The Perception of Facial Emotion in Typical and Atypical Development

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Abstract

The ability to perceive emotional facial expressions is an important building block for many aspects of social and emotional functioning. Not surprisingly, this ability emerges early in life, with development continuing through adolescence. We begin this chapter by briefly reviewing current theoretical models of face emotion processing in adults, with a particular emphasis on the neural bases of this ability. We then present an overview of the developmental literature, from birth to late childhood. A secondary focus pertains to atypical patterns of development, in particular, in children with autism and children with an anxiety disorder. In particular, we review the early development and neural basis of attentional biases to fearful or threatening facial emotions, in typical development and as they relate to individual risk profiles for anxiety disorders. Finally, we highlight recent advances in the understanding of the perceived valence of facial expressions in development and the variations of emotional facial expressions perception across different human cultures.

A major component of the human ability to socially connect with other people is the ability to understand and "read" facial emotion. Humans of all cultures, including individuals who are blind (Galati, Sini, Schmidt, & Tinti, 2003), display a variety of spontaneous facial expressions when experiencing different emotions (Duchenne, 1862). The production of facial expressions is a relatively recent adaptation in phylogenetic history, being generally present in mammals but most pronounced in primates (Darwin, 1872). The perception of emotional faces is critical to social functioning and social communication (for a discussion about the definition of social communication in an evolutionary context, see, e.g., Scott-Phillips & Kirby, 2013; Scott-Phillips, 2008) and involves the interplay between emotional and perceptual processes (Tamietto & de Gelder, 2010). The development of emotional face perception is differentially affected by autism spectrum disorders (Dawson, Webb, & McPartland, 2005; Krebs et al., 2011), affective and psychiatric disorders (Brennan, Harris, & Williams, 2014; Leppänen, Milders, Bell, Terriere, & Hietanen, 2004), early visual deprivation (Gao, Maurer, & Nishimura, 2013), and early experiences of violence or neglect (Moulson

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et al., 2015; Pollak, Cicchetti, Hornung, & Reed, 2000). The adaptive significance of the ability to "read" facial emotion, the relative complexity and evolutionary recentness of this ability, and its sensitivity to a range of conditions and developmental circumstances motivate the investigation of the development and developmental mechanisms of facial emotion perception. As a first step to this end, we briefly review the theoretical models and neural bases of facial emotion perception in adults.

Explaining Emotional Facial Expression Perception: Setting the Stage

Variant and Invariant Streams of Information Embedded in Faces

Faces convey a range of hierarchically embedded information such as gender, race, identity, age, expression, gaze, and speech movements. Facial features that play a particularly important role in discriminating facial expressions include the eye, mouth, and nose regions (Lee & Anderson, 2017; Schyns, Petro, & Smith, 2007). Thus, accurately perceiving facial emotion necessitates the extraction of information from relevant facial features that also carry other information, such as gaze direction or face gender (Burton, Bruce, & Dench, 1993). This embedding of information on different timescales (Jack, Garrod, & Schyns, 2014; Jack & Schyns, 2015) poses specific computational problems related to the need to combine invariance and sensitivity. For example, while humans perceive varying expressions on an individual face (sensitivity), they can extract its identity regardless of its expression (invariance). Such a trade-off is general to the problem of object recognition (Marr, 1982). In the case of faces, this trade-off is commonly understood as the relative dissociation between variant (e.g., emotional expression, gaze direction) and invariant (e.g., identity, gender, race) streams of information within face processing networks, which occurs as a result of the structural encoding of the face (Bruce & Young, 1986). Such dissociation is most evident in behavioral or lesion studies: some patients with acquired brain lesions experience selective behavioral impairments in face identity recognition (i.e., prosopagnosia) but not facial expression recognition, and vice versa (reviewed in Bruce & Young, 1986). This relative dissociation between variant and invariant processing streams for face perception has found additional support from neuroimaging studies (reviewed in Haxby, Hoffman, & Gobbini, 2000) revealing preferential processing of variant, dynamic facial information in the superior temporal sulcus (STS) but preferential processing of invariant, static facial information in the fusiform gyrus (FG). Developmentally, face identity can be extracted independently from expression and vice versa as early as about 7 months of age in human infants (e.g., Nakato, Otsuka, Kanazawa, Yamaguchi, & Kakigi, 2011), suggesting that facial emotion perception prior to this age could be more influenced by face identity, and perhaps other invariant aspects of the face (e.g., gender), than at later ages. For example, infants younger than 6–7 months of age (but not older infants) typically do not dishabituate to different facial expressions when presented by different models but may do so with expressions presented by the same model (Leppänen & Nelson, 2009; Nelson, 1987).

While the dissociation between emotion processing and other aspects of face processing is important to understand in terms of functional specificity and computational trade-offs, this dissociation is not complete (Calder & Young, 2005). Conversely, factors affecting the earliest face processing stages can still affect dynamic and static face processing differentially. For example, a recent case study of a patient with acquired prosopagnosia (a selective impairment in recognizing facial identity) from a bilateral lesion in the occipito-temporal cortex revealed a distinct pattern of impairment in identifying static facial expressions but preserved performance in identifying dynamic expressions with the exception of fear (Richoz, Jack, Garrod, Schyns, & Caldara, 2015). This patient's lesion affected their occipital face area (OFA), involved in extracting facial features, but not the STS, a higher-order area involved in the multimodal perception of dynamic stimuli (Haxby et al., 2000; Said, Moore, Engell, & Haxby, 2010). Further investigations revealed that this patient was specifically impaired in extracting emotional information from the eye region of the face, even when instructed to do so (Fiset et al., 2017). In summary, a deficit in facial feature processing can cause downstream effects on both identity processing (prosopagnosia) and static emotion processing while relatively sparing dynamic facial emotion processing.

Another line of work that highlights the incomplete segregation of facial emotion processing from other aspects of face processing concerns the integration of information between the processing streams involved in decoding facial expressions specifically versus other aspects of faces. These interactions occur across several levels. For example, angry faces tend to be perceived as more masculine, a bias that can be partly captured by variations in specific facial features such as brow thickness (Bayet, Pascalis, et al., 2015). In another example, event-related potential (ERP) studies in humans reveal an early (170 ms) sensitivity to emotional facial expressions, followed by gaze direction (190 ms) and finally (200–300 ms) the conjunction of expression and gaze (Conty, Dezecache, Hugueville, & Grezes, 2012). Similarly, smiling expressions act as cues to face familiarity in behavioral tasks (Baudouin, Gilibert, Sansone, & Tiberghien, 2000), information typically associated with modulations of neural responses around 250 ms (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). The mechanism underpinning these perceptual biases is unknown but may include an inference based on the typical association of familiarity and smiling in everyday experience.

Finally, interactions between emotional expression and other facial dimensions may involve higher-level cognitive processes including stereotypes or other semantic knowledge that is not rooted in perceptual experience. For example, white American adults (Hehman, Ingbretsen, & Freeman, 2014) and children as young as 4 years (Dunham, Chen, & Banaji, 2013) tend to associate Black- or African-American faces with the emotion of anger. A recent fMRI study has identified the fusiform gyrus and the orbitofrontal cortex as possible neural loci of this effect of stereotypes on social perception (Stolier & Freeman, 2016). Thus, our understanding of the development of the ability to perceive facial emotion must account for the development of these complex interactions between facial emotion perception and other aspects of face processing including identity, gaze, race, and gender.

The Perception of Emotional Faces in the Brain

The perception of emotional facial expressions in the human brain engages both visual and emotional processing pathways (Adolphs, Damasio, Tranel, & Damasio, 1996; Tamietto & de Gelder, 2010; Vuilleumier, 2005; for a meta-analysis, see, e.g., Fusar-Poli et al., 2009). After early, feature-based processing in the OFA, facial expression processing is thought to be continued in the STS and to a lesser extent in the FFA (Haxby et al., 2000; Said, Haxby, & Todorov, 2011). Cortical and subcortical structures involved in emotion processing include the amygdala nuclei (Ahs, Davis, Gorka, & Hariri, 2014), the pulvinar, the orbitofrontal cortex (OFC), and the anterior cingulate cortex (ACC), among others (Kesler-West et al., 2001; Said et al., 2011; Tamietto & de Gelder, 2010; Vuilleumier, 2005). While the specific, causal function of subcortical (versus cortical) structures in processing facial emotion remains debated, their general involvement is not (de Gelder, van Honk, & Tamietto, 2011; Pessoa & Adolphs, 2010, 2011). Similarly, while there is little doubt that emotion processing pathways (e.g., involving the pulvinar) exist alongside and in interconnection with the primary visual pathway, their specific role and importance remain unclear and are difficult to test (de Gelder et al., 2011; Pessoa & Adolphs, 2010, 2011).

