CHAPTER 9

The Perception of Facial Expressions of Emotion

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Humans communicate social and motivational internal states through complex dynamic nonverbal facial signals that have been shaped by *biological*, *evolutionary*, and *social* constraints. The mutual understanding of emotion plays a critical functional role in regulating human social interactions. These communicative signals can be expressed voluntarily or involuntarily and typically involve dynamic facial expressions that rapidly unfold from one expressive signal to another. As perceivers, we decode and interpret the meaning of these signals and act on this interpretation. A facial signal of fear may prompt us to become more alert to our environment for potential threats of danger, or a facial signal of displeasure may indicate that a conciliatory response is necessary to facilitate a desired social outcome or improve social bonds.

How accurately we interpret facial expressions of emotion is critical to the quality of our relationships and social functioning (e.g., Denham et al., 2003). Consequently, facial expressions of emotion are commonly understood as *biologically* relevant communicative social signals (Frith, 2009; Jack & Schyns, 2015). Their significance in social communication is thought to have evolved in part as a method of nonverbal communication between conspecifics (Fridlund, 1994). Originally, facial expressions may have had behavioural advantages for the person expressing the emotion, for example, through sensory regulation by increasing or decreasing the perceiver's sensory exposure to the environment (e.g., opening the eyes wide for the expression of fear or closing the nostrils in disgust; Susskind et al., 2008). With the developing awareness that others perceived and understood their expressions, those expressing the emotion could also choose to control what were previously involuntary expressions adapted for sensory regulation (Parkinson, 2005). As both expressor and perceiver became aware that their expressions are *socially* communicative signals, expressions no longer needed to be tied to their original behavioural function and evolved to be understood as emotional signals within the context of social communication (Frith, 2009). Through *evolutionary* pressure, facial expressions

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have also developed to become as orthogonal as possible, minimising the overlap in diagnostic information between each expression to generate distinct communicative signals that can be optimally decoded by those perceiving them.

The brain perceives, decodes, and interprets these visual signals of emotion by recruiting multiple distributed neural systems that subserve emotion recognition. Visual and emotional pathways are engaged during the processing of expressions (e.g., Vuilleumier & Pourtois, 2007). However, the precise mechanisms, processes, and representations involved in these neural activations continue to be debated (Frith, 2009; Said, Haxby, & Todorov, 2011). Considering the evolution of facial expressions as a social communication system, some form of neural substrate is thought to have evolved for processing faces (Kanwisher, 2000) and emotional expressions (Leppänen & Nelson, 2009), which shall be discussed in 'The Development of Facial Expression Recognition'.

Two fundamental distinctions are made between subcortical mechanisms that bypass the primary visual cortex, which involve coarse and automatic processing of transient and salient features, and the occipital and temporal visual neocortical processing streams (Adolphs, 2002). The subcortical route involves the superior colliculus, the pulvinar, and the amygdala, and is important for general face processing but is not specific to fear processing as previously thought (see Chapters 3 and 19 for details). A subcortical connection between the pulvinar and the amygdala is involved in early but not late visual processing (Garvert, Friston, Dolan, & Garrido, 2014), with the anterior insula and ventral medial prefrontal cortex playing a critical role in the processing of all emotions (Xu, Peng, Luo, & Gong, 2021). In the subcortical route, the amygdala's primary involvement is to extract emotional significance from facial expressions. The amygdala enhances vigilance towards emotionally salient stimuli, aiding in the rapid recognition of fear- or threat-related facial expressions (Adolphs, 2002). The pulvinar is thought to play a role in the integration of emotional information across different sensory modalities, due to its connectivity with different brain regions (Vuilleumier, Armony, Driver, & Dolan, 2003). However, its specific role in emotion recognition is still an active area of research and more studies are required to fully understand its function. The superior colliculus is known for its role in visual processing, particularly in the generation of eye movements and the orientation of attention. This brain structure also contributes to the processing of emotional facial expressions through its involvement in attention and gaze direction (e.g., Vuilleumier et al., 2003).

To date, the cortical neural networks implicated in facial expression processing have largely been described within overarching models of general face perception, which include the occipital face area (OFA) and fusiform face area (FFA) in the ventral pathway, and the posterior superior temporal sulcus (pSTS) and inferior frontal gyrus (IFG) in the dorsal pathway. Early models, developed before many human neuroanatomical studies were available, distinguished between the brain's processing of invariant versus variant visual information from the face (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000). Invariant visual information, such as face identity, was thought to involve an OFA-to-FFA processing pathway that is distinct from the OFA-to-pSTS pathway implicated in the processing of variant information, such as facial expressions. More recent findings have demonstrated that the purported distinct functional pathways for identity and expression processing in earlier models are not supported by neuroimaging data, as the ventral stream, previously attributed to the processing of invariant information uniquely, also contributes to facial expression processing via the FFA (for a review, see Bernstein & Yovel, 2015). Conversely, the dorsal pathway, previously thought to process variant information exclusively, is more responsive to dynamic compared to static faces, and is therefore also thought

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to be involved in the processing of identity information conveyed by dynamic faces more specifically. Given these recent findings, Duchaine and Yovel (2015) proposed a revised neural framework for face processing, which includes two distinct pathways that interact. The ventral route, including the OFA, the FFA, and the anterior temporal lobe, processes form information (e.g., age, identity) but also responds to static facial expressions. The dorsal stream, which comprises the pSTS, the anterior superior temporal sulcus (aSTS), and the IFG, is tuned to both form and motion information, such as dynamic facial expressions (e.g., Richoz, Jack, Garrod, Schyns, & Caldara, 2015). The processing of emotional and non-emotional information from the face does not therefore involve entirely distinct neural networks as previously thought.

