produce discrete facial displays (De Waal, 2003). Thus, it is typical for humans and great apes to be able to produce graded facial expressions (De Waal, 2019; Kret et al., 2020). The large repertoire of facial expressions in humans and great apes is generated by their complex facial muscular system, in which muscles blend and single muscles cannot easily be distinguished (Burrows et al., 2006; Darwin, 1899; Cattaneo and Pavesi, 2014). The muscular system also has a large interindividual variation (Cattaneo and Pavesi, 2014; Schmidt and Cohn, 2001).

The facial muscles are controlled by two neural systems: the emotional motor system, involving the mesencephalic periaqueductal grey and higher limbic regions (Holstege and Subramanian, 2016), and the cortical control system. The latter is especially well developed in humans and great apes (Cattaneo and Pavesi, 2014). Interestingly, the cortical control of the upper and lower part of the face differ. The upper part of the face receives bilateral projections from the motor cortex, whereas the lower part of the face is mainly contralaterally controlled by the cortex (Müri, 2016; Ross et al., 2007, 2016; Schmidt and Cohn, 2001). In addition, the cortical control of the lower part of the face is stronger than that of the upper part, a specialization associated with the former's role in the production of fully articulated speech (Ross et al., 2007). The differential cortical control of the upper and lower part of the face implies that it is easier to lie with the mouth than with the eyes – an observation already made by Duchenne (Duchenne, 1862; see also Cattaneo and Pavesi, 2014; Ekman, 2003; Ross et al., 2007).

3.2. Recognition of facial expressions of emotion

The ability to recognize facial expressions of conspecifics is not unique for humans. It has been described for instance for dogs, monkeys and great apes (Calcutt et al., 2017; Ferretti and Papaleo, 2019; Nahm et al., 1997; Parr, 2003; Thompkins et al., 2018).

Since Darwin's treatise *The expression of the emotions in man and animals* (1899) - in which he claimed that emotional expressions are innate and universal - the universality of emotional expressions has been debated (Ekman et al., 1972; Ekman and Friesen, 1975; Jack, 2013). Ekman, in his seminal work on the recognition of emotional expressions across the world, distinguished six basic and mostly universal expressions: happiness, anger, fear, sadness, disgust and surprise (Ekman et al., 1972; Ekman and Friesen, 1975). However, nowadays it is agreed that only some facial expressions, i.e., happiness and anger, are universally recognized. For other facial expressions, such as disgust and fear, far less cross-cultural agreement exists (Elfenbein and Ambadi, 2002; see also section 3.3).

3.2.1. Capacities of the human newborn to recognize emotional expressions

Field et al. (1982) indicated that 2–3-day-old infants have some capacity to imitate happy, surprised and sad expressions. This implies that they are able to discriminate these expressions to some extent. Later studies investigated newborns' abilities in more detail. Addabbo et al. (2018) reported that newborn infants can discriminate dynamic facial expressions of happiness and disgust. Other studies revealed that newborns aged a few days preferentially look at happy faces compared to neutral and fearful faces and that this preference occurs only when the happy expression is accompanied by direct gaze instead of averted gaze (Farroni et al., 2007; Rigato et al., 2011). The studies indicate that already shortly after birth infants have some capacity to process

information on facial expressions. Also that they have a preference for happy faces with direct gaze, i.e., the facial condition that favours positive social interaction. It is this situation, the eye-to-eye interaction with a happy, smiling face that infants frequently experience, starting soon after birth (Klaus et al., 1970; Papoušek and Papoušek, 1984). During the first months after birth, the infant's capacity to distinguish facial expressions remains limited, but after the age of 4 months this ability gradually improves with increasing age (Flom and Bahrick, 2007).

In standard laboratory conditions, i.e., in decontextualized settings, happy expressions are recognized with the highest accuracy and the shortest reaction times and fearful expressions with the lowest accuracy and longest reaction times (Wells et al., 2016). The ease of recognition of happy expressions is associated with its large experience from birth onwards 3.2.1.

3.2.2. Context dependency of recognition of facial expression

The evaluation of emotion in general is context specific (Wilson-Mendenhall et al., 2011). Likewise, the perception of facial expressions depends on the situation. The specific situation of the other race is discussed in Section 3.2.2.1. The contextual factor may originate in the expresser, in the observer and in the external aspects of the situation (Aviezer et al., 2017; Barrett et al., 2011; Wieser and Brosch, 2012). Examples of expresser-related factors are the tone of the expresser's voice (a sad voice increases the likelihood that a face is perceived as sad and a happy voice enhances the chance that a face is perceived as happy; De Gelder and Vroomen, 2000), the expresser's body posture (body postures largely facilitate the evaluation of ambiguous facial expressions; Aviezer et al., 2017; Wieser and Brosch, 2012) and the face's trustworthiness. Trustworthiness is an invisible social cognitive dimension that may be attributed to the owner's face on the basis of a single glance, i.e., with a viewing time less than 100 ms (Todorov, 2008). Happy expressions of a trustworthy face are evaluated as more happy than the same expression in a face perceived as untrustworthy. In a similar vein, expressions of anger in an untrustworthy face are rated as more angry than the same expression in a face perceived as trustworthy (Oosterhof and Todorov, 2009).

Examples of observer related factors are the observer's mood (happy, neutral and ambiguous expressions are perceived as more happy during a positive than during a negative mood; Stephen et al., 2021) and the observer's gender (females are more accurate in recognition of facial expressions than males; Olderbak et al., 2019). Finally, external factors that may impact the perception of facial expressions are, for instance, the degree of distraction by the environment (in a distracting environment fearful faces are more easily recognized than neutral or happy faces – an effect even present when only the eye region of the face is visible; Yang et al., 2007), the background colour (a red background is associated with a more negative evaluation of ambiguous facial expressions than a grey or green background; Sivananthan et al., 2021), and situational information (knowledge that the person with an ambiguous facial expression is in a situation eliciting anger facilitates the perception of anger in the facial expression; Carroll and Russell, 1996). The contextual factors especially modulate the perception of ambiguous facial expressions – a situation frequently encountered in daily life (Aviezer et al., 2017; Wieser and Brosch, 2012).

Some studies in Western Caucasian individuals suggested that the ease of recognition of emotional expressions is affected by gaze direction (Adams and Kleck, 2005; Milders et al., 2011). The studies indicated that expressions of fear and sadness, that were interpreted as avoidance oriented emotions, were most easily detected when the eyes showed an averted gaze, whereas happy and angry expressions – considered to be approach oriented emotions – were most easily recognized in the presence of direct gaze (Adams and Kleck, 2005; McCrackin and Itier, 2019).