It has also been suggested that motor or somatosensory portions of the cortex could play a role in processing facial emotion, perhaps related to motor mirroring (Said et al., 2011). For example, the frontal operculum (FO) is more activated by emotional than neutral facial expressions during passive viewing (Montgomery & Haxby, 2008). However, its causal role remains unclear, as is the role of the *production* of facial expressions in *perceiving* facial expressions. For example, it is interesting to note that deficits in identifying but not imagining facial expressions have been reported in adults with bilateral facial paralysis from Moebius syndrome (Bate, Cook, Mole, & Cole, 2013; Bogart, Matsumoto, & Bogart, 2010; Calder, Keane, Cole, Campbell, & Young, 2000). However, these deficits may stem from more general impairments in oculomotor control (Bate et al., 2013), which are essential to optimal face perception, including emotional facial expressions (e.g., Peterson & Eckstein, 2012).

Given the large number of cortical and subcortical areas involved in processing emotional facial expressions, it is important to note that only a small number of these areas are routinely accessible by common spatially resolved neuroimaging techniques used in developmental studies involving infants or very young children. Functional near-infrared spectroscopy (fNIRS), most notably, provides good coverage of superficial cortical areas (Minagawa-Kawai, Mori, Hebden, & Dupoux, 2008). Importantly, in the case of facial emotion processing, these regions include the STS (Nakato et al., 2011), frontal regions (Minagawa-Kawai et al., 2009), and occipital regions of the superficial cortex. Neural activity in the fusiform gyrus, while inaccessible by fNIRS, can be at least partly recovered from electroencephalography (EEG) (Guy, Zieber, & Richards, 2016; Johnson et al., 2005). However, subcortical structures (such as the amygdala or pulvinar) are usually considered inaccessible by EEG or fNIRS. Future progress in source reconstruction methods for EEG or magnetoencephalography (MEG) signals in developmental participants (Guy et al., 2016; Kuhl, Ramirez, Bosseler, Lin, & Imada, 2014; Lew et al., 2013), as well as future advances in pediatric functional magnetic resonance imaging (Deen et al., 2017; Weaver, 2015), may help in unveiling the involvement of ventral or subcortical structures in facial emotion processing early in life.

In addition to spatially resolved neuroimaging methods, time-resolved methods such as EEG or MEG have revealed the time-course of emotional facial expression processing in human adults. EEG studies in adults have shown that the face-sensitive ERP N170, a negative component measured at temporal electrodes at a latency of about 170 ms, is sensitive to specific emotional facial expressions (Batty & Taylor, 2003; Eimer & Holmes, 2007; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Luo, Feng, He, Wang, & Luo, 2010; Schyns et al., 2007). The amplitude of the earlier component P1, measured occipitally at a latency of about 100 ms, also appeared to be modulated by emotional facial expressions, at least when contrasting emotional to neutral expressions (Batty & Taylor, 2003; Leppänen et al., 2007; Luo et al., 2010; Vlamings, Goffaux, & Kemner, 2009). In this context, it is interesting to note that the neural source of the N170 is estimated to be localized in the fusiform gyrus (Deffke et al., 2007) and the STS (Itier & Taylor, 2004).

A joint ERP-fMRI study found that trial-level modulations of N170 amplitude in an emotion perception task correlated with trial-level modulations of amygdala activity measured with concurrent fMRI (Conty et al., 2012), suggesting that the amygdala could be sensitive to facial emotions at this latency. MEG and intracranial EEG have been used to directly examine the time-course of neural activity in the amygdala (versus extra-striate visual cortex) in response to emotional faces in general and fearful faces in particular, with relatively mixed results (Dumas et al., 2013; Garvert, Friston, Dolan, & Garrido, 2014; Krolak-Salmon, Hénaff, Vighetto, Bertrand, & Mauguière, 2004). Overall, the evidence suggests that emotional facial expressions are extracted alongside other aspects of the face from at least 170 ms in the adult human brain.

Most of the neuroimaging or electrophysiological studies reviewed so far concern where or when in the brain facial emotions are differentiated. Such a direct approach has considerable merit, but its first theoretical limitation is that interpreting facial emotions often requires the integration of other emotional cues (e.g., body posture, tone of voice) as well as an understanding of how the current context is likely to cause specific emotional experiences (Barrett, Mesquita, & Gendron, 2011; Hassin, Aviezer, & Bentin, 2013; Saxe & Houlihan, 2017). A second, related theoretical limitation of this approach is that perceiving a facial emotion in isolation from other cues and the broader context is often insufficient to produce an adaptive response: for example, an adaptive response to an angry face clearly depends on whether the angry expression is directed at the observer or not (Conty et al., 2012). Both limitations highlight the importance of appraisal in interpreting facial expressions, inferring the underlying emotional experience of the producer, and selecting an adaptive response.

Recent neuroimaging research has shown, for example, that supra-modal representations of other people's emotional experiences can be extracted from neural activity in the medial prefrontal cortex (MPFC), which could be a locus for integrating emotional cues originating from context understanding and person perception (Peelen, Atkinson, & Vuilleumier, 2010; Skerry & Saxe, 2014). Electrophysiological approaches have demonstrated the time-course of emotional cue integration in the human brain, such as the integration of gaze, gesture, and emotional cues (Conty et al., 2012). Computational studies have shown how Bayesian models can capture human inferences in the emotional domain (Ong, Asaba, & Gweon, 2016; Saxe & Houlihan, 2017). These lines of research highlight the need to understand how during development the perception of emotional facial expressions is integrated with that of other cues to produce an adaptive response and an understanding of other people's emotions in context.

Early Development: From Birth to Toddlerhood

Facial emotion perception engages a complex and efficient processing network. Understanding the development of this ability uniquely illuminates the mechanisms by which such a network is built in human ontogeny. These developmental insights may help elucidate how atypical processes lead to social or emotional disorders in adulthood and shed light on the experience-dependent nature of facial emotion perception more generally. Because developmental studies of facial emotion perception in infants and toddlers typically employ different methods than studies in children and adolescents, here we review the literature on these two developmental periods separately starting with early development. Developmental studies of facial emotion processing in the first 2 years of life (for reviews see, e.g., Leppänen & Nelson, 2009; Nelson, 1987) have pointed to a developmental change in the perception and discrimination of certain isolated expressions between 5 and 7 months of age and to the emergence of contextual understanding toward the end of the first year.

Emotional Facial Expression Perception in Very Young Infants

Newborns and fetuses from 24 weeks of gestation can produce facial expressions, within the range of their facial motor repertoire (Reissland, Francis, Mason, & Lincoln, 2011; Steiner, 1979; Steiner, Glaser, Hawilo, & Berridge, 2001; Trapanotto et al., 2004). Perceiving, discriminating, and identifying facial expressions of emotion follow a more protracted developmental trajectory. Relatively few studies have examined the perception of facial emotion in infants under the age of 4–5 months, and methodological difficulties complicate the interpretation of existing studies. A large body of work has examined the ability of newborns and infants under 2 months of age to imitate live, dynamic facial expressions such as smiling or tongue protrusion (for a review, see, e.g., Oostenbroek, Slaughter, Nielsen, & Suddendorf, 2013). However, the existence, limits, and mechanism (e.g., arousal response, reflex, or motor mirroring) of neonatal imitation remain quite controversial due to differences in experimental controls and parameters across studies (Coulon, Hemimou, & Streri, 2013; Kaitz, Meschulach-Sarfaty, Auerbach, & Eidelman, 1988; Meltzoff et al., 2018; Meltzoff & Moore, 1977, 1983; Oostenbroek et al., 2013, 2016).

The imitation of tongue protrusion appears to be the more reliable form of neonatal imitation (Meltzoff et al., 2018), but how this behavior relates to emotional facial expression is unclear. At the very least, it appears that newborns and very young infants can differentiate between high-intensity, live dynamic expressions of surprise, sadness, or smiling produced by a live female model, as measured by behavioral habituation-dishabituation (Field, Woodson, Greenberg, & Cohen, 1982). More recent studies using static pictures of emotional facial expressions have additionally shown that newborns will look longer toward smiling than neutral or fearful female faces in paired preferential looking paradigms (Farroni, Menon, Rigato, & Johnson, 2007; Rigato, Menon, Johnson, & Farroni, 2011) and that newborns do not differentiate neutral and fearful female faces in behavioral habituation-dishabituation paradigms (Farroni et al., 2007).