As noted at the beginning of this section, current research continues to debate the precise mechanisms, processes, and representations involved in the neural activations responding to emotional faces. Similar debate has surrounded the question of whether specific facial expressions of emotion produce specific or overlapping activations in the brain. This debate will be touched on after examining how faces signal emotions and the historic promotion of basic emotion theory in the literature.

Facial Expressions of Emotion as Visual Signals

This chapter focuses on different factors shaping the perception and decoding of facial expressions of emotion, and provides, where possible, an overview of the brain's interpretation of these signals. To begin with, we shall briefly consider how these nonverbal dynamic social signals are produced, as this is pertinent to the understanding of predominant research methods and current advances in the field.

The contraction of specific muscles in the face produces distinct spatio-temporal dynamics that render expressions of emotional signals in humans and animals. Facial features briefly change form with muscle movement, and this change in form can express or disguise our current experience of emotion. Each facial expression of emotion is produced by the activation of its own unique pattern of muscles. This activation may vary in intensity, leading to an expression that is perceived as more or less pronounced. In the nineteenth century, Darwin (1872) observed that changes in the appearance of faces (i.e., facial expressions) were similar amongst a wide range of species. This observation had, and still has, strong conceptual implications on the production of facial expressions of emotion, as Darwin concluded that this similarity between animals and humans must be due to shared ancestral – biological – roots, inherently promoting a universal explanation for expression production. Studies showing that people with congenital blindness spontaneously produce some prototypical expressions, or that facial expressions are present in utero (Reissland, Francis, Mason, & Lincoln, 2011), have been suggested as further evidence of universality (Matsumoto & Willingham, 2009; Tracy & Matsumoto, 2008). However, counter-evidence suggests that such individuals learn about regularities between facial movements and emotional states through other sensory modalities and direct instruction (see Bedny & Saxe, 2012 for a review).

In the twentieth century, Paul Ekman and Wallace V. Friesen (1978) adopted an anatomical taxonomy to systematically measure facial muscle movements: the Facial Action Coding System (FACS). The FACS was used to develop FACS-coded image databases that are still used in current facial expression research. Within this system, each muscle movement is defined as an individual action unit (AU), and each facial expression is composed of the movement of a unique set of AUs. This systemised coding of facial AUs has facilitated the reproduction and analysis of expressions in diverse research domains, which has been widely employed due to these features (Cohn & Ekman, 2005; Jack & Schyns, 2015).

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Since Eckman's early studies, the long-running debate concerning the universality of basic emotions has endorsed the biological – universal – nature of facial expressions. Most notably, a large body of cross-cultural studies using the six basic FACS-coded expressions – happiness, fear, anger, disgust, sadness, and surprise – has led to the predominant view in emotion research that these six expressions represent universal 'basic emotions' (e.g., Ekman, Sorenson, Friesen, 1969; Ekman et al., 1987). Evidence from researchers questioning universality has continued to develop since the initial Ekman studies. These developments provide greater understanding of cultural and individual differences in facial expression recognition, which we shall subsequently discuss in more detail. Significant advances in research methods have also helped to achieve these important theoretical developments.

Psychophysical methods have been used in recent years to parametrically determine the *quality* and *quantity* of visual signal necessary to achieve facial expression recognition (Bayet et al., 2017; Rodger, Lao, & Caldara, 2018; Rodger, Vizioli, Ouyang, & Caldara, 2015; Stoll et al., 2019; Wyssen et al., 2019). *Bubbles*, a low-bias sampling reverse correlation technique, has been used to identify the diagnostic information of each of the six basic facial expressions of emotion (e.g., the mouth for happiness, the eyes for fear; Smith, Gosselin, Cottrell, & Schyns, 2005). These findings have demonstrated that the face, as a transmitter, maximises orthogonal emotional signals that poorly overlap and have low correlations between them (i.e., they are highly distinguishable) to decrease ambiguities and increase categorisation performance. The results have also demonstrated that the perceiver, as a decoder, further decorrelates these signals. A novel response classification technique using a genetic algorithm to sample expression space has more recently been developed to overcome one of the limitations of the Bubbles method: the large number of trials it requires (Binetti et al., 2022). This technique can determine an expression's diagnostic information with only a few hundred trials and highlights the importance of individual differences in information use to categorise expressions. Importantly, the decoding of these unimodal – visual – static or dynamic facial expressions of emotion is not superior in the deaf expert visual system. This suggests that these signals do not benefit from the multimodal knowledge associated with facial expressions in the hearing population, at least when decoded in the visual modality uniquely (Rodger et al., 2021; Stoll et al., 2019). Finally, recent cross-cultural studies using a novel data-driven, dynamic, FACS-based Generative Face Grammar have provided evidence that, contrary to previous beliefs, FACS-coded expressive faces do not represent universally understood signals of emotion (Jack, Caldara, & Schyns, 2012; Jack, Garrod, & Schyns, 2014) but are specific to Western facial expressions. Ultimately, the inherent properties of facial expressions of emotion as highly variant, dynamic signals dependent on social context (Aviezer et al., 2008) require continuous monitoring to draw meaningful inferences. These properties naturally give rise to multiple potential interpretations of what the expressions signal and how they are represented according to the perceiver. Overall, this research has shown that a unique set of FACS cannot account for human diversity in the communicative expression of emotional signals and the complex ecological contextual settings, which characterise the social interactions of everyday life (Barrett, Adolphs, Marsella, Martinez, & Pollak, 2019).