During recognition tasks of facial emotional expressions Western Caucasian individuals fixate especially the eye region of the face. This tendency is most pronounced in the assessment of fearful faces (Scheller

et al., 2012; Wells et al., 2016). However, when the cognitive load of the recognition task is increased and does not only consist of recognition of the type of emotion, but also of its intensity, dwell times of fixation of the mouth increase, in particular when the face has a happy expression (Eisenbarth and Alpers, 2011). Already the first glances to faces with an emotional expression are emotion specific. The gaze of Western Caucasian persons first orients towards the eyes of expressions of sadness and shame, towards the eyes and the nasion of fearful faces, to the eyes and eyebrows of angry faces, to upper lip, nose and mouth of faces expressing disgust, and to the mouth of happy faces (Schurgin et al., 2014). Even subliminally perceived emotional expressions (only presented for 50 ms) trigger gaze orientations to specific parts of the face, i.e., to the eyes of a fearful face and to the mouth of a happy face (Bodenschatz et al., 2019).

3.2.2.1. Cultural differences in recognition of facial expressions of emotion. Ekman and colleagues strongly supported the idea that facial expressions of emotion are universally recognized. Nevertheless, they also observed that the universal agreement was higher for happiness and anger than for surprise and fear (Ekman et al., 1972; Ekman and Friesen, 1975). The reviews of Elfenbein and Ambadi (2002) and Jack (2013) supported the idea that not all facial expressions of emotion are recognized equally easily across the world. Happiness and anger are most easily and universally recognized, whereas fear and disgust cause the most confusion. Fear is often miscategorised as surprise and disgust as anger (Jack, 2013; Jack et al., 2009). Mis-categorization occurs more frequently in a surrounding environment of faces with various expressions; this effect is stronger in East Asian than in Western individuals (Stanley et al., 2013). This may be explained by the difference in culture: more collectivistic in East Asia and more individualistic in Western society (Argyle et al., 1986; Krämer et al., 2013; Stanley et al., 2013; Wu and Keysar, 2007). It should be realized, however, that when facial expressions are displayed in their relevant context, the recognition of emotions achieves high cross-cultural agreement (Matsumoto and Hwang, 2016). The finding that emotional expressions of faces of the own culture are more easily recognized than those of other cultures indicates that the development of the ability to recognize emotional expression is the result of a continuous interaction of 'nature' and 'nurture' (Elfenbein and Ambadi, 2002). The 'in-group' advantage is larger for the 'difficult' expressions of fear and disgust than for the 'easy' expressions of happiness and anger (Elfenbein and Ambadi, 2002). Faces of the own culture are also perceived as more trustworthy than those of other cultures (Sofer et al., 2017).

The way in which Western Caucasian people assemble information of emotional expressions of static faces differs from that of East Asian people. Western Caucasian persons scan all parts of the face with a predominance of the eye region, whereas East Asian individuals have a strong preference to fixate the eyes (Jack et al., 2009). Likewise, East Asian persons rely for the classification of facial emotions more on information of the eye region than Western Caucasian individuals do (Jack et al., 2012; Xia et al., 2017; Yan et al., 2016; Yuki et al., 2007). This difference is reflected in the keystroke emoticons that are used in Japan and in the Western world: in Japan the (^_^) and (;;) symbols are used to indicate a happy and a sad face, respectively, whereas the corresponding symbols in the West consist of :) or :-) to denote a happy face and :(or :- (to indicate a sad face. This suggests that the focus in the Japanese emoticons is more on the eyes; that in the Western ones more on the mouth (Yuki et al., 2007). This difference may be explained by culturally determined differences in nonverbal behaviour: Japan's culture is more reserved, implying that its norm encourages people to restrict emotional expressions, including those of the face, whereas the Western culture is in general more expressive in its nonverbal behaviour (Argyle et al., 1986; Matsumoto and Hwang, 2016). As the perioral muscles can be better controlled than those around the eyes, cultural restraint will especially eliminate the emotional expressions of the mouth, leaving the

eyes as markers of emotion.

The effect of gaze direction on the perception of emotional expressions in Western and East Asian cultures is discussed in Section 4.2.3.

3.2.3. Neural substrate of the recognition of facial emotional expressions

The neural networks involved in the recognition of facial emotional expressions form - like those partaking in facial identity recognition - part of the social brain (Adolphs and Birmingham, 2011; Dricu and Frühholze, 2016; Liu et al., 2021; Pessoa, 2017). The neural encoding of facial expressions and that of facial identity occurs in partially shared pathways and not in entirely distinct networks (Barraclough and Perrett, 2011; Rhodes et al., 2015). The areas that are most consistently activated during the recognition of facial emotions consist of the inferior frontal cortex, the dorsal medial frontal cortex, the STS, the fusiform gyrus, the intraparietal sulcus, the visual association areas, and the amygdala. These sites are activated bilaterally. In addition, the left thalamus and left insula are involved (Dricu and Frühholze, 2016; see Fig. 1B). Overall, this implies that the evaluation of emotional expressions occurs in large-scale networks involving major parts of the nervous system. It involves bottom-up and top-down processing of information. The latter includes activity in fronto-parietal networks (Kajal et al., 2020). The function of the networks involved in the processing of facial expressions is highly dynamic and context sensitive (Pessoa, 2017). The context specificity is, for instance, reflected by the study of Gamond et al. (2017) showing that the processing of emotional expressions is affected by minimal group membership. The latter implied that group membership was only determined by a random assignment to a colour-code group. In situations, in which the emotional expression did not match the observer's expectation (e.g., an angry face of in-group member), group membership affected directly through recruitment of the medial prefrontal cortex the further processing of emotional expressions in the STS and temporo-parietal junction. The networks involved in the processing of emotional expressions also show a large interindividual variability, in which network activity is partially dependent on the presence or absence of trait anxiety (Leppänen and Nelson, 2009).

The amygdala plays a specific role in the processing of facial emotions (Adolphs, 2010; Dricu and Frühholze, 2016; Pessoa, 2017). It is activated in the early stages of emotion processing - possibly within 30 ms (Leppänen and Nelson, 2009). The amygdala has widespread projections, including projections to the frontal, temporal and insular cortices, hypothalamus and brainstem (Pessoa, 2017). Amygdala activation enhances - through its projections to the temporal areas - a more detailed processing of facial information in the fusiform gyrus and STS (Leppänen and Nelson, 2009). Amygdala's projections to the orbito-frontal cortex (Pessoa, 2017) may result in preparatory activation of the fusiform gyrus, which may explain why specific emotional expressions may enhance face identity recognition (see Section 2).