These results can be interpreted in the light of the limitations in visual acuity in newborns and young infants (e.g., discussed in Nelson, 1987), as well as of the converging evidence that dynamic movement plays an important role in the perception of newborns and young infants (e.g., Kellman & Spelke, 1983). As a result, studies using static pictures may underestimate the perceptual abilities of newborns and young infants in less controlled situations. Similarly, higher facial expression discrimination performance is evident in young (4-month-old) infants using audiovisual presentations, as opposed to unimodal stimuli (Flom & Bahrick, 2007). Similar studies in infants younger than 5 months of age have generally reported a visual preference for smiling over frowning or neutral faces, at least under some conditions (Bayet, Quinn, et al., 2015; Kuchuk, Vibbert, & Bornstein, 1986; La Barbera, Izard, Vietze, & Parisi, 1976), which could reflect the relative familiarity of this salient and positive expression (Malatesta, Grigoryev, Lamb, Albin, & Culver, 1986). Five-month-old infants do not exhibit the same looking preference for smiling faces (Peltola, Leppänen, Mäki, & Hietanen, 2009) but show some ability to differentiate smiling from sad (Caron, Caron, Maclean, & Url, 1988), fearful (Bornstein & Arterberry, 2003), neutral (Bornstein, Arterberry, Mash, & Manian, 2011), and, in some cases, surprise (Caron, Caron, & Myers, 1982; Young-Browne, Rosenfeld, & Horowitz, 1977) expressions.

However, typically the ability to differentiate facial emotions diminishes (but see Bornstein & Arterberry, 2003; Caron et al., 1982; Serrano, Iglesias, & Loeches, 1992) as habituation-dishabituation paradigms become more demanding by varying the identity of the model between habituation and testing or throughout both habituation and testing ("generalized discrimination"). Smiling versus angry expressions appear to be particularly confusing for infants at this age (but see Serrano et al., 1992), perhaps due to the presence of exposed teeth in both of these facial expressions (Caron, Caron, & Myers, 1985; Oster, 1981). Interestingly, at least two studies have reported interactive effects of gaze and facial emotion perception in 3- to 4-month-old infants when ERPs are utilized, namely, the interaction of fear with averted gaze (Hoehl, Wiese, & Striano, 2008) and the interaction of anger with direct gaze (Striano, Kopp, Grossmann, & Reid, 2006). In Hoehl et al. (2008), the amplitude of the Nc (negative central) ERP component was found to be larger at the right frontoparietal sites in response to objects that had been previously presented with a fearful face gazing toward it, compared to objects that had been previously presented with a neutral face gazing toward it. The effect was absent when faces were gazing away from the object or when the faces were gazing toward a different object than the one presented at test. In Striano et al. (2006), the amplitude of the PSW (positive slow wave) component was found to be larger in response to angry faces with direct compared to averted gazed; the effect was absent for happy or neutral faces. Overall, young infants appear to show burgeoning abilities to differentiate between several emotional facial expressions, including the ability to respond differentially to some expressions as a function of gaze direction, and show a visual preference for smiling faces in some conditions. However, their processing strategies appear more reliant on specific features (e.g., teeth) rather than the extraction of expressions invariantly from the identity of the face.

A current, open question regarding the perception of facial emotion by very young infants and newborns concerns the role of familiarity and experience in shaping this ability. Interestingly, infants from the age of at least 4 months appear to expect adults to produce facial expressions in social interactions, as evidenced in the still-face paradigm (Rochat, Striano, & Blatt, 2002), demonstrating expectations that reflect their everyday experiences (Malatesta et al., 1986). Studies of 5-month-old infants of clinically depressed mothers, who are less likely to produce facial expressions in general and positive expressions in particular, do show delays in discriminating facial expressions (Bornstein et al., 2011); these perceptual delays however do not appear specific to discriminating facial expressions and extend to discriminating objects (Bornstein, Mash, Arterberry, & Manian, 2012). Maternal characteristics (positive emotionality, sensitive parenting style, or anxiety) more generally appear to affect facial emotion processing in older, 7-month-old (de Haan, Belsky, Reid, Volein, & Johnson, 2004; Taylor-Colls & Pasco Fearon, 2015) as well as 9-month-old infants (Otte, Donkers, Braeken, & Van den Bergh, 2015).

Studies comparing infants' discrimination of facial emotions produced by familiar (caregiver) or unfamiliar (stranger) models have demonstrated improved discrimination of expressions from caregivers (versus strangers) at 3.5 months (Kahana-Kalman & Walker-Andrews, 2001; Montague & Walker-Andrews, 2002) but not at 6.5 months (Safar & Moulson, 2017). At least one study has found an effect of face gender on the looking preferences of 3.5-month-olds for smiling versus neutral expressions (Bayet, Quinn, et al., 2015), which could be due to experience as female faces are typically more familiar to infants due to imbalances in caregiving patterns across genders (Ramsey-Rennels & Langlois, 2006; Rennels & Davis, 2008; Sugden, Mohamed-Ali, & Moulson, 2014).

In short, some evidence suggests that expressions from familiar faces may be better perceived by very young infants and that their perception of emotions could be additionally shaped by perceptual experience with faces across the dimensions of gender and race. Theoretically, this could be explained by a relative deficit in structural encoding (e.g., separation of emotion from identity, race, or gender) in young infants (Gliga & Dehaene-Lambertz, 2005; Kobayashi et al., 2011; Kobayashi, Otsuka, Kanazawa, Yamaguchi, & Kakigi, 2012; Nakato et al., 2009, 2011). In other words, the perception of facial emotion could be more integrated with other aspects of the face in very young infants. However, definite evidence for a role of experience in shaping emotional facial expressions perception in early infancy is currently lacking. Future research in this areas as well as larger scale studies that parametrically map the limits of dynamic and static facial expression perception in newborns in young infants will help clarifying the critical experiences and building blocks that set the stage for the emergence of more mature emotional facial expressions perception abilities during the second half of the first year of life.

Early Biases Toward the Facial Expression of Fear

A striking feature of early facial emotion perception abilities in the second half of the first year of life is an attentional bias toward fearful faces emerging between the ages of 5 and 7 months. This fear bias has been evidenced across a range of experimental paradigms and measures, including behavioral, electrophysiological, and physiological measures (Leppänen & Nelson, 2012). For example, 7- but not 5-month-old infants exhibit a visual preference (i.e., longer looking times) for fearful over smiling faces (Leppänen et al., 2007; Nelson & Dolgin, 1985), although a preference for smiling versus neutral, angry, or sad faces may also still be observed (La Barbera et al., 1976; Soken & Pick, 1999; Striano, Brennan, & Vanman, 2002). In a similar vein, 7-month-old infants habituate more slowly to fearful than to smiling expressions (Nelson, Morse, & Leavitt, 1979). At the same age, a central fearful face will increase saccadic reaction times to a peripheral target compared to a central neutral or smiling face, or even to a neutral face with fearful eyes (Peltola, Leppänen, Mäki, et al., 2009; Peltola, Leppänen, Palokangas, & Hietanen, 2008; Peltola, Leppänen, Vogel-Farley, Hietanen, & Nelson, 2009). Importantly, the effect is not replicated by a neutral face with fearful eyes (Peltola, Leppänen, Vogel-Farley, et al., 2009), or a cheek blowing expression, which is potentially as novel to infants as the fearful expression (Peltola et al., 2008). Taken together, these results suggest that the fearful expression itself is attention-grabbing, although it is always possible that the fearful expression is relatively more novel than other expressions in infancy. Documenting the real-life experience of infants with facial expressions using head-mounted cameras (Sugden et al., 2014) will help in disambiguating these alternative explanations.

The attention holding effect of fearful faces at this age is further demonstrated by stronger orienting responses to fearful than smiling faces as indexed by cardiac deceleration (Leppänen et al., 2010; Peltola, Leppänen, & Hietanen, 2011). However, pupil dilation, another index of orienting and arousal, shows the opposite pattern, that is, stronger response to smiling than fearful faces (Jessen, Altvater-Mackensen, & Grossmann, 2016). Infants also do not appear to experience any overt distress or fear in response to fearful faces. ERP responses in 7- but not 5-month-olds additionally reveal a modulation of the Nc (negative central), an ERP component related to attention (Reynolds & Richards, 2005), by fearful versus happy faces (Jessen & Grossmann, 2015; Leppänen et al., 2007; Nelson & De Haan, 1996). The effect may be observed even when fearful and happy faces are presented below the psychophysical threshold for consciousness (Jessen & Grossmann, 2014, 2015, 2016). Intriguingly, conscious processing of fearful faces is also associated with a modulation in face-sensitive ERPs, suggesting the allocation of increased cortical processing resources (N290, P400; Jessen & Grossmann, 2015; Leppänen et al., 2007).