Together, these recent findings give impetus for greater consideration of the stimuli employed to represent facial expressions of emotion, a development that is currently emerging within the research domain and will be discussed in the final section. Facial expression research has gradually moved towards more deeply examining the multifarious nature of what facial expressions signal and how they are decoded. In the next sections we shall discuss how facial expression recognition develops throughout infancy and

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childhood, how experience influences the recognition of facial expressions, the recognition of dynamic versus static facial expressions, and developments in ecological experimental designs. To conclude, we will consider five outstanding questions and challenges for the field, after considering the evidence for whether specific neural activations can be associated with specific facial expressions of emotion.

Neural Activations Associated with Facial Expressions of Emotion

Guided by Basic Emotion Theory, neuroimaging studies have largely examined whether recognition of each of the six basic emotions elicits specific neural activations. Findings have shown that certain neural patterns are associated with the processing of different emotions; however, these activations are not completely distinct (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). Functional MRI (fMRI) and electroencephalographic studies have shown that there is some overlap in the neural circuits activated by different emotions. For example, regions like the amygdala and insula are often implicated in the processing of a range of emotions rather than being specific to one emotion, such as fear and disgust, as previously thought (Pessoa & Adolphs, 2010; Uddin, Nomi, Hébert-Seropian, Ghaziri, & Boucher, 2017). A meta-analysis of the brain basis of emotion revealed that during emotion perception the main regions showing consistent activation (including the left ventrolateral prefrontal cortex, the right occipitotemporal cortex, the dorsomedial prefrontal cortex, the insula, amygdala, and dorsal anterior cingulate cortex) had increased levels for not one but several or all of the basic emotions (Lindquist, Jackson, Leshin, Satpute, & Gendron, 2022).

Evidence for the role of the different brain regions implicated in specific emotions, however, has also been provided from studies of patients with brain damage. An early study revealed that patients with bilateral amygdala damage had poorer performance in fear recognition compared with healthy controls, leading to the common belief that the amygdala has a specific role in fear processing (Adolphs, Tranel, Damasio, & Damasio, 1994). Similarly, impaired recognition of disgust in patients with insula damage (Calder, Keane, Manes, Antoun, & Young, 2000; Phillips et al., 1997) led to the initial belief that the insula's role was specific to disgust recognition. Since these earlier studies, understanding of these regions has developed. The amygdala's role in visual processing, similarly to that of the pulvinar, is now known to involve the coordination of functional cortical networks in the evaluation of biologically relevant affective stimuli (Pessoa & Adolphs, 2010).

While there is ongoing research into the neural correlates of different emotions, and progress has been made in identifying common patterns associated with certain emotions, it is essential to recognise the complexity and variability in emotional processing. The field of affective neuroscience continues to explore how different brain regions contribute to the experience and recognition of emotions.

The Development of Facial Expression Recognition

The adaptive decoding of facial expressions of emotion is fundamental to the development of an infant's and child's social understanding. As such, many studies have investigated facial expression recognition abilities during infancy. Interest in infant studies originally stems from the question of whether the ability to recognise facial expressions of emotion is innate – biologically rooted – or develops with experience. Theoretical accounts of recognition ability have traditionally alternated between nativist perspectives of an innate preparedness to recognise 'basic emotions' (e.g., Ekman, 1994) and empiricist accounts, which highlight the role of experience in developing these abilities (e.g., Russell, 1994).

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Behavioural studies have shown that within the first few months of life infants are able to discriminate between some facial expressions; one study revealed that infants as young as 36 hours old could discriminate between happy, sad, and surprised expressions posed by a live model (Field, Woodson, Greenberg, & Cohen, 1982). Face detection in noisy stimuli at 3.5 months old is boosted when faces are fearful compared to happy (Bayet et al., 2017). Happy expressions are discriminated from early infancy (Farroni, Menon, Rigato, & Johnson, 2007), and can be categorised – that is, examples of the same expression can be grouped together – from 7 months onwards (Safar, Kusec, & Moulson, 2017). However, it is important to note that the discrimination of an expression does not equate to recognition of the emotional state being expressed. There is also growing evidence that other negative expressions can be categorised from 7 months onwards (see Ruba & Repacholi, 2020 for a review of preverbal infants' understanding of discrete facial expressions of emotion). Behavioural studies therefore find evidence of both early facial expression processing abilities and of the development of these abilities during infancy.

Developmental neuroimaging studies have critically fed into the debate of nativist versus experiential perspectives of face-processing abilities by assessing evidence of domain-specific face-processing regions in the infant brain, or of the need for further development of these neural systems. The inherent challenges of conducting neuroimaging studies with young infants have determined that such studies remain limited in number. Of those that do exist (see Bayet & Nelson, 2020 for a review), the findings indicate some functional specificity for faces in 4- to 6-month-old infants. At this age, the right-hemisphere neural response is stronger for faces, including those of different expressions and genders, compared with other complex object stimuli such as houses, animals, or fruit. This response is observed at 1.2 Hz on electrode P8, where the N170 is found in adults (de Heering & Rossion, 2015). Sensitivity to facial expressions has been shown in 7-month-old infants for specific ERP components, such as the N290, P400, and Nc components, as amplitudes vary according to the combinations of expressions presented (Leppänen, Richmond, Vogel-Farley, Moulson, & Nelson, 2009; Poncet et al., 2022; Xie, McCormick, Westerlund, Bowman, & Nelson, 2018).