The amygdala is recruited in the processing of any emotion, but presumably in particular during facial expressions of fear (Adolphs, 2010; Leppänen and Nelson, 2009; Whalen et al., 2004). This increased amygdala activation may be explained in part by the increased pupillary size associated with arousal, as Demos et al. (2008) demonstrated that artificially enlarged pupils in pictures of happy and neutral faces were also associated with increased amygdala activation. Amygdala's responsiveness to fearful faces also depends on the race of the face: increased activity occurs especially when viewing fear in faces of the own race, not when the fear is expressed in faces of another race (Chiao et al., 2008). In addition, the race effect is modulated by gaze direction: the amygdala response to fearful faces of the own race is larger during averted gaze than during direct gaze; for fearful faces of the other race the gaze effect is just opposite: direct gaze is associated with higher amygdala activation (Adams et al., 2010). One of amygdala's specific roles may be its capacity to shift overt attention to those parts of the face that are diagnostically most relevant, i.e., to the eyes of fearful faces and to the mouth of happy faces (Gamer and Büchel, 2009; Gamer et al.,

2013). The latter idea corresponds to observations in patients with bilateral amygdala lesions: these patients have an impaired recognition of fearful faces and an increased likelihood to rate unknown faces as trustworthy (Adolphs et al., 1998, 2005). The impaired recognition of fear of these patients could not be explained by an impaired ability to process basic visual information, but has been attributed to an impaired capacity of the amygdala to direct attention to the salient signals of the face (Adolphs, 2010; Adolphs et al., 2005).

It is generally assumed that the STS plays a prominent role in the processing of emotional expressions of the face. It is especially involved in the processing of the variable and dynamic characteristics of the face, whereas the FFA and OFA are recruited to a similar extent during the evaluation of dynamic and static faces (Bernstein et al., 2018). The STS' prominent role in the evaluation of emotional expression is in line with the idea that the STS acts as a hub in the evaluation of social signals (Deen et al., 2015). Especially the posterior part of the STS (pSTS) participates in the assessment of facial expressions. It is able to analyse a large number of facial actions by means of both categorical and continuous representations of facial expressions (Srinivasan et al., 2016). It should be noted however, that a recent meta-analysis of functional neuro-imaging studies indicated that the role of the STS may be less prominent than previously thought (Liu et al., 2021).

The ERP-study of Dzhelyova et al. (2017) indicated that emotional expressions can be detected in the cortex in a single glance, i.e., within 84 ms. In the processing of facial expressions presumably also two pathways can be distinguished: a quick subcortical route via the superior colliculus and thalamus to the amygdala and a somewhat slower cortical route (Schyns et al., 2009; Vuilleumier et al., 2003). The subcortical route has been demonstrated in a person with bilateral cortical blindness and affective blindsight (Burra et al., 2019a). Faces with fearful expressions activated in this person the right amygdala without inducing awareness of the expression. Fearful faces that were filtered so that they only contained low spatial frequencies elicited similar right amygdala activity, whereas fearful faces containing only high spatial frequencies did not result in amygdala activation (Burra et al., 2019a). These findings underline the sensitivity of the subcortical pathway for low spatial frequency information.

Minimal group membership (discussed above) affects the processing of unexpected emotional expressions already at the early stage by recruiting the medial prefrontal cortex (Gamond et al., 2017). The latter also illustrates that the flow of information in the 'emotion networks' is not unidirectional, but bidirectional and includes top-down processing (Spunt and Adolphs, 2019). ERP-studies showed that emotion decoding in the temporal cortex occurs in the time window of the N170, i.e., between 140–200 ms after stimulus onset (Schyns et al., 2009). The amplitude of the N170 is largest during angry expressions (Hinojosa et al., 2015). Yet, this effect is only present when the facial information is relevant, e.g., in a gender discrimination task, and not when the facial information is irrelevant, e.g., in a 'find the missing pixel' task (Burra and Kerzel, 2019). The amplitude of the N170 is larger in response to fearful faces than in response to neutral or happy faces (Leppänen et al., 2007), an effect that occurs both during recognition tasks of emotional expression and facial identity (Turano et al., 2017). The effect has been attributed to the fact that fearful faces draw the observer's attention to the eyes. Fixation of the eyes - also of faces with neutral or happy expressions - results in higher N170 amplitudes than fixation on other parts of the face (Neath and Itier, 2015; Nemdorov et al., 2014). The context of the fearful expression also matters: fearful faces in a fearful context elicit higher N170 amplitudes than similar faces in a neutral context (Righart and De Gelder, 2006).

Notwithstanding that all facial expressions are basically processed in the same neural networks, subtle emotion-specific differences occur. This was elegantly illustrated by the study of Poncet et al. (2019), that evaluated EEG-activity in response to fast periodic visual stimulation with facial expressions. The authors concluded that each emotion studied (happy, anger, sad, disgust, fear) had its own ERP-signature with

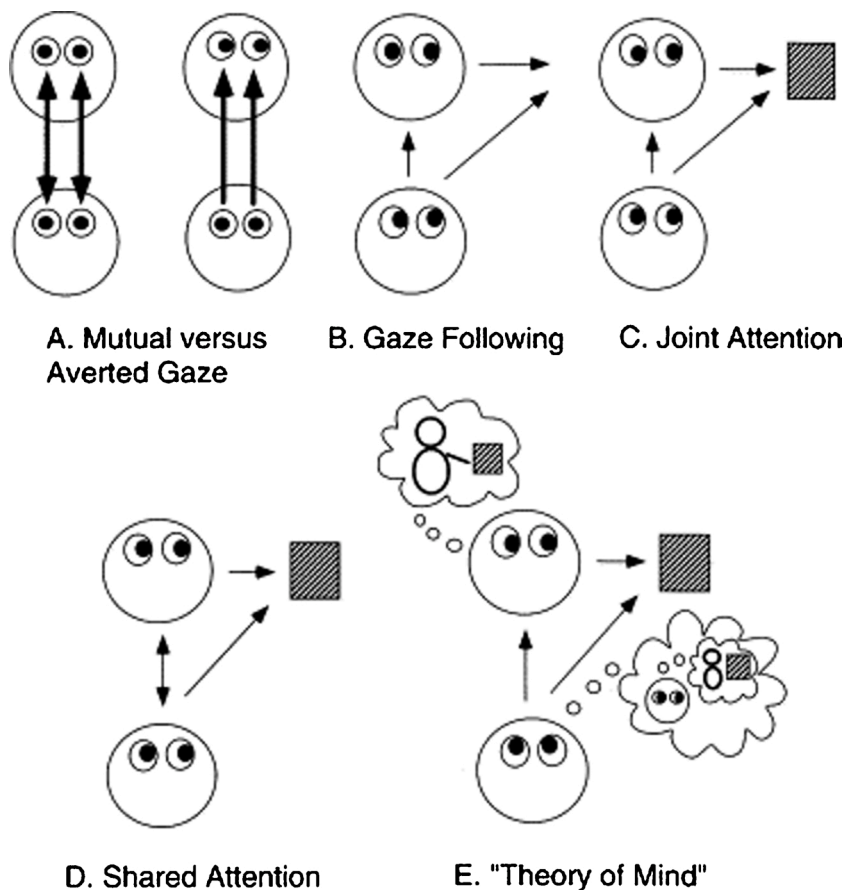


Fig. 2. A. Mutual gaze is where the attention of individuals A and B is directed to one another. Averted gaze is where individual A is looking at B, but B is looking elsewhere. B. Gaze following is where individual A detects that B's gaze is not directed towards him or her, and follows the line of sight of B onto a point in space. C. Joint Attention is the same as Gaze Following except that there is a focus of attention (such as an object), so individuals A and B are looking at the same object. D. Shared Attention is a combination of Mutual Attention and Joint Attention, where the focus of individual A and B's attention is on the object of joint focus and each other (i.e. "I know you're looking at X, and you know that I'm looking at X"). E. Theory of mind, probably uses a combination of the previous A-D attentional processes, and higher-order cognitive strategies (including experience and empathy) to determine that an individual is attending to a particular stimulus because they intend to do something with the object, or believe something about the object. From Emery (2000), with permission from the author and Elsevier Publishers.