The fear bias appears to decrease in strength toward the end of the first year of life (Peltola, Hietanen, Forssman, & Leppänen, 2013). Importantly, however, the attentional bias to fear at 7 months is sensitive to individual genetic variations in serotonin synthesis pathways as well as to current maternal stress and depression, which are both relevant to later social-emotional development and function (Forssman et al., 2014), and is predictive of attachment security in toddlerhood as measured in a standardized behavioral task (Peltola, Forssman, Puura, Van Ijzendoorn, & Leppänen, 2015). This suggests that the fear bias at 7 months could act as an early marker of and precursor to social-emotional development.

A robust body of work has demonstrated the emergence of a fear bias between the ages of 5 and 7 months, but it is unknown whether this emergence represents a discrete developmental shift. For example, it has been suggested that the emergence of the fear bias could reflect the onset of functional connections between emotion processing and attentional networks (Leppänen & Nelson, 2009). Animal models additionally suggest that such a shift could correspond to the closing of a critical period for familiarity formation and the onset of fear learning in development (Leppänen & Nelson, 2012). Unfortunately, limitations in the functional neuroimaging of the infant brain during visual tasks and, more specifically, its current restriction to cortical structures on the surface of the brain (Minagawa-Kawai et al., 2008; but see Biagi, Crespi, Tosetti, & Morrone, 2015; Deen et al., 2017; Tzourio-Mazoyer et al., 2002) have prevented from testing this hypothesis directly. Most notably, recent resting-state fMRI studies suggest that functional connections between the amygdala and cingulate and frontal cortices are present at rest from birth (Graham, Pfeifer, Fisher, Carpenter, & Fair, 2015; Rogers et al., 2017; Sylvester et al., 2018); however, it remains unknown whether such functional connections are more active in response to facial emotions (for fMRI data on auditory emotion processing in infants, see, e.g., Blasi et al., 2011; Graham, Fisher, & Pfeifer, 2013).

Alternatively, the emergence of the attentional fear bias at 7 months could reflect the maturation of attentional networks more generally. It has also been proposed that low-level perceptual biases could guide the emergence of attentional biases to fear, followed by fear learning; indeed, there is behavioral evidence for the emergence of perceptual or attentional biases (attention-grabbing, faster detection, or better detection) to threatening stimuli (shape and spider shapes, angry faces, and fearful faces) in young infants both before and after the pivotal age of 7 months (Bayet et al., 2017; DeLoache & LoBue, 2009; Heck, Hock, White, Jubran, & Bhatt, 2016; LoBue, 2012; LoBue & Deloache, 2010; LoBue & Rakison, 2013; LoBue, Rakison, & DeLoache, 2010). Some ERP studies also suggest that some sensitivity to fearful versus smiling faces exists before the age of 7 months, although to a much lesser degree and less robustly so than at 7 months, again suggesting a possibly more continuous development of fear processing during the first year than suggested by earlier studies. For example, a sensitivity to fear has been evidenced by finer analyses of ERP data at 5 months (Yrttiaho, Forssman, Kaatiala, & Leppänen, 2014), and in an object referencing ERP paradigm at 3.5 months (Hoehl et al., 2008).

As studies of young infants tend to be relatively small-scaled (Oakes, 2017), replicating these results in larger, ideally longitudinal samples will be instrumental in uncovering the developmental trajectory of fearful faces and threat perception across the first year of life. Taken together, these results in young infants still provide modest evidence (but see Grossmann & Jessen, 2017) against the notion that the emergence of the attentional fear bias is causally triggered by the onset of locomotion (Heck et al., 2016), as infants are generally unlikely to be mobile as early as 5 months of age. However, as previously suggested (Leppänen & Nelson, 2009, 2012) on the basis of animal models (e.g., Sullivan & Holman, 2010), the developmental time-locking between the onset of a robust perception of fearful faces and threat sensitivity and the onset of locomotion and independent exploration may still have been evolutionary selected for its adaptiveness—even though those events are not directly and causally related in ontogeny.

Categorical Representation of Facial Emotions Across Different Identities

As sensitivity to different facial expressions may be driven by irrelevant features, or be driven by low-level perceptual properties of these expressions, an important line of research has assessed whether and when the perception of emotional facial expressions emerges as truly categorical (for a review, see, e.g., Leppänen & Nelson, 2009; Nelson, 1987). Experimentally, this has involved modifying standard habituation-dishabituation procedures so that the exemplars for each emotional category presented during habituation and test show sufficient variety (e.g., different models). In doing so, the modified habituation-dishabituation task measures the ability to extract the emotion information itself invariantly from model identity or other aspects, i.e., exhibit generalized discrimination (Nelson & Dolgin, 1985). Such identity-invariant, categorical discrimination of smile and several other emotions (surprise, sadness, fear) is clearly evident from 6 to 7 months of age in infants (e.g., Caron et al., 1982; Ludemann & Nelson, 1988; Nelson et al., 1979; Nelson & Dolgin, 1985). However, no evidence has been found for a valence-based categorization of emotional expressions at this age (Ludemann, 1991). An additional way to test for categorical representations of emotional facial expressions is to test for the existence of categorical boundary effects, i.e., stronger dishabituation to novel stimuli that cross the boundary of the habituated category than to novel stimuli that do not, given the same perceptual distance. Again, this approach has demonstrated the existence of a categorical boundary between fear and smiling expressions in 7-month-old infants (Kotsoni, de Haan, & Johnson, 2001).

In addition to these behavioral studies, ERP and fNIRS studies provide insights in the time-course and cortical areas involved in processing emotional facial expressions at 7 months of age. In line with results in adults, fNIRS studies have shown differential responses to angry and smiling expressions in temporal cortical areas, which could correspond to the STS (Nakato et al., 2011). ERP studies have shown differences, in particular larger amplitudes for face- and attention-related components (N290, Nc, P400), in response to fearful compared to smiling or neutral expressions at this age (Jessen & Grossmann, 2015; Leppänen et al., 2007; Nelson & De Haan, 1996; Peltola, Leppänen, Mäki, et al., 2009). However, larger amplitudes for these components were found in older, 9- to 10-month-olds in response to smiling versus fearful or neutral faces (van den Boomen, Munsters, & Kemner, 2019). ERP studies comparing responses to fearful and angry faces (Hoehl & Striano, 2008; Kobiella, Grossmann, Reid, & Striano, 2008; Nelson & De Haan, 1996), or smiling and angry faces (Grossmann, Striano, & Friederici, 2007), have had more mixed results but generally reported different responses to these expressions at 7 months (but see Nelson & De Haan, 1996), as measured by face- and attention-related components (N290, Nc, P400).

Cross-modal matching, suggestive of an abstract representation of emotional categories, has also been evidenced at this age for smiling and angry expressions in behavioral and ERP paradigms (Grossmann, Striano, & Friederici, 2006; Soken & Pick, 1992). Of particular note is a recent ERP study conducted in 9- to 10-month-old infants, which focused on the effect of low (coarse) and high (fine) spatial frequency information in processing smiling, fearful, and neutral facial emotions in infancy (van den Boomen et al., 2019). Low spatial frequency information plays an important role in facial emotion processing in adults (Vuilleumier, Armony, Driver, & Dolan, 2003). However, in that study, face-sensitive components (N290, P400) were found to be significantly modulated by emotion only when high spatial frequency information was presented, with higher amplitudes for smiling than fearful or neutral expressions (van den Boomen et al., 2019). However, an attention-related component (Nc) was modulated by emotion for both low and high spatial frequency stimuli, with a more negative amplitude for smiling than fearful or neutral expressions (van den Boomen et al., 2019). These results are in line with the notion that infants' (Dobkins & Harms, 2014) and children's (Vlamings, Jonkman, & Kemner, 2010) face processing is more reliant on high-frequency information, relative to their acuity, than adults.

Overall, behavioral and neuroimaging studies converge to suggest that the 6–7-month period corresponds to the developmental emergence of emotional facial expression perception abilities organized around a few categories that include smiling, fear, and anger.

Emergence of Contextual Understanding

While younger infants demonstrate sensitivity to some emotional facial expressions, toward the end of the first year of life, infants additionally begin to integrate their perception of facial expressions within their growing understanding of context and social interactions. In particular, toward the end of the first year of life, infants begin to demonstrate at least some understanding of the relations between facial expressions and internal states. For example, 8- to 10-month-old infants expect agents who achieve their goals to display a positive (smile) rather than negative (sad) expression (Skerry & Spelke, 2014). Conversely, 12-month-olds show evidence of expecting agents who look to one of two objects and display a positive expression toward it to reach to that object over another (Phillips, Wellman, & Spelke, 2002). Taken together, these results suggest that toward the end of the first year of life, infants connect positive displays of emotion with achieving goals, which perhaps represents one essential step toward building a theory of mind and an understanding of emotions (e.g., Wu & Schulz, 2018).