From early childhood onwards, a greater range of behavioural and neuroimaging methodologies are evidently available to investigate facial expression recognition abilities. Behavioural studies have typically sought to measure changes in recognition performance throughout development to identify at which age specific emotions can most accurately be recognised. While different tasks, age ranges, and stimuli have yielded heterogeneous findings, the concordant findings are that facial expression recognition does not develop uniformly for each expression throughout childhood (see Figure 9.1) and that this development is protracted (Herba & Phillips, 2004; Rodger et al., 2015, 2018).

As described, categorical abilities for happiness emerge in early infancy. This expression's unique status as the easiest emotion to recognise is sustained throughout childhood and into adulthood, with ceiling effects for the recognition of happiness frequently found (Figure 9.1; Herba & Phillips, 2004; Rodger et al., 2015; Richoz, Lao, Pascalis, & Caldara, 2018). This facility with happiness could be related, in typically developing children, to our frequent exposure to smiling faces during early childhood combined with the visual distinctiveness of happiness from other expressions (Calvo & Marrero, 2009). By contrast, fear is consistently found to be one of the most difficult expressions to recognise, especially in paradigms using multiple expressions as it is frequently miscategorised as surprise (e.g., Rodger et al., 2015, 2018). This suggests that for optimal recognition of fear additional information is required, perhaps from several modalities and/or of a contextual or temporal nature. In addition, most

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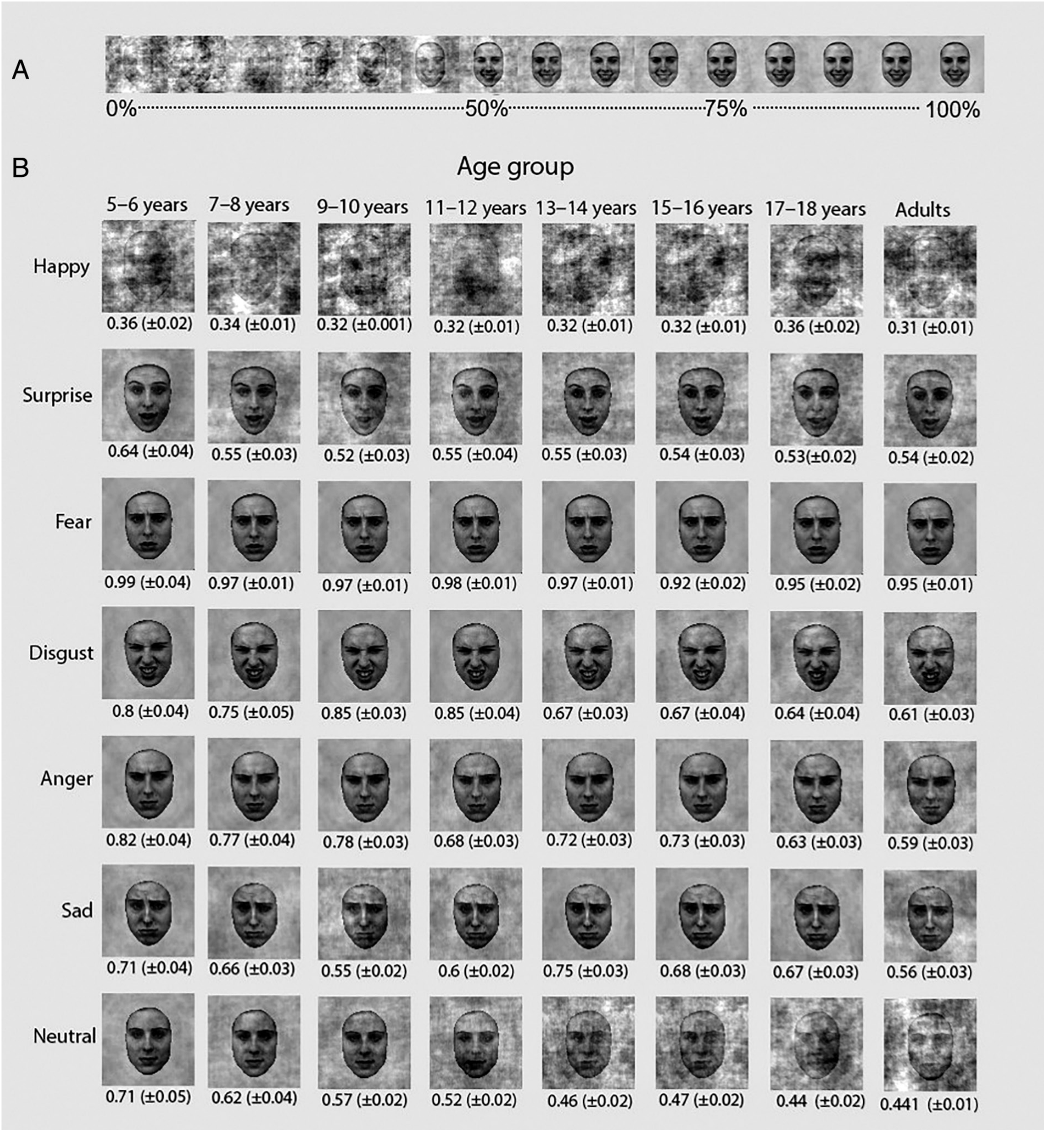

Figure 9.1 Mean recognition signal thresholds across development. (A) Signal strengths ranging from 0% to 100% (for image purposes the signal strength increments in steps of 6.66%) for the expression of happiness. (B) Mean recognition signal thresholds for each emotional expression per age group. Numbers in parenthesis report the ± standard errors of the mean. Happiness was recognised with the lowest signal strength across age groups. Fear was recognised with the highest signal strength across age groups (Rodger et al., 2015).

developmental findings are based on studies using adult facial expression stimuli. More studies using own-age faces are necessary as the question of whether there is an own-age advantage for the recognition of some, or all, expressions during development continues to be debated (e.g., Hauschild, Felsman, Keifer, & Lerner, 2020).