emotion-specific response sites. For instance, responses to anger and sadness were most prominent at medial occipital and parietal sites (for anger more right and laterally; for sadness more medially), whereas those in response to happy and disgust were most clear in the lateral parts of the central parietal region. Fear elicited the most widespread response, including all occipito-temporal sites, with the left side being more involved than the right side.

ERP-studies indicated that gaze direction affects the processing of facial expression in a task-specific way, i.e., the duration of the stimulus presentation affects the response (see also Section 4.2). Angry faces with direct gaze presented for 1300 ms were associated with larger N170 amplitudes than angry faces with averted gaze (El Zein et al., 2015). But a study presenting the angry faces for only 500 ms did not find a modulatory effect of gaze direction on the N170 (McCrackin and Itier, 2019). In this study the modulatory effect was found between 220–290 ms at the frontal sites.

3.2.4. Summary of the recognition of facial emotional expressions

Humans have a repertoire of at least sixty facial expressions controlled by the emotional motor system and cortical control system. The mouth region is stronger controlled by the cortical system than the eye region. Among the many expressions some are universal, such as happiness and anger. Other widely used expressions are fear, shame, disgust and surprise; they are often recognized, but less flawless. Happiness is recognized quickest and most accurate. It is also the expression which can be discriminated to some extent by newborn infants and it is the first one that can be recognized during ontogeny. The recognition of expressions is experience dependent - explaining why emotional expressions of faces of the own culture are most easily recognized - and context dependent. The context especially affects the perception of ambiguous expressions.

Like face identity recognition, the recognition of facial expression

involves active scanning of the face. The strategy used is culture dependent: Western Caucasian people scan the entire face with a preferential dwelling on the eye region, whereas East Asian people have a virtually strict preference for the eye region, i.e., the region that has least cortical control.

The emotional expressions of the face are processed in the social brain network. Similar to the neural handling of facial identity, it is assumed that the processing of emotional expression occurs in two parallel pathways, a subcortical one, including the thalamic pulvinar and amygdala, and an extensive cortical network. In the networks dealing with emotional expressions the amygdala and presumably also the STS have a prominent role. Accumulating evidence indicates that the evaluation of facial expression involves bottom-up and top-down processing of information, the latter involving the orbitofrontal cortex.

4. Perception of gaze

The human eyes are often said to be the "windows of the soul" (Emery, 2000; Grossmann, 2017; Kleinke, 1986). The eyes' gaze provides information on animacy (Looser and Wheatley, 2010), love (Shakespeare, 1590ies: "love, first learned in a lady's eyes", Craig, 1984), attention and intention (Klein et al., 2009). Gaze cannot only be expressed by the eyes, but also by the body and the head (Rosati and Hare, 2009). Gaze following based on all parts of the other's body is common throughout the primate order and has also been documented in ravens; the other's gaze informs the observer about the environment (Emery, 2000; Frischen et al., 2007; Klein et al., 2009; Rosati and Hare, 2009). In these animals it occurs more often in situations of competition than in the context of collaboration (Klein et al., 2009). In most primates, including most monkeys, this behaviour is an automatic response to attention capturing gaze cues (Rosati and Hare, 2009). The response does not only induce an overt direction of the viewer's gaze, but also a

covert shift of attention in the gaze direction (Deaner and Platt, 2003). In chimpanzees, bonobos, and perhaps also in rhesus monkeys, gaze may also provide knowledge about what the other sees (Rosati and Hare, 2009; Tomasello, 2014). However, it is typically human to prioritize the signals derived from the eyes to obtain information on gaze (Tomasello et al., 2007; Leopold and Rhodes, 2010).

The use of eye information is promoted by the specific human eye morphology: from the 88 primate species studied, the human eyes do not only have the largest width-height ratio, but also are the only ones with a white sclera (Kobayashi and Kohshima, 2001). The width-height ratio correlates with the eyeball's scanning movements and the relative size of the neocortex (Kobayashi and Hashiya, 2011). The evolutionary changes in eye morphology and those in the brain, including an increased specialization in the processing of visual information (Emery, 2000), facilitated the emergence of the unique human features of joint and shared attention (Tomasello et al., 2007: the cooperative eye hypothesis; Call, 2009: the shared intentionality hypothesis). In joint attention two individuals look at the same target, in shared attention this joint attention is interchanged with mutual gaze, therewith sharing the experience of looking at the same target (Fig. 2; Emery, 2000). Unfortunately, most researchers in the area of joint and shared attention do not distinguish between the two conditions and also use the term joint attention for shared attention (Pfeiffer et al., 2013). The following text adopts this terminology tradition. This implies that from this point onwards joint attention generally means shared attention. Joint attention is one of the building blocks of the 'theory of mind', i.e., the ability to impute unobservable mental states, such as intentions, desires and beliefs to others (Heyes and Frith, 2014). After decades of research it is still controversial whether non-human species have a theory of mind (Horschler et al., 2020a, b; Kano et al., 2020). It is well known that the explicit form of mind reading involving the ability to exchange thoughts about mental states is specific for humans. Nonetheless, increasing evidence suggests that great apes do possess an implicit form of mind reading. The latter allows to predict behaviour and to get information of others (Call and Tomasello, 2008; Heyes and Frith, 2014; Kano et al., 2019; Krupenye et al., 2016; Premack and Woodruff, 1978).

4.1. Gaze perception in the human newborn

The human preference for direct gaze is already present during early ontogeny: newborn infants preferentially look at faces with direct rather than averted gaze (Batki et al., 2000; Farroni et al., 2006). This difference is absent when the face is inverted, suggesting that the context of the face matters (Farroni et al., 2006). The study of Guellai et al. (2020) indicated that the preference for direct instead of averted gaze cannot be attributed to the difference in horizontal location of the iris: newborns also prefer to look at direct gaze rather than to a 'faraway' look, i.e., a gaze directed toward the infant's face but to a location above the infant's eyes. This suggests that newborn infants have a preference for socially relevant stimuli in which direct gaze plays an important role (Farroni et al., 2006; Gliga and Csibra, 2007). The direct gaze is often provided by the mother, whose pregnancy and postpartum hormonal status, i.e., her oxytocin levels, has prepared her for this situation: oxytocin facilitates maternal direct gaze and maternal bonding behaviour (Feldman et al., 2007). The maternal propensity to provide direct gaze and the infant's preference for this gaze pave the way for the infant's social skill development.