In addition, at the end of the first year at least, infants appear to respond more strongly, and possibly attribute a higher positive value, to smiles from their own mother compared to smiles from a stranger (Minagawa-Kawai et al., 2009). More specifically, a fNIRS study found increased activation in the orbitofrontal cortical region of 9- to 13-month-old infants (mean age 11.7 months) in response to their own mother smiling, compared to a neutral expression; less activation was found in response to smiles from a female stranger (Minagawa-Kawai et al., 2009). Because the orbitofrontal cortex is involved in emotion and reward processing, this could mean that infants at this age perceive their mother's smiles as particularly rewarding, indicating that at this age, familiarity and attachment already shape infants' emotional response to smiles.

In addition to an increased contextual understanding of facial expressions in respect to goals and familiar relationships, and in line with their more complex understanding of social situations, infants toward the end of the first year appear to actively seek information from the facial expressions of their caregivers when faced with an ambiguous situation (e.g., a novel toy)—a behavior known as social referencing (Feinman, 1982; Nelson, 1987; Smith & Walden, 1998; Walden & Ogan, 1988). For example, 12-month-olds will actively look for their mother's face in a context of uncertainty and sometimes alter their behavior if the mother displays a negative (e.g., fearful expression) expression (Sorce, Emde, Campos, & Klinnert, 1985).

However, not all infants actually exhibit social referencing in ambiguous situations, and of those who do, not all of them seem to actually use the information gathered to guide their own behavior (e.g., Sorce et al., 1985; also discussed in Nelson, 1987). In more constrained behavioral studies, infants watch an adult display a facial expression directed at one of two novel objects, and the behavior (e.g., looking, reaching) of the infant toward both objects is compared. Even very young (3–6 months) infants demonstrate increased attention to novel objects that were referenced with a fearful or surprised face by an adult, while older (8–9 months and above) infants appear to demonstrate a more contextual and integrated understanding of these situations. That is, older infants do not allocate additional attention to harmless, nonambiguous toys even if they were referenced by an agent with a fearful expression (Hoehl & Pauen, 2011; Hoehl & Striano, 2010; Pauen, Birgit, Hoehl, & Bechtel, 2015). Intriguingly, one emerging finding from this literature has been the notion of a negativity bias, i.e., that infants (and adults) use negative emotions more than positive emotions when learning, attending, and interacting with objects and agents (Vaish, Grossmann, & Woodward, 2008, 2015). While discussing the negativity bias falls outside of the scope of this chapter, it is interesting to note that such bias can be understood as encompassing the perceptual and attentional fear bias found in infants around the age of 7 months. Biases in attention in young infants, and biases in referencing in older infants, could reflect the same underlying bias toward negative valence in attention and learning.

Childhood and Adolescence

Studies examining the development of emotional facial expression perception in childhood and adolescence have typically been complicated by difficulties in equating task difficulty (e.g., verbal difficulty associated with producing or understanding emotion labels) across different age groups or tasks, accounting for differences in variability and noise levels across age groups (e.g., in neuroimaging studies), and teasing out the effects of perceptual, emotional, and cognitive development on task performance. The relative lack of studies targeting early childhood (13–48 months of age) additionally obfuscates the trajectory of facial emotion perception between infancy and childhood. Despite such difficulties, there is now a large body of data documenting typical and atypical developmental trajectories of facial emotion perception during childhood and adolescence.

Typical Trajectories

The perception of facial emotion has been assessed in childhood with a variety of tasks such as sorting, matching, or labeling. Typical performance increases with age but depends heavily on the specific task and facial emotions presented (for a review, see, e.g., Gross & Ballif, 1991; Herba & Phillips, 2004; Vicari, Reilly, Pasqualetti, Vizzotto, & Caltagirone, 2000). For example, performance in facial emotion labeling tasks reflects children's understanding of emotion labels (Vicari et al., 2000). However, understanding emotion labels is not the sole driving force in the development of emotion identification, as emotion identification is generally more accurate for faces than voices in early childhood (Chronaki, Hadwin, Garner, Maurage, & Sonuga-Barke, 2015). Smiling facial expressions are identified earliest and most accurately, followed by angry facial expressions (Durand, Gallay, Seigneuric, Robichon, & Baudouin, 2007; Gao & Maurer, 2009, 2010; Gosselin, Roberge, & Lavallée, 1995; Mancini, Agnoli, Baldaro, Ricci Bitti, & Surcinelli, 2013; Montirosso, Peverelli, Frigerio, Crespi, & Borgatti, 2010; Rodger, Vizioli, Ouyang, & Caldara, 2015; Székely et al., 2011; Widen & Russell, 2003). The identification of sad, neutral, surprised, fearful, or disgusted (often confused with anger in children; Widen & Russell, 2013) expressions follows a more protracted developmental trajectory throughout childhood and up to early adolescence (Camras & Allison, 1985; Gosselin et al., 1995; Mancini et al., 2013; Rodger et al., 2015; Rottman, 2014).

While the driving forces behind these developmental trajectories in childhood remain unclear, it has been suggested that they reflect the progressive refinement of emotional categories, from broad categories of happiness and anger or sadness to subtler emotional distinctions such as disgust versus anger (Widen, 2013; Widen & Russell, 2003, 2008). Studies of the composite face effect (where the processing of a part of a face is impaired by alignment with a counterpart from another face) have additionally shown that children from the age of at least 5 years use holistic (Maurer, Le Grand, & Mondloch, 2002) information for emotional faces identification (Durand et al., 2007). Recent studies have also investigated perceptual thresholds for the identification of emotional facial expressions, using stimuli mixed with noise (Rodger et al., 2015), or expressions of varying intensity (Gao & Maurer, 2009, 2010). Those studies have provided normative data on the thresholds for facial emotion identification in typically developing children and confirmed the higher accuracy for the identification of smiling faces in childhood. The identification of "basic" facial emotions (such as anger, sadness, smiling, or fear) appears adult-like by early adolescence, as measured in such behavioral tasks. In contrast, the identification of complex, social emotions such as contempt or sexual interest continues to develop through adolescence and might be driven by pubertal stage rather than age (Motta-Mena & Scherf, 2017). Intriguingly, there appears to be a paradox between the lower accuracy in identifying fearful facial expressions in childhood, and the early biases to fearful faces found in infancy. While a lower accuracy for fear in identification tasks may sometimes be attributed to its perceptual resemblance with the expression of surprise (Rodger et al., 2015), it appears to persist even when the expression of surprise is not included in the task (e.g., in Székely et al., 2011). This paradox is perhaps related to the higher accuracy for fear that has been reported in 3-year-old children in a perceptual matching task, as opposed to an identification task (Székely et al., 2011). The mechanism explaining the dissociation is unclear, but early biases and perceptual matching may reflect implicit processing, while identification may reflect explicit recognition. In line with comparable results in adults, neuroimaging studies of emotional facial expressions perception using fMRI or MEG in children have uncovered activation in the amygdala (Herba & Phillips, 2004; Hung, Smith, & Taylor, 2012; Thomas et al., 2001), STS (Lobaugh, Gibson, & Taylor, 2006), ventral medial prefrontal cortex (Wu et al., 2016), and FG (Lobaugh et al., 2006). However, activations in dorsal areas such as the ACC appear to develop later and increase with age in childhood and adolescence (Herba & Phillips, 2004; Hung et al., 2012; Phillips, Drevets, Rauch, & Lane, 2003). Interestingly, neutral faces appear to result in greater amygdala activation than fearful faces in children aged of about 9–13 years as measured with fMRI, while the opposite pattern is found in adults (Thomas et al., 2001). Electrophysiological studies have also revealed subtle differences in facial emotion processing between children and adults. For example, it has been reported that early (e.g., P100) ERP components to facial emotions are sensitive to emotion categories in young children, while face-sensitive components (N170) are not sensitive to emotion categories until 14–15 years (Batty & Taylor, 2006). However, the later could be attributed to higher variability in younger groups. About 40–60% of the variability in ERP responses to emotional faces at age 12 is estimated to be of genetic origin (Anokhin, Golosheykin, & Heath, 2010). MEG studies (Hung et al., 2012) reveal a more complex pattern of results, with early (100–150 ms) amygdala activations to unattended smiling and fearful faces in 7- to 10-year-olds compared to neutral faces, but not in 12- to 15-year-olds who instead show fear specific activations in the ACC at early and 100–150 and 250–280 ms (Hung et al., 2012). The complexity of the functional changes in neural activations underlying the development of facial emotion processing in childhood may explain some of the discrepancies between studies (Hung et al., 2012), perhaps especially when grouping together children based on larger age ranges.