In alignment with behavioural studies of school-aged children, neuroimaging findings show protracted development in the neural systems subserving facial expression processing. Again, similarly to behavioural studies, most neuroimaging studies are cross-sectional as opposed to longitudinal, which limits conclusions about the

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exact nature of development (Bayet & Nelson, 2020). Studies have found neural responses to emotional faces in the amygdala (e.g., Thomas et al., 2001), superior temporal sulcus (STS), and fusiform gyrus (Lobaugh, Gibson, & Taylor, 2006) are frequently comparable to those in adults but also show some differences. In a rare longitudinal study of children at the ages of 10 and 13 years, roughly corresponding with pre- and post-puberty as identified by self-report, activity in the amygdala, thalamus, and visual cortical areas at age 10 was found to increase in magnitude and extent by age 13 (Moore et al., 2012). At 13, pubertal development was also correlated with stronger face responses in the temporal pole, the ventrolateral prefrontal cortex, and the dorsomedial prefrontal cortex. The enhanced responses in the amygdala, hippocampus, and temporal pole in early adolescence compared to late childhood indicates an association between pubertal development and the neural processing of socio-emotional stimuli. Further studies have also revealed significant neuroanatomical development during adolescence, a period marked not only by the onset of puberty, but also by changes in social experiences and a widening social environment that includes closer peer relationships, all of which have an important impact on social cognition. Imaging studies of brain areas implicated in social cognition show that grey matter volume reaches its peak around the onset of puberty and thins out during the remainder of adolescence (Burnett & Blakemore, 2009). Together, these developments in the face-sensitive cortices of the brain reveal that specialisation for facial expression perception develops into adulthood, so while there is evidence of face-specific regions in infancy, domain specificity increases during adolescence up to adulthood (Kadosh & Johnson, 2007; Leppänen & Nelson, 2009).

Finally, theoretical models of the development of facial expression processing reconcile the dichotomy of face-specific versus domain-general processing by proposing two potential mechanisms that underpin emotion processing. These mechanisms incorporate both nativist and empiricist theoretical perspectives of biological preparedness and experience for this ability: an experience-expectant mechanism and an experience-dependent mechanism (Leppänen & Nelson, 2009). They suggest it is possible that we have evolved to ‘expect’ some emotional expressions due to their presence throughout evolutionary history. Therefore, brain mechanisms may have evolved that are biased towards processing emotionally salient signals from the face. The early maturation of emotion-related brain circuits, functional coupling of these circuits with cortical perceptual areas, and behavioural evidence of attentional biases for emotional compared to neutral facial expressions are cited as evidence that is compatible with a foundational experience-expectant mechanism for emotion recognition in the developing brain. The role of experience in the development of emotion recognition, which shall be further discussed in the following section, is underpinned by an experience-dependent mechanism that is necessary for the development of a mature system. Our perceptual representations of facial expressions are therefore initially coarsely specified and develop into a mature system with adult-like specificity only through exposure to species-typical emotional expressions.

The Influence of Experience on Facial Expression Recognition

As we have seen, the recognition of emotion from faces is a complex process that develops over an extended period and is influenced by many factors. The predominant view in the emotion literature, as we have discussed, has been the ‘basic emotion’ theory in which facial features and muscle movements are necessary and sufficient cues to recognise the emotion a person is experiencing (e.g., Ekman, 1994). Over time, however, alternative, constructivist views, which hold that experience and contextual information influence emotion

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perception are necessary for emotion recognition, have continued to reveal evidence in support of this view (e.g., Aviezer et al., 2008; Barrett, Lindquist, & Gendron, 2007; Russell, 1994).

A non-exhaustive list of factors shown to influence the development of facial expression recognition include emotional experience (e.g., Pollak & Kistler, 2002), cultural experience (e.g., Caldara, 2017), and socio-economic experience (e.g., Caspi, Taylor, Moffitt, & Plomin, 2000; Goodyer, 2002).

Emotional Experience

A number of studies have shown the disruption caused to typical development by species-atypical parenting and social deprivation, providing evidence for the experience-dependent nature of facial expression processing (Pollak & Kistler, 2002). By testing different developmental cohorts, including children who had grown up in hostile environments and were exposed to physical abuse and those who had not, the effect of emotional experience on emotion processing was revealed. Children from hostile environments consistently recognised anger more rapidly, or with fewer physical cues, than those from non-hostile environments. Moreover, the children studied had similar socio-demographic and family backgrounds, with the exception of the experience of physical abuse, so the explanation of this heightened sensitivity for anger recognition in comparison to other emotions included in the study reveals that affective experience can influence our perceptual representations of emotions.

Neuroanatomical studies of children who have experienced early life adversity have found differences in the brain regions implicated in socio-emotional functioning compared with those who have not. Hand-tracing of the amygdala and hippocampus from MRI images of children with three different types of early life adversity – physical abuse, early caregiving neglect, and low socio-economic status – showed smaller amygdala volumes in children from these three groups, as well as smaller hippocampal volumes in children who had experienced physical abuse or who were from low socio-economic households (Hanson et al., 2015). A recent review of the effects of childhood maltreatment on the brain emphasises structure, function, and connectivity are all impacted by adverse experiences, with consistent findings of heightened amygdala responses to threatening stimuli, and diminished ventral striatal responses to anticipated or received rewards (Teicher, Samson, Anderson, & Ohasi, 2016). However, understanding of the neurobiological mechanisms that underpin the effects of adverse experiences is still limited (Smith & Pollak, 2021).