Newborns can follow moving eyes to a limited extent (Farroni et al., 2004b). Gaze following on the basis of information of head and eyes gradually improves with age, especially after the age of 6 months (Butterworth and Jarrett, 1991; Del Bianco et al., 2019; Gredebäck et al., 2010). It is initially based on the information of the head and eyes. In the second year infants start to rely more on the information of the eyes than that of the head (Moore and Corkum, 1998; Tomasello et al., 2007). At this age gaze following has become a robust phenomenon (Grossmann, 2017). The improved gaze following with increasing age is experience

dependent. This was demonstrated, for instance, by the study of Senju et al. (2015): infants of blind mothers looked less at an object that was gaze-cued by an adult than infants of mothers without visual impairment.

4.2. Context dependency of gaze perception

In many species eye contact (also called mutual gaze) and direct gaze (being looked at regardless of eye contact) generate aversive responses, as direct gaze signals threat (Fig. 2; Senju and Johnson, 2009). In human beings, however, eye contact plays a major role in communication, social interaction and affective bonding (Argyle and Dean, 1965; Frischen et al., 2007; Senju and Hasegawa, 2005; Senju and Johnson, 2009). The duration of eye contact has a large interindividual variation, but it lasts generally longer in women than in men (Argyle and Dean, 1965). Direct gaze functions as an attention grabber, both in photos, videos (Itier and Batty, 2009) and painted portraits (Kesner et al., 2018). The attention grabbing function of direct gaze is absent when information of face and gaze is irrelevant (Framorando et al., 2016). Yet, when the information of direct gaze is relevant, it is associated with heart rate deceleration, larger skin conductance responses and higher feelings of arousal accompanying direct gaze (Akechi et al., 2013; Hietanen et al., 2008). The psychophysiological response does not only occur during direct gaze of a human being, but also – be it somewhat less intensive – in response to direct gaze of a humanoid robot (Kilavuori et al., 2021). However, in a negative emotional context, an averted gaze elicits more arousal than direct gaze (McCrackin and Itier, 2021). Eye contact also increases the time spent on looking at the gazer's face, it delays the disengagement from it to look at a target elsewhere (Senju and Hasegawa, 2005), it evokes positive social judgements (Chen et al., 2017), and it plays a coordinative role in shared attention during real conversations (Wohltjen and Wheatley, 2021). In addition, eye movements ending in direct gaze induce by capturing attention a shortening of subjective time during social interaction (Burra and Kerzel, 2021).

4.2.1. Context and 'watching eye' effect

Humans have an a priori expectation that other people's gaze is directed towards them (Mareschal et al., 2013; Schultze et al., 2013); they share this sensitivity of being watched with many vertebrates (Klein et al., 2009). In humans the angular range of the perception of being looked at ('cone of direct gaze') varies between 4 and 9 degrees and depends on interpersonal distance and facial expression (Gamer and Hecht, 2007). The cone of direct gaze is wider for happy and angry facial expressions than for neutral and fearful expressions (Lobmaier and Perrett, 2011; Schulze et al., 2013). The idea of being looked at by 'watching eyes' promotes pro-social behaviour and self-awareness (Argyle and Dean, 1965; Conty et al., 2016). The latter can be illustrated by the effect of watching eyes on the Stroop task. This task consists of naming the actual colour of the ink in which a colour name is printed; this naming is delayed when the ink colour does not match the colour's name (e.g. when the word 'green' is printed in pink). Performing the Stroop task under watching eyes delays the naming (Conty et al., 2010).

The positive effect of watching eyes on pro-social behaviour has been reported in the following conditions: it has been associated with less bicycle thefts (Nettle et al., 2012); with less littering of public area (Bateson et al., 2013); with higher gifts in donation boxes in a museum or student cafeteria (Bateson et al., 2006; Kelsey et al., 2018) and with increased ratings of trustworthiness of truth-ambiguous statements (Kreysa et al., 2016). The effect of watching eyes in experimental economics games, such as the ultimatum and the dictator game, is debated. Some studies reported a positive pro-social effect (Baillon et al., 2013; Burnham and Hare, 2007; Haley and Fessler, 2005; Hietanen et al., 2018), while a similar pro-social effect was absent when auditory cues instead of watching eyes suggested the presence of others (Haley and Fessler, 2005). However, the review and meta-analyses of Northover

et al. (2017) did not find evidence for a consistent pro-social effect of watching eyes in economic games. The above findings may imply that the pro-social effect of watching eyes occurs is context specific and especially arises when the actor is surrounded by other people (Bateson et al., 2013). In this respect it is interesting to mention that Norenzayan et al. (2016) hypothesized that the cultural development from small-scale groups in the gatherer-hunter era to large-scale societies in later times was facilitated by pro-social religions characterized by gods whose eyes monitored human behaviour.

4.2.2. Context and gaze effect on orientation toward and appreciation of objects

Seeing someone looking at a specific target, i.e., the gaze of the viewer is averted to the target, automatically draws the observer's attention to the target location (Fig. 2). This orienting effect is stronger than the orienting effect of an arrow (Tipper and Bayliss, 2018). The gaze orienting effect has been extensively investigated in laboratory experiments. Typically, participants in such experiments see a face projected on a screen with either direct or averted gaze. Next, targets appear laterally to the face, either at the location cued by the gaze or not. The studies revealed that persons react faster to targets that have been pre-cued by gaze direction, even when they intend to look at the contralateral direction (Driver et al., 1999; Friesen and Kingstone, 1998). The gaze orienting effect is also present when only the eye region is presented (Bayless et al., 2011). When the contrast polarity of the eyes is reversed, the gaze orienting effect largely disappears (Ricciardelli et al., 2000). The gaze orienting effect is affected by the situation, in particular by the characteristics of the expresser and observer (Dalmaso et al., 2020). The presence of fearful or surprised expressions in the expresser's face – expressions that are associated with more widely opened eyes – enhances the gaze cueing effect (Bayless et al., 2011). Also faces perceived as more dominant or having a higher social status promote the gaze orienting effect (Dalmaso et al., 2020). Factors of the observer that affect the gaze orienting effect are gender (larger effect in females than in males), age (smaller effect in elderly people) and self-esteem (larger effect in persons with low self-esteem) (Dalmaso et al., 2020).