Neural structures involved in social cognition or the processing of social stimuli such as faces (the "social brain," Adolphs, 2009; Frith & Frith, 2007) undergo a second period of profound maturation in adolescence (Blakemore, 2008; Nelson, Leibenluft, McClure, & Pine, 2005). The development of the social brain in puberty and adolescence has been proposed to reflect adolescents' increased sensitivity to sociocultural cues in their environment (Blakemore & Mills, 2014) and increased social interest toward peers rather than caregivers (Nelson et al., 2005; Picci & Scherf, 2016). Neural activations to emotional faces are exaggerated in adolescents as a function of pubertal development across multiple regions including the amygdala, fusiform gyrus, extra-striate cortex, thalami, temporal pole, and ventral prefrontal cortex (Guyer et al., 2008; Killgore & Yurgelun-Todd, 2007; Monk et al., 2003; Moore et al., 2012; Nelson et al., 2003; Passarotti, Sweeney, & Pavuluri, 2009; Swartz, Carrasco, Wiggins, Thomason, & Monk, 2014). In particular, amygdala reactivity to threat-relevant (anger or fear) faces increases in adolescence as a function of hormonal changes associated with puberty (Spielberg et al., 2013; Spielberg, Olino, Forbes, & Dahl, 2014). Functional connectivity between the ACC and the amygdala during emotional face perception also appears to shift from positive to negative during the teenage years (Wu et al., 2016).

Atypical Trajectories and Individual Differences

Here we focus on three distinct categories of atypical developmental trajectories, which uniquely illuminate the developmental mechanisms of facial emotion processing: individual differences based on atypical visual or psychosocial experience or deprivation, autism spectrum disorders, and anxiety disorders.

The development of face processing is a largely experience-expectant and activity-dependent phenomenon (Arcaro, Schade, Vincent, Ponce, & Livingstone, 2017; Nelson, 2003; Pinel et al., 2015). However, the evidence for an effect of atypical visual or emotional experience on the development of facial emotion perception is relatively mixed. As an example, adults who suffered early visual deprivation due to congenital cataracts (Maurer, Lewis, & Mondloch, 2005), and who correspondingly show deficits in invariant face recognition or holistic face processing (Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002; Le Grand & Mondloch, 2004; Le Grand, Mondloch, Maurer, & Brent, 2003), also show differences in similarity judgments of facial emotions but relatively mild deficits in facial emotion identification (Gao et al., 2013). These results suggest that the perception of facial emotion builds on face perception and early visual experience but can be acquired despite persistent difficulties in expert, holistic face processing.

Studies of facial emotion perception in children exposed to adverse socio-emotional experience have confirmed the relative robustness of facial emotion perception abilities as these experiences appear mostly to tweak the categorical boundaries and thresholds for identifying specific emotional facial expressions. As an example, 8- to 10-year-old children exposed to profound early psychosocial deprivation from living in an institution early in life only exhibit slightly higher perceptual thresholds for the identification of smiling expressions (Moulson et al., 2015), with no detectable differences in ERP responses to facial emotions at 12 years of age compared to controls (Young, Luyster, Fox, Zeanah, & Nelson, 2017) despite differences in infancy and toddlerhood (Parker, Nelson, & The Bucarest Early Intervention Project Core Group, 2005).

Children who have experienced physical abuse show lower thresholds for identifying facial expressions of anger and higher thresholds for identifying expressions of fear or sadness mixed with anger (Pollak & Kistler, 2002; Pollak, Messner, Kistler, & Cohn, 2009; Pollak & Sinha, 2002). Children with an experience of neglect, however, do show a more general difficulty in differentiating between different facial emotions (Pollak et al., 2000). Overall, the evidence suggests that different experiences can shape or fine-tune the perceptual learning of emotional faces in development, perhaps depending on which facial emotions are most salient in the child's environment (Pollak et al., 2009). However, the resulting differences in identifying emotional facial expression appear relatively mild compared to other social-emotional domains (Moulson et al., 2015; Young et al., 2017) and may be adaptive in the context of the child's environment: as an example, a superior identification of angry expressions at low intensities may allow chronically abused children to predict, and perhaps avoid, new instances of physical abuse. A first implication of these results is that the amount of experience necessary to acquire functional facial emotion identification abilities could be relatively low. A second implication is that the relatively mild differences in facial emotion identification do not appear likely to underlie the larger difficulties in socio-emotional functioning experienced by many children exposed to deprivation or violence (for a discussion, see, e.g., Young et al., 2017).

Research on face perception abilities or impairments in adults and children with autism spectrum disorders (ASD) have generally been inconsistent due to considerable heterogeneity across participants and tasks (Harms, Martin, & Wallace, 2010). At least two recent meta-analyses however have concluded on the presence of a moderate deficit in facial emotion identification in individuals with ASD compared to the general population (Uljarevic & Hamilton, 2013), which may increase with age as improvements in children with ASD lag behind those of their typically developing (TD) peers (Lozier, Vanmeter, & Marsh, 2014). Interestingly, unaffected siblings of children with ASD are also more likely to show mild impairments in facial emotion perception compared to typically developing children (Oerlemans et al., 2014).

ASD is also associated with differences in sensory perception (Ben-Sasson et al., 2009), physiological reactivity (Bal et al., 2010), face processing (Weigelt, Koldewyn, & Kanwisher, 2012), social interest and attention to faces (Grelotti, Gauthier, & Schultz, 2002; Osterling & Dawson, 1994), joint attention (Charman, 2003), theory of mind (Frith, 2001), and emotion awareness (Hill, Berthoz, & Frith, 2004), all of which could contribute to development of deficits in facial emotion perception, discrimination, and identification (Nuske, Vivanti, & Dissanayake, 2013). Thus, a first question is whether deficits in facial emotion identification in ASD can be accounted for by a combination of these differences, or if they reflect a distinct impairment specific to ASD (Nuske et al., 2013).

For example, it has been proposed that deficits in facial emotion identification in ASD may be driven by co-morbid alexithymia, suggesting difficulties in interpreting the emotional meaning of facial expressions (Bird & Cook, 2013; Cook, Brewer, Shah, & Bird, 2013; Hill et al., 2004), perhaps in combination with atypical face processing strategies (Wallace, Coleman, & Bailey, 2008). ERP studies have reported atypical, slower responses of reduced amplitudes to emotional faces in children with ASD (Dawson, Webb, Carver, Panagiotides, & McPartland, 2004; Monteiro, Simões, Andrade, & Castelo Branco, 2017). Faster face-related ERP (N290) latencies to neutral faces in the left hemisphere at age 3 years are associated with improvements in autism symptoms as well as lower autism severity in adolescence (Neuhaus et al., 2016). Another study has reported an association between facial emotion identification performance in young adults with ASD and differences in the amplitude of an early visual ERP component (P1) in response to low-intensity emotional faces (Luyster, Bick, Westerlund, & Nelson, 2019). It may be that only subsets of individuals with ASD, perhaps associated with differential genetic variants, show deficits in facial emotion identification (Nuske et al., 2013). Overall, the evidence suggests that there is an impairment of facial emotion identification in autism, but this deficit is not present in all individuals with ASD and could be accounted for by other impairments or comorbidities.

A second question is thus whether training in facial emotion identification generally improves social functioning in individuals with ASD. Recent research has demonstrated the potential of targeted interventions or assistive technology in remediating facial emotion identification in individuals with ASD (e.g., Bauminger, 2002; Kandalaft, Didehbani, Krawczyk, Allen, & Chapman, 2013). These have included behavioral intervention (Bauminger, 2002), computer games or training software (Cockburn et al., 2008; Silver & Oakes, 2001), virtual reality (Georgescu, Kuzmanovic, Roth, Bente, & Vogeley, 2014), and augmented reality (Chen, Lee, & Lin, 2015). Integrated interventions (e.g., Bauminger, 2002) have targeted a range of social cognitive skills with the goal of facilitating real-life functioning, rather than the improvement of facial emotion identification per se. Further research is needed to determine the relative merit of training facial emotion identification specifically, as opposed to other social-emotional skills, in improving real-life social functioning.