Culture

Experience is heavily shaped by culture. Humans adapt to their environment through a unique amalgamation of culture and biology. Historically, it has long been presumed that across cultures humans perceive the world in a comparable manner, viewing objects and attending to salient information in similar ways. Recently, however, a growing body of literature has disputed this notion by highlighting fundamental differences in perception between people from Eastern (China, Korea, and Japan) and Western cultures, even for important biologically relevant tasks such as face recognition and the decoding of facial expressions of emotion (e.g., Blais, Jack, Scheepers, Fiset, & Caldara, 2008; for a review, see Caldara, 2017). With biological and evolutionary origins, facial expressions of emotion have long been considered hardwired human behaviour. The universality in decoding facial expressions of emotion was mainly based on findings that all facial expressions were categorised above chance level by different cultures, while ignoring the large statistical differences in performance across intercultural groups (Izard, 1971). In the past decade, this common assumption has been challenged by studies investigating whether the transmission of emotional signals is universally achieved across cultures. An early study monitored the eye

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movements of Western and Eastern observers while they decoded facial expressions of emotion from Western and Eastern faces (Jack, Blais, Scheepers, Schyns, & Caldara, 2009). By using novel spatio-temporal analysis to extract the occurrence of systematic eye movement sequences, the findings provided the first demonstration that observers from different cultures use different eye movements to decode facial expressions of emotion (see Figure 9.2). Westerners sample all facial features whereas Easterners persistently fixate the eye region, which causes significantly greater confusions in emotion decoding (i.e., between fear and surprise, and between anger and disgust). This difference resonates with the use of emoticons across cultures whereby Easterners code transitions of expressions from happy to sad with the eyes – that is, ^_^ and T_T – while Westerners do so with the mouth – :-) and :-(.

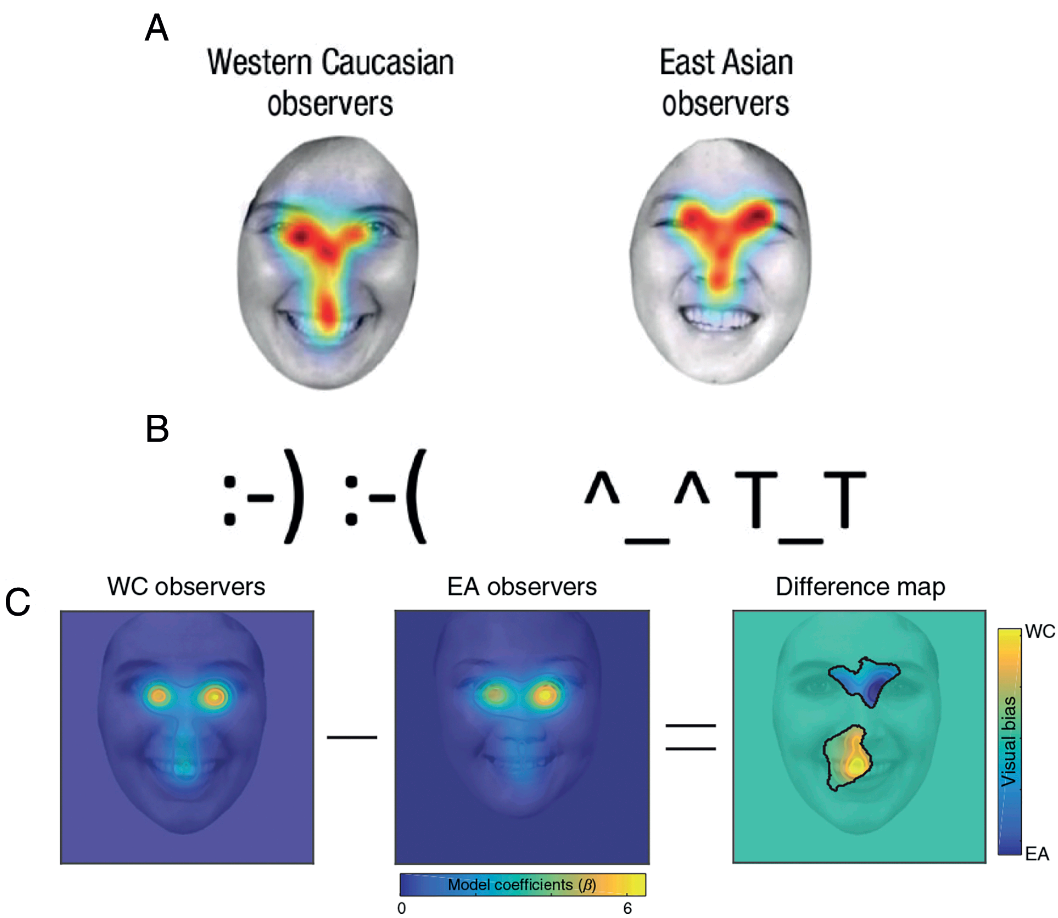

Figure 9.2 Fixation patterns and emoticons reflecting cultural differences in emotion-expression recognition and transmission, respectively. (A) Shown are Western Caucasian (WC) and East Asian (EA) fixation distributions averaged across the six basic emotion expressions (happiness, surprise, fear, disgust, anger, and sadness) plus a neutral expression. The averaged pattern is displayed on a happy expression for illustration purposes only (Jack et al., 2009). Note that Eastern observers did not fixate the mouth even for the happy expression. (B) Illustration of the distinctly different emoticons used by each culture to convey expressions of emotion (here, happy and sad, respectively; Yuki, Maddux, & Masuda, 2007), which accord with these observations. (C) Shown is a similar pattern of fixation distributions observed in Western Caucasian and East Asian 7-month-old infants (Geangu et al., 2016). Adapted from Caldara (2017).