The complexity of the effect of human gaze in the appreciation of objects may be illustrated by the studies of Bayliss and colleagues. They demonstrated that gaze cueing was stronger when the gazing face had a happy than a disgusting expression, but this was only true when the observed object had a positive valence. When objects with a neutral or negative valence were presented the expression of the gazing face did not affect gaze cueing (Bayliss et al., 2010). In another experiment Bayliss and co-workers showed that a gazing individual evaluates objects more positively when his/her gaze is followed by another person's gaze, i.e., in the presence of joint attention (Bayliss et al., 2013).

4.2.3. Cultural differences in the perception of gaze

Western Caucasian people maintain more eye contact during social interaction than East Asian people (Argyle et al., 1986). As a result Western Caucasian individuals have more experience with mutual gaze than East Asian persons, which could be the reason that Western Caucasian persons are more accurate in determining whether another person (with a similar cultural background) is looking at them than East Asian individuals (Uono and Hietanen, 2015). Yet, when tested with subtle gaze deviations both East Asian and Western Caucasian individuals show higher perceptual sensitivity to direct gaze in own-race faces than to direct gaze in other-race faces (Collova et al., 2017). This difference has been attributed to less perceptual expertise with faces of the other race (Collova et al., 2017).

East Asian people perceive direct gaze of faces of the own culture as more unpleasant, more unapproachable and angrier than Western Caucasian people do (Akechi et al., 2013). Yet, the perceived intensity of happy and angry faces in both cultures is not affected by gaze direction of faces of the same culture. In addition, persons of both cultures

perceive both expressions as more intensive when expressed by faces with direct (and not averted gaze) of the other culture (Krämer et al., 2013). Finally, the gaze orienting effect is affected by culture: in East Asian persons, but not in Western Caucasian individuals, the gaze orienting effect is affected by mismatching gazes of surrounding faces (Cohen et al., 2017). This may be the result of the cultural differences in social orientation and information processing: a more collectivistic oriented society with holistic information processing in East Asia and a more individualistic society with analytic information processing in the Western industrialized world (Argyle et al., 1986; Nisbett and Miyamoto, 2005; Rule et al., 2013).

4.3. Neural substrate of gaze perception

Similar to the characteristics of the face, gaze perception is processed in the network of the social brain (Grosbras et al., 2005; Nummenmaa et al., 2010, Fig. 1C). It is unknown which parts of the brain are involved in gaze processing in newborn infants. The youngest age at which gaze perception has been studied is 4 months. A combined Near infrared spectroscopy and EEG study in 4-month-olds indicated that getting engaged in direct gaze is associated with increased activity in the superior posterior temporal cortex and the frontal-polar cortex (Grossmann et al., 2008). In addition, the amplitude of the N290 (the infant equivalent of the N170) is larger during direct gaze than during averted gaze, an effect that is absent during face inversion (Farroni et al., 2002, 2004a). The study of Vermetti et al. (2018) indicated that this differential effect of gaze direction on the N290 is experience dependent, as it was lacking in 6–10-month-old sighted infants of blind mothers.

In adults, the details of the situation determine which parts of the network are most active. For instance, the perception of dynamic gaze shift (irrespective of its direction) is associated with increased activity in the STS, intraparietal sulcus and fusiform gyrus (Pelphrey et al., 2003). When the gaze shift results in mutual as opposed to averted gaze a specific recruitment of the STS follows (Pelphrey et al., 2004). Another example is brain activity involved in the gaze orienting effect; it consists of activity in the inferotemporal gyrus, medial temporal cortex, inferior frontal gyrus, ventral and dorsal medial prefrontal cortex, paracentral lobule, and amygdala (Schilbach et al., 2011).

For the evaluation of mutual gaze (eye contact) Senju and Johnson (2009) proposed a dual pathway model – in analogy to Johnson's construct of the neural processing of faces (Section 2.2). The first route is the fast subcortical pathway that is also involved in the first and crude processing of facial information. It comprises the superior colliculus, pulvinar and amygdala. A study using positron emission tomography was able to confirm higher activity in the right (not the left) amygdala during direct as opposed to averted gaze (Kawashima et al., 1999). Burra et al. (2013), who assessed gaze perception in a person with extensive bilateral damage of the primary visual cortex, showed that direct gaze resulted in higher right amygdala activity than averted gaze, even though the person was unaware of gaze and gaze direction. The activation of the amygdala did not depend on the spatial frequency information of the gaze, which contrasts with the known frequency dependency of the amygdala in response to facial information (see Sections 2.3 and 3.2.3). Burra et al. (2013) suggested that the salient stimulus of the white sclera is apparently sufficient to drive the amygdala response (Burra et al., 2013).

The information of the subcortical pathway modulates the activity in the second pathway, i.e., the cortical networks involved in the evaluation of mutual gaze. The latter comprises in particular the aSTS, pSTS and medial prefrontal cortex (Senju and Johnson, 2009). The STS has a specific sensitivity to gaze. Studies in macaques indicated that both aSTS and pSTS have gaze-specific cells that are activated by gaze signals of body, head and eye, with especially the aSTS having cells that respond to eye-gaze signals (Barraclough and Perrett, 2011; Carlin and Calder, 2013). Yet, according to fMRI studies in humans, it is the pSTS that plays a pivotal role in the processing of social gaze, that is, eye contact that is

perceived as communicative (Senju and Johnson, 2009) or joint attention (Nummenmaa and Calder, 2009; Pfeiffer et al., 2013; Redcay et al., 2010). The finding that the pSTS does not only mediate gaze perception, but also forms part of the networks involved in action observation and theory of mind, underlines its crucial role in the processing of social information (Yang et al., 2015). As Senju and Johnson's bottom-up model may suggest that cortical activity only occurs as a second and slower step in the processing of gaze information, Burra, Mares and Senju (2019b) extended the model by explicitly including the notion that task- and context specific information in the cortex may affect the early phases of gaze processing by means of top-down modulation.

The pSTS plays a pivotal role in joint attention. Other parts of the brain involved in joint attention are the right temporoparietal junction and the dorsal medial prefrontal cortex, the cortex that is suggested to be involved in 'meeting the minds' (Pfeiffer et al., 2013; Redcay et al., 2010). The study of Schilbach et al. (2010) indicated that the dorsal medial prefrontal cortex, in particular its anterior part, is activated when the other initiates joint attention, whereas self-initiated joint attention especially recruits the ventral striatum, that forms part of the so-called reward circuitry.

The context and task specificity of the neural processing of gaze information is illustrated by the controversial ERP findings on the effect of direct as opposed to averted gaze on the N170. Studies that reported that direct gaze was associated with a smaller N170 amplitude than averted gaze, mostly used exposure times of at least 1 s and/or included the evaluation of facial characteristics, e.g. emotional expression or mouth movements (Latinus et al., 2015; Puce et al., 2000; Stephani et al., 2020; exception: Itier et al., 2007). The studies that found that direct gaze was associated with a larger N170 amplitude mostly used an exposure time of 500 ms and restricted themselves to the evaluation of the effect of gaze (Conty et al., 2007; Mares et al., 2018; Pönkänen et al., 2011; exception Conty et al., 2012). Two studies that used exposure times of 500 or 600 ms while persons were engaged in a gender categorization task (Burra et al., 2018) or a theory of mind judgement task (McCrackin and Itier, 2021), indicated that the N170 was not affected by gaze direction. Rather, gaze direction was associated with higher EEG-activity in an early time window (100–140 ms) at the N170 site (Burra et al., 2018) and in a relatively late time window (300–600 ms, Burra et al., 2018; 540–800 ms, McCrackin and Itier, 2021) at the centroparietal and parieto-occipital sites.