Anxiety disorders, social anxiety in particular, are associated with atypical processing of facial emotions in general and negative facial emotions in particular (Binelli et al., 2014; Brühl, Delsignore, Komossa, & Weidt, 2014; Etkin & Wager, 2007; Freitas-Ferrari et al., 2010; Hattingh et al., 2013; Machado-de-Sousa et al., 2010), in line with disrupted attention to threat-relevant cues (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007). For example, facial emotion identification has been found to be moderately impaired in adults (though not necessarily in children) with anxiety (Demenescu, Kortekaas, den Boer, & Aleman, 2010; Easter et al., 2005; McClure, Pope, Hoberman, Pine, & Leibenluft, 2003; Reeb-Sutherland et al., 2015). Perhaps even clearer is the moderate but specific tendency of anxious participants (including children and adults, clinical and nonclinical participants) to exhibit heightened sensitivity to threat-related emotional faces (e.g., increased detection, attention allocation, difficulty disengaging, or avoidance), in dot-probe or similar behavioral tasks compared to controls (Bar-Haim et al., 2007; Fox, Mathews, Calder, & Yiend, 2007; Georgiou et al., 2005; Mogg, Garner, & Bradley, 2007; Morales, Fu, & Pérez-Edgar, 2016; Puliafico & Kendall, 2006; Roy et al., 2008; Salum et al., 2013; Waters, Mogg, Bradley, & Pine, 2008; Weissman, Chu, Reddy, & Mohlman, 2012).

Such a threat bias is part of a larger pattern of biased emotional processing in individuals with anxiety (Mathews & MacLeod, 2005). Faster latencies or higher amplitudes of ERPs to fearful or angry faces have been found in anxious children and adults compared to non-anxious individuals (Bar-Haim, Lamy, & Glickman, 2005; Eldar, Yankelevitch Roni, Lamy, & Bar-Haim, 2010; Kujawa, MacNamara, Fitzgerald, Monk, & Phan, 2015). These differences are thought to originate from an altered or exaggerated amygdala activity (Bas-Hoogendam et al., 2016; Shin & Liberzon, 2010), and lower activity in regions implicated in attentional control such as the rostral anterior cingulate cortex (Swartz, Phan, et al., 2014). For example, altered reactivity of the amygdala in response to at least some (e.g., fearful, ambiguous or neutral, negative) facial emotions has been reported in adults with social anxiety (Cooney, Atlas, Joormann, Eugène, & Gotlib, 2006), in adults with subclinical tendency toward anxiety (Calder, Ewbank, & Passamonti, 2011; Stein, Simmons, Feinstein, & Paulus, 2007), in adults with social phobia or social anxiety as a function of social anxiety symptoms (Phan, Fitzgerald, Nathan, & Tancer, 2006; Shah, Klumpp, Angstadt, Nathan, & Phan, 2009), in adolescents as a function of anxiety symptoms (Killgore & Yurgelun-Todd, 2005; van den Bulk et al., 2014), or in children with panic or generalized anxiety disorder (Thomas, 2001). Perhaps one of the most consistent findings is the hyperactivation of the amygdala and temporal lobe in response to threatening facial emotions in adults with social anxiety compared to controls (Brühl et al., 2014; Bui et al., 2017; Etkin & Wager, 2007; Freitas-Ferrari et al., 2010; Hattingh et al., 2013; Shah et al., 2009).

Overall, these results suggest that the atypical processing of emotional faces in anxiety disorders reflects more general individual differences in emotional reactivity and negative valence processing (McKay & Tolin, 2017), rather than perceptual differences per se. Thus, the first question is whether individual differences in responses to negative faces may identify individuals at risk for developing anxiety disorders (McKay & Tolin, 2017) and help characterize the neural systems implicated in individual risk for anxiety. Indeed, there is some evidence that heightened responses and attentional bias to threat or emotional faces are present in children at risk for anxiety disorders because of temperament (Fox, Henderson, Marshall, Nichols, & Ghera, 2005; Kagan, Reznick, & Snidman, 1988; Morgan, 2006; Thai, Taber-Thomas, & Pérez-Edgar, 2016), or exposure to maternal or direct stress or trauma (de Haan et al., 2004; Otte et al., 2015; Pine et al., 2005; Taylor-Colls & Pasco Fearon, 2015). A developmental approach is particularly relevant to this endeavor, as anxiety disorders emerge in childhood and adolescence (Beesdo, Knappe, & Pine, 2009) and early emotional regulation difficulties in preschoolers predict later anxiety in childhood (Bosquet & Egeland, 2006).

Animal models suggest that genetic dispositions and stressors occurring during developmental windows of vulnerability may prime individuals to develop anxiety or depressive disorders later in life (Leonardo & Hen, 2008). In the context of facial emotion processing, it is interesting to note that a large-scale study ($N = 338$) of preschoolers with a longitudinal follow-up after 6 months found that shyness and anxiety scores predicted lower emotional faces identification at the first time-point, but also less improvement in emotional faces identification between the two time points, marking a developmental effect of anxiety on facial emotion identification (Strand, Cerna, & Downs, 2008).

Conversely, it has been proposed that attentional biases toward threat and negative emotions in young children may reflect individual (e.g., genetic) risk profiles for the development of anxiety disorders and could act as maintaining factors in anxiety (Eldar, Ricon, & Bar-Haim, 2008). This is especially compelling because attentional biases to threat and negative facial emotions are evident from infancy (Leppänen & Nelson, 2009; LoBue & Rakison, 2013) and thus could be leveraged to predict anxiety risk from an early age, perhaps in association with other risk factors such as low effortful-control or other aspects of temperament and executive function (Helzer, Connor-Smith, & Reed, 2009; Lonigan, Vasey, Phillips, & Hazen, 2004; Morales et al., 2016; Puliafico & Kendall, 2006). For example, behavioral attentional biases toward fearful faces at 12 months were found to be associated with negative affect at this same age, although they were not significantly related to negative affect at later time points (Nakagawa & Sukigara, 2012).

A second question is whether individual differences in responses to negative faces may differentiate between closely related clinical profiles and perhaps predict treatment responses (for a review on neurobiological markers of treatment outcomes in anxiety disorders, including neural responses to emotional faces, see, e.g., Lueken et al., 2016). For example, one fMRI study in adults reported differential patterns of responses to fearful versus angry faces in adults with social phobia versus generalized anxiety (Blair et al., 2008). Another study reported a positive relationship between treatment efficacy and pretreatment amygdala response during a series of facial emotion processing tasks in adolescents with generalized anxiety (McClure et al., 2007; see also Burkhouse et al., 2017). These are very promising results, but a limitation of this approach is that because of its high cost, fMRI is probably not a realistically scalable method for routine clinical assessments. Behavioral metrics, or cheaper neural methods including EEG or fNIRS, could circumvent this issue. However, none of these methods can provide a direct assessment of the reactivity of the amygdala or other limbic and subcortical structures implicated in anxiety and risk for anxiety (but see Bunford, Kujawa, Fitzgerald, Monk, & Phan, 2018). It is encouraging to note that despite this important limitation, at least one EEG study in children with anxiety disorders has reported a relation between treatment efficacy and pretreatment EEG responses during an emotional face processing task (Bunford et al., 2017). Another study using EEG demonstrated increased neural responses to fearful faces in adults with social anxiety restricted to performance situations (McTeague et al., 2018).

On the one hand, differences in facial emotion identification in children and adults with atypical early visual or psychosocial experience have confirmed the relative robustness of facial emotion identification to differential experience, although both visual and psychosocial experience subtly shape this faculty. For example, early visual deprivation affects face recognition more profoundly than facial emotion identification, in accordance with the dissociation of these two abilities. On the other hand, differences in facial emotion processing in children and adults with anxiety or autism spectrum disorders reveal the role of emotion understanding, emotional attention, and attentional regulation, in shaping individual differences in facial emotion processing.

Outstanding Questions

Perceived Emotional Valence of Facial Expressions in Development

Behavioral and neuroimaging studies in infants and very young children have mostly focused on the ability to differentiate between, or differentially respond to, different facial emotions. However, a different question is the degree to which infants and very young children may extract the specific emotional content of these expressions. For example, studies in infants have demonstrated attentional biases toward some negative valence (fear, anger) expressions. However, it is unclear whether infants subjectively experience these faces as emotionally negative. Similarly, very young infants typically attend to smiling faces preferentially, but it is not entirely clear whether they experience these faces as particularly rewarding or simply as familiar.