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Using a psychophysical technique (four-dimensional reverse correlation) to estimate the spatio-temporal dynamics of the cultural and observer-specific internal representations of the six basic facial expressions of emotion, the results confirmed that Eastern observers coded facial expressions of emotion based on information from the eye region, whereas Western Caucasian observers more frequently used the mouth (Jack, Garrod, Yu, Caldara, & Schyns, 2012). More recently, these cultural differences were shown to be already present in 7-month-old infants (Geangu et al., 2016). Together, these findings demonstrate that culture shapes the development of perceptual strategies for processing facial expressions of emotion from an early stage in life. More recently, facial expression recognition of the six basic emotions, using the seminal Ekman Western database (Ekman & Friesen, 1976), was also tested across 12 *occidental* countries (Quesque et al., 2022), revealing significant differences in recognition performance even among countries sharing Western cultures. Overall, these cross-cultural findings have shown that future studies need to adapt the stimuli according to the culture of the participants. Otherwise, biases are found that are not representative of the participants' actual capacity for emotion recognition and instead represent differences in their mental representations of these expressions.

To date, fully cross-cultural neuroimaging studies investigating the processing of facial expressions of emotion are scarce. Findings show that cultural differences in transmitting and decoding facial expressions of emotion are reflected in the representational structure of the right fusiform gyrus (Brooks, Chikazoe, Sadato, & Freeman, 2019), which mirrors cross-culture differences in the conceptual structure of emotions. Fear generates larger amygdala activations when expressed by members within the same cultural group (Chiao et al., 2008). More recently, Harada et al. (2020) reported that greater activations in the bilateral amygdala relate to in-group biases during the evaluation of negative expressions. Some cross-cultural neurofunctional signatures have also been found for positive expressions (Park, Tsai, Chim, Blevins, & Knutson, 2016). For example, European Americans show greater bilateral ventral striatal activations associated with reward and affect while viewing excited versus calm expressions, whereas Chinese participants showed greater activity in response to calm versus excited expressions. However, to the best of our knowledge, the literature is still missing a comprehensive study investigating the neural bases of cross-cultural differences for the recognition of the six basic facial expressions of emotion. This is an important theoretical gap that needs to be addressed. Likewise, how facial expressions of emotion are transmitted and decoded by the many different cultures of the world is largely unexplored (e.g., studies in the African continent are lacking). Future large-scale behavioural and neurofunctional comparative studies are necessary to progress understanding of this important question. Such studies could provide novel insights into human diversity and the very nature of social communication signals, and the evolutionary forces behind them.

Individual Differences

Until recently, individual differences in human behavioural science have been considered as a source of *noise* in data rather than *signal*. Many psychological theories have been developed based on *average* group effects. However, research in face recognition has been increasingly addressing individual differences in face identity processing and is now beginning to investigate this issue in facial expression processing. Eye movement studies have been critical to this work, as they provide a functional signature of how various perceptual tasks are achieved by feeding the neural system with diagnostic information for a given task to a specific observer. During face recognition, it has been shown that the idiosyncratic facial features fixated longer elicit unequivocal stronger neural face discrimination

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responses (Stacchi, Ramon, Lao, & Caldara, 2019). This neural tuning occurred regardless of the difference in observer-specific preferred facial features (e.g., eye versus mouth lookers). Effective processing of identity therefore involves idiosyncratic, rather than universal, face representations and refutes the concept of a single face representation format shared across observers.

Relevant findings on individual differences in facial expression processing have initially been provided by studies investigating the ongoing question of how eye movement strategies relate to emotion recognition performance (Rodger, Sokhn, Lao, Liu, & Caldara, 2023; Yitzhak, Pertzov, Guy, & Aviezer, 2020). As specific expressions have distinct diagnostic information (Smith et al., 2005), it has been assumed that to recognise an emotional expression this information must be processed. However, recent studies have also revealed that consistent idiosyncratic fixation strategies can achieve comparable recognition performance, and that some individual fixation strategies do not appear to process diagnostic information (Yitzhak et al., 2020). This observation has underlined the importance of using extra-foveal paradigms to establish whether diagnostic information is processed parafoveally. Recent findings suggest that observers largely rely on foveated visual sampling strategies, as the recognition strategies for natural viewing versus restricted gaze-contingent viewing appear similar (Rodger et al., 2023). Future studies are required to verify whether this observation is maintained at the individual level. Overall, these observations suggest the existence of idiosyncratic rather than universal face representation formats to decode facial expressions of emotion as has been found for identity (see Figure 9.3).