ERP and fMRI studies indicated that facial expression affects the neural processing of gaze (Fichtenholtz et al., 2007; Graham and LaBar, 2012; McCrackin and Itier, 2019). Moreover, Adams et al. (2010) showed that this effect may be modulated by race: averted gaze (as opposed to direct gaze) in own-race faces with a fearful expression was associated with increased activity in the face and gaze networks, including bilateral amygdala, whereas the reverse was true for other-race face with a fearful expression in which direct gaze was associated with the higher neural activity.

4.4. Summary of gaze perception

Gaze reflects attention and intention. Human eye morphology promotes that human gaze behaviour is predominantly communicated via the eyes. Direct and especially mutual gaze facilitate social interaction, prosocial behaviour ('watching eyes') and affective bonding. Newborn infants already preferentially look at faces with direct rather than averted gaze. Averted gaze directs attention away from the viewer, often to a specific target. The strength of this gaze orienting effect is context specific. The combination of gaze shift to a target and mutual gaze results in joint attention (or rather shared attention), which is the cornerstone of the theory of mind, the human's capacity to create cognitive representations of others' mental states.

Culture affects eye contact: East Asian persons have less eye contact than Western Caucasian persons. This difference may reflect that East Asian persons in general are rather oriented to the community than to

the individual, in contrast to the major orientation of Western Caucasian persons.

Like the processing of face identity and facial expression, the processing of eye gaze involves parts of the social brain network. Two pathways have been described: (1) a fast and crude subcortical pathway including the superior colliculus, pulvinar and amygdala; and (2) a slower and more accurate cortical pathway. The type of the task determines which part of the cortical network is recruited preferentially and to what extent it relies on bottom-up and top-down processing of information. In mutual gaze the STS and medial prefrontal cortex are involved; in gaze shifts the STS, intraparietal sulcus and fusiform gyrus; in joint attention the pSTS, medial prefrontal cortex and temporoparietal junction, and in the gaze orienting effect major parts of the social brain network.

5. Concluding remarks and suggestions for future research

The newborn human infant is already able to perceive and process information of face and gaze to some extent. The early emergence of face and gaze processing abilities underlines the importance of face and gaze signals in social interaction. Some evidence is available that the recognition of face-like stimuli starts in utero (Reid et al., 2017). Yet, replication of the study of Reid and colleagues is needed, taking into account the methodological issues raised by Scheel et al. (2018) and Reid et al. (2018). In addition to replication, a longitudinal design that also includes the evaluation of hand-face movements is recommended. This design would allow to investigate whether the foetus' increasing ability to adapt hand movements to the delicacy of the facial target (avoiding movements towards the eyes; Zoia et al., 2013) is associated with an increasing ability of the foetus to turn its head to face-like stimuli. The presence of such an association would support the foetal emergence of neural face maps that may facilitate the perception of face-like stimuli. Studies on the foetal emergence of the perception of facial expression and gaze direction are very hard to design. When studies on the foetal recognition of face-like stimuli can be accomplished successfully, the next step to be endeavoured might consist of studies evaluating the foetus' ability to discriminate dynamic light displays of expressions of happiness and disgust.

The eye region often plays a crucial role in the recognition of identity and genuine emotional expression. The genuine aspect is due to the limited cortical control of the muscles in the upper half of the face. The eyes' gaze tell the observer about the other's attention and intention and furnishes information about the other's mental state. Hence the expression that the eyes are "the windows of the soul", i.e., the other's mind (Emery, 2000; Grossmann, 2017; Kleinke, 1986).

The perception and processing of face identity, facial expression and gaze is clearly context dependent. The context is determined by a variety of factors. In the first place, the context of each of the three types of facial information (identity, expression, gaze) consists of the status of the other two types (e.g., the context of identity recognition is formed by expression and gaze direction). This interdependency of the three face signals underscores the notion that the appreciation of social facial information largely improves when information of the entire face is available. Second, the context is formed by other characteristics of the expresser and by characteristics of the observer and the environment. Also, the role of the eyes in the perception of facial identity and expression is context dependent. It depends, for instance, on culture and specifics of the situation (e.g., still face vs dyadic live interaction). The complexity and context dependency of the perception and processing of face and gaze information impact two societal trends, i.e., the increase in video-conferencing and in the use of robots. In video-conferencing, participants lack a shared environment and miss large parts of the others' body context. Moreover, participants see themselves frequently on the screen, resulting in increased self-awareness that distracts from attention to the others (Bickmeyer, 2021). Future research needs to address the impact of the video-conferencing context on the perception

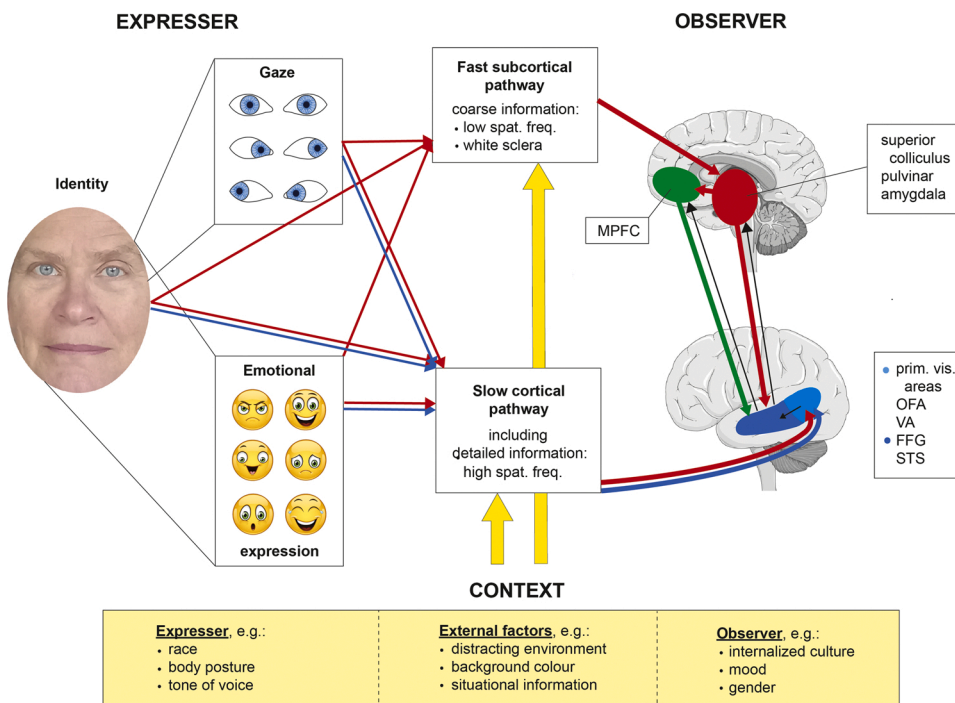


Fig. 3. Schematic depiction of subcortical and cortical pathways, contextual modulation, and bottom-up and top-down processing.