An approach consists in drawing from the circumplex model of affect in adults (Russell, 1980), i.e., the organization of affects according to the dimensions of valence in addition to arousal, to ask whether children can extract the valence of facial emotions and how the representational space of facial emotions develops over time (Russell & Bullock, 1985, 1986). This line of inquiry has led to interesting insights. Most strikingly, children as young as 2 years appear to spontaneously organize facial emotions along a two-dimensional space that roughly corresponds to the dimensions of valence and arousal (Russell & Bullock, 1985, 1986). However, the children's labeling of facial expressions has suggested that they may only gradually learn to differentiate among different negative expressions (Russell & Widen, 2002; Widen, 2013; Widen & Russell, 2003, 2008). More recent approaches in adults have proposed additional dimensions to inferred emotional experience (e.g., certainty, morality, safety) that more closely account for neural responses, i.e., an appraisal space that comprises more dimensions than valence and arousal (Skerry & Saxe, 2015). Because the dimensions of this proposed appraisal space (Skerry & Saxe, 2015) have varying degrees of abstraction (e.g., others' knowledge, distant past; versus expectedness, pleasantness), it would be interesting to see how social experience, cognitive, and theory of mind development affect the dimensions of perceived emotions across development in early childhood.

The attribution of valence to facial expressions of emotions by preverbal participants is more difficult to study, due to limitations in infants' behavioral repertoire. For example, 7-month-old infants do not appear to discriminate negative from positive facial emotions, although 10-month-olds show signs of doing so (Ludemann, 1991). Because infants cannot provide verbal reports of their own experience of emotions, it is thus tempting to turn to reverse inference for clues to the perceived emotional valence of facial emotions in infants (but see, e.g., Anderson & Adolphs, 2014, for an alternative approach in nonverbal animals that does not rely on subjective reports or reverse inference). For example, neuroimaging results (Goksan et al., 2015) have been used to infer the nature of the experience of pain in newborns. In the same vein, one may infer from the orbitofrontal activation observed in infants watching videos of their own mothers' smiling that they attribute a particularly positive valence to these smiles (Minagawa-Kawai et al., 2009). However, this approach is generally limited by at least two factors.

One limitation concerns the relative inaccessibility of many cortical and subcortical (e.g., the amygdala) regions involved in emotion processing by usual methods of neuroimaging in awake infants (EEG and fNIRS; but see, e.g., Deen et al., 2017; Tzourio-Mazoyer et al., 2002; Weaver, 2015). These areas may also undergo significant functional changes over development, which limits the validity of reverse inferences comparing the localization of neural activity in infants and adults or even children. A second limitation concerns the complex nature of emotion and valence attribution. With the exception of a few candidate areas (e.g., the ventral medial prefrontal cortex and positive valence; Lindquist, Satpute, Wager, Weber, & Barrett, 2016), there are no areas of the brain whose isolated activity clearly and reliably distinguishes emotions or even valence (as opposed to co-activation patterns or single-neuron activity, e.g., see Lindquist et al., 2016; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Namburi et al., 2015; Wager et al., 2015): emotion pervades subjective experience. A similar argument can be made from the field of linguistics, as very few languages have grammatical structures dedicated to the expression of affects only. Instead, the expression of affects often parsimoniously borrows from existing grammatical structures such as those used for the expression of action, possession, or being acted upon (Hagège, 2006). Thus, it seems unlikely that an unambiguous marker of valence, let alone specific emotions, may be reverse inferred from neural measures. Overt behavior provides an additional set of cues. For example, contraction of the facial muscle corrugator supercilii has been used as a nonverbal indicator of negative valence in newborns (Trapanotto et al., 2004). Conversely, it is striking that 7-month-old infants differentiate between several facial expressions of emotion and exhibit an attentional bias to the expression of fear, yet do not show any behavioral sign of distress to negative facial emotions such as angry or fearful faces. This suggests that infants may not experience these faces as negative in valence. Another behavioral indicator of valence attribution by infants comes from the information that infants appear to extract from facial expressions: for example, the association of smiling with achieving a goal (Skerry & Spelke, 2014), or liking a specific object (Pauen et al., 2015; Phillips et al., 2002). While such approach does not require verbal reports, it remains constrained by infants' cognitive and behavioral limitations. Despite these challenges, and independently of the experienced valence of facial emotions by infants, perhaps the association of genetic variants or dimensions of attachment and temperament with infants' neural or behavioral responses to negative and positive facial emotions (Forssman et al., 2014; Grossmann et al., 2011; Peltola et al., 2015) can provide the most compelling evidence for a developmental continuity of positive and negative valence processing systems from infancy. For example, increasing numbers of stressful life events currently affecting infant's mothers are associated with larger attentional biases to fear as measured behaviorally (Forssman et al., 2014), suggesting that even at this early age, attentional biases to fear faces might be driven by or reflect emotional functioning. A converging argument for the relative continuity of emotional experience from infancy to early childhood might be made from the relative developmental stability of functional networks involving the amygdala during this period (Gabard-Durnam et al., 2018). Future longitudinal work linking early measures of facial emotion processing to multiple markers of emotional functioning or understanding, possibly longitudinally and across multiple types of facial emotions, will help establishing the emotional quality of early facial emotion processing and its relevance to emotional functioning.

Commonalities and Variations in Facial Emotion Identification Across Cultures

There is a universal propensity to perceive emotions expressed through facial movements. Early cross-cultural work on facial emotion perception has often emphasized this pan-cultural aspect by advancing the notion that a small, shared, core set of "basic" facial emotions are universally identified and produced in a similar fashion across cultures (Ekman, 1980; Ekman & Friesen, 1971; Ekman, Sorenson, & Friesen, 1969). More recent research, however, has begun to uncover fascinating cultural variations in the perception of facial expressions of emotion (Barrett, Lindquist, & Gendron, 2007; Chen & Jack, 2017; Gendron, 2017; Gendron, Roberson, van der Vyver, & Barrett, 2014; Nelson & Russell, 2013).

As an example, Eastern and Western observers differ in their responses when labeling random facial expressions displayed on artificial faces (Jack, Garrod, Yu, Caldara, & Schyns, 2012; Jack, Sun, Delis, Garrod, & Schyns, 2016) and in their scanning patterns to emotional faces (Jack, Blais, Scheepers, Schyns, & Caldara, 2009). Such differences in scanning patterns to emotional faces between Eastern and Western observers can be found in infants as early as 7 months of age (Geangu et al., 2016). Perhaps even more striking is the interpretation and usage of the wide-eyed, gasping "fear" face with direct gaze as an expression of anger and interpersonal threat in some cultures, as demonstrated by a study of facial emotion perception in adolescents from the Trobriand Islands in Papua New Guinea (Crivelli, Russell, Jarillo, & Fernández-Dols, 2016). Smiles, in contrast, were readily identified by these participants (Crivelli et al., 2016). This suggests an intriguing possibility that the attention-grabbing, canonical "fear" face may be universally perceived as indicative of a threat but that its specific interpretation (perceived threat versus threatening display) varies across cultures. This could potentially explain the relative lag in the explicit understanding of fearful (versus angry) faces in young children, despite early biases toward this expression. Alternatively, the "fear" face may have been "culturally recycled" for their attention-grabbing property, acquiring a new meaning in Trobriander culture through cultural evolution. While the relative degree to which facial emotion perception varies across cultures remains controversial (Sauter & Eisner, 2013), these converging results open a new area of investigation to uncover how and why specific facial expressions acquire new, cultural meanings in development and over cultural time, while others (such as the smile) may be identified universally and relatively early in development (Chen & Jack, 2017; Gendron, 2017; Nelson & Russell, 2013). Insights and methods from the quantitative, psychological science of culture, language, and cultural evolution (Barrett et al., 2007; Greenfield, 2013; Michel et al., 2011; ojalehto & Medin, 2015) may prove instrumental in tackling such problems in future work.

Conclusion

The ability to perceive, discriminate, and identify emotional facial expressions appears remarkably robust. Yet, the cultural usage and fine-grained interpretation of emotional facial expressions exhibit exquisite variations. The perception of facial emotion develops in a nonlinear fashion, with critical aspects coming on line around the age of 7 months, followed by a more protracted emergence of contextual understanding and a refinement of emotional labels over late infancy and childhood, with additional improvements in interpreting more complex facial emotions occurring in adolescence. The perception of smiling is notable by its developmental precedence and possible universality. Fearful faces remarkably evoke increased attentional and perceptual responses in infancy, with implications for understanding the neural circuits underlying individual liability for anxiety as fearful or angry faces have proven useful to probe individual differences in attention to threat. Fearful expressions are paradoxically hard to identify for young children, perhaps due to their higher cognitive difficulty and lower familiarity. Future research may help clarifying the cognitive and neural processes involved in interpreting, rather than perceiving or discriminating, facial emotions, which could help specify and disentangle the mechanisms by which differences in culture, emotion understanding abilities, or experience, differentially affect this ability.

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