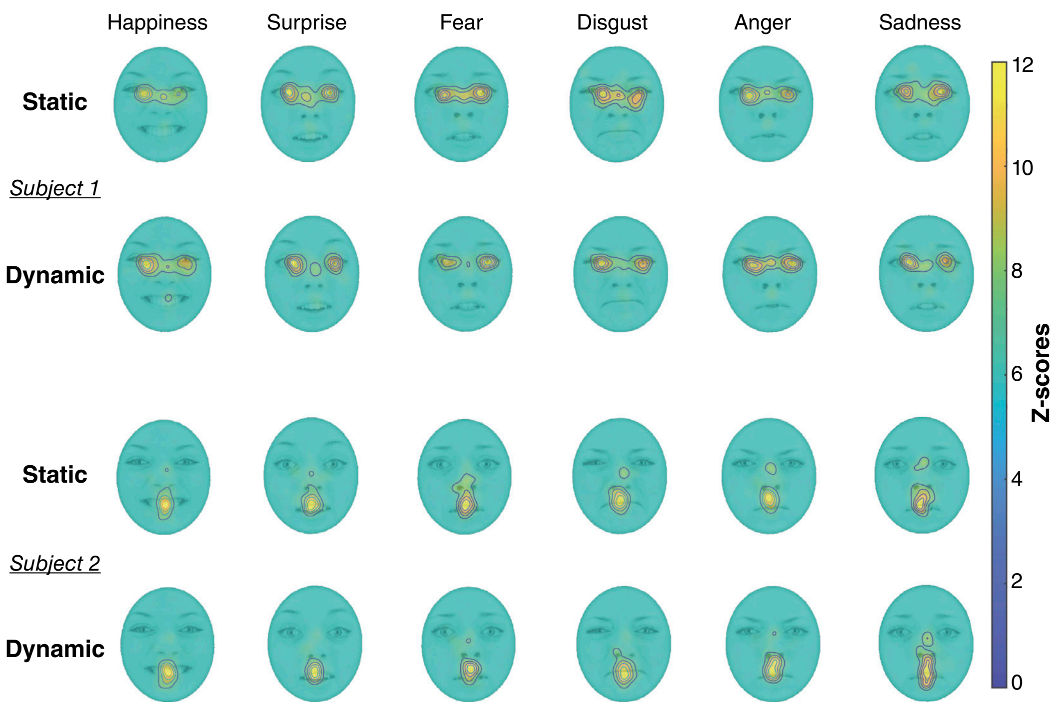

Figure 9.3 Fixation patterns acquired during the recognition of the six basic static and dynamic facial expressions of emotion for two observers (subjects 1 and 2). Areas showing a significant statistical probability of fixation are delimited by a violet border ($Z > 4.25$ corrected for multiple comparisons; $p < 0.05$). The observers show idiosyncratic visual sampling strategies (subject 1, eye looker; subject 2, mouth looker), while reaching similar behavioural recognition performance. Notably, the presentation of static or dynamic faces did not modulate the nature of the fixation idiosyncrasies. Data from Paparelli, Sokhn, Stacchi, Coutrot, Richoz, and Caldara (2024).

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A recent study using a novel genetic algorithm also confirmed the existence of significant individual differences in the representations of different emotional expressions. The method allows participants to select three-dimensional (3D) facial expression images that most closely represent their own mental images of a specific expression using a genetic-algorithm toolkit (Binetti et al., 2022). Crucially, this method overcomes the challenge of representing the high-dimensional space that facial expressions occupy, which is too large to be fully tested by conventional paradigms. By combining genetic algorithms with photorealistic 3D avatars, the sampling of the multidimensional space of facial expressions is reduced as participants select the images most closely representing their mental image of a specific facial expression. Across a large sample of participants, the findings revealed that there are large individual differences in the expressions defined by participants from a typical adult population, and that these differences account for differences in recognition performance. Differences in emotion responses may not, therefore, reflect differences in the mechanisms subserving recognition, but rather differences in individuals' categorical representations of emotions.

These findings imply not only differences across cultures in the representations of emotional expressions but also individual differences within specific adult populations, which underlines the importance of using representative stimuli. Recent theoretical perspectives in emotion research reflect these findings in individual differences in the representations of emotional expressions. They argue that emotion categories are non-entitative; that there is no consistent 1:1 mapping between specific emotion categories and dedicated biological mechanisms. Instead, emotion categories name populations of instances that are variable (Lindquist, Jackson, Leshin, Satpute, & Gendron, 2022). In this way, emotion categories are conceived of as inherently heterogeneous, with adults using multimodal and contextual signals to categorise these instances in their own, often unique, way.

The Recognition of Static versus Dynamic Facial Expressions

The transmission of facial expressions of emotion is temporally and hierarchically optimised to be socially advantageous (Jack et al., 2014). However, surprisingly, while real-life social interactions are flooded with dynamic signals, most of the scientific literature and knowledge about facial expression recognition has been developed with the use of static face images. This scientific bias towards the use of static images can be partly accounted for by both technological limitations typical of early research in facial expression recognition, and the subsequent replicability of these studies. Technology has now extensively evolved, and dynamic stimuli can easily be acquired and implemented in experimental designs. Surprisingly, this progress in technology is not yet paired with greater use of these means in this field of research, as the large majority of studies continue to use static rather than dynamic face images. Knowledge about the processing of dynamic expressions is therefore lacking. Importantly, of the studies that have been conducted using dynamic facial expressions, evidence from different perspectives is beginning to converge, which suggests notable differences in the processing of these distinct types of communicative emotional signals.

From an *evolutionary* perspective, both human and non-human animal brains are naturally tuned to perceive and interpret dynamic visual information, as living organisms have primarily been exposed to dynamic inputs throughout evolution. The perception of static images, by contrast, is unique to humans and represents a relatively recent cultural development, given that static images are human-made artefacts. In particular, the perception of static faces is a recent emergence in human history, with early examples such as painted portraits originating in ancient Egypt. While static representations of faces—through paintings, statues, and later photography have gradually become more common, regular and widespread exposure to static faces has only truly intensified in the past century with

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the advent of cameras and, more recently, digital technologies and social media. As a result, our perceptual systems are primarily adapted to dynamic rather than static visual inputs. Equally, during the first years of life, infants are much more frequently exposed to dynamic emotional signals as opposed to static signals. Considering our daily *exposure* to dynamic faces, as well