The red arrows represent the flow of coarse, low spatial frequency information of face and gaze signals. This information is used by the fast subcortical pathway. The blue arrows represent the detailed, high spatial frequency information of face and gaze signals. This information is processed by the slow cortical pathway. The contextual information (yellow) affects both pathways. The information of the subcortical pathway may recruit the networks in the medial prefrontal cortex (MPFC) allowing for preparation of the higher order visual cortical networks (including the fusiform regions) for the evaluation of the incoming information via the slow cortical pathway. This preparatory top-down modulation is represented by the green arrow. It should be noted that (a) face identity, emotional expression and gaze are interdependent, i.e., each aspect forms part of the context of the other two; this is not depicted in the diagram; (b) neural information flow is often bidirectional (some of it is indicated by the black arrows); and (c) the neural systems are not depicted in anatomical detail; for details see Fig. 1.

FFG = fusiform gyrus with fusiform face area; OFA = occipital face area; prim. vis. areas = primary visual areas; spat. freq. = spatial frequency; STS = superior temporal sulcus; VA = visual association areas.

frequency; STS = superior temporal sulcus; VA = visual association areas.

of face and gaze signals and how this affects the social communication and understanding of the participants.

Robots, including social robots, are nowadays commonly used (Giger et al., 2019). Their abilities, such as perception, movements and interaction, get increasingly human-like (Ajoudani et al., 2018). In general, people see robots as more acceptable for household chores than for social interaction, as robots often induce an eerie feeling (Giger et al., 2019; Zlotowski et al., 2015). An experiment evaluating identical gaze behaviour of humans and robots indicated that participants required less attentional effort to interpret the human's gaze than that of the robot (Ghiglini et al., 2021). The greater ease to read the human gaze may not only be attributed to the larger experience with this gaze, but also to its human facial context. Future research needs to address the question which human-like aspects of robotic face and gaze are associated with social appreciation or rather with dislike of robots – and in which context. First, when it is clear that a human-like face and gaze of robots are appreciated, it is wise to take the challenging step to develop robots equipped with the intricate non-verbal human-like skills involved in the production and processing of face and gaze signals.

Culture is an acknowledged contextual factor in face and gaze processing. For people in monoracial environments it is easier to recognize faces of the own-race and expressions expressed by faces of the own culture than those of other races and cultures, respectively, due to the large experiential advantage of faces of the own race and culture and to social categorization. The East Asian culture is associated with less eye contact than the culture in Western industrialized countries. In identity recognition of still faces with a neutral expression of the own-race Western Caucasian individuals gather the information on the critical eye region by direct scanning of that region, whereas East Asian people collect this information by focussing on the nose. Yet, in other situations, e.g., faces with an emotional expression or faces encountered in dyadic social interaction, Western Caucasian persons preferentially scan eye and mouth regions, whereas East Asian primarily fixate the eye region – the facial part that is relatively resistant to the East Asian cultural norm

of suppression of emotional expression.

Up until now, most research in face and gaze perception and processing has been carried out in relatively artificial laboratory situations. These conditions have the advantage that interfering environmental contextual factors can be controlled. Yet, daily life is characterized by a continuously changing context. Technical tools to assess the way in which individuals assess faces in ecologically valid situations are currently available. These include malleable virtual environments in which, for instance, two live persons wearing head-mounted eye-trackers (see e.g. Haensel et al., 2021) interact. Such tools would allow to further elucidate the role of the cultural environment, as the environment can be easily changed from multiple people from a single race (own or other race) to a multiracial mix of people, and because it allows for inclusion of not only Western Caucasian and East Asian participants, but also of e.g., black individuals from Africa and the Americas. Moreover, such tools allow to assess the role of the race of the interacting persons, that of their dynamic changes in gaze and facial expression, and that of their social categorization and implicit racial bias. When three dimensional video recording is added to the recording facilities also the changes in body posture and gestures as contextual modifiers may be captured and accounted for.

Face and gaze processing occurs in parts of the social brain, i.e., the networks that deal with social cognition. The majority of studies on the neural processing of face and gaze signals in human beings focus on the cortical networks. Nevertheless, accumulating evidence suggests that the processing of facial identity, facial emotional expression and gaze involves two parallel and interacting pathways: (1) a fast and crude subcortical route, including the superior colliculus, pulvinar and amygdala; and (2) a slower cortical pathway. The cortical networks include in particular the fusiform gyrus, STS, the intraparietal sulcus, the temporoparietal junction and medial prefrontal cortex. The information flow in the networks is bidirectional, consists of a combination of bottom-up and top-down processing, and is highly context specific. The context assists the anticipation and the later processing of facial

information (Fig. 3). Future research needs to address the specifics of the contribution of the subcortical pathways and top-down processing. For instance, it could address the question of whether the effect of quick, coarse, low spatial frequency facial input, associated with social categories, prepares - via recruitment of the orbitofrontal cortex - the fusiform cortex to process facial information in a specific way. Novel techniques have become available to unravel the contributions of subcortical pathways and orbitofrontal cortex. Examples are the combination of fMRI with magnetoencephalography (MEG; allowing for a better spatial resolution of the source location than EEG; Lin et al., 2021); MEG in combination with masking (allowing for unravelling the contribution of top-down processing; Kajal et al., 2020); the application of steady-state visual evoked potentials and eye-tracking (allowing for fixation related evoked potentials; Wieser et al., 2016); or hyper-scanning in which two individuals interact in real time while the brain activity of both persons is scanned in an fMRI machine or recorded with EEG or MEG (Czeszumski et al., 2020; Misaki et al., 2021). The studies using a single brain approach, i.e., record brain activity in only one person, could use as stimulus videoclips of daily life situations using three versions of the same clip: the original unfiltered version of the clip, one containing only the original's low spatial frequency information, and one containing only the original's high spatial frequency information. The use of such stimulus set would allow a further determination of the role of the subcortical pathways in face and gaze processing in ecologically valid situations.

In conclusion, face and gaze perception in the human is a complex process. Its development starts already in the prenatal phase. It is strongly experience dependent and largely context specific. Its processing involves large parts of the social brain network, and does not only include bottom-up, but also top-down processing (e.g., during social categorization).

Data availability

N.A.

Declaration of Competing Interest

None.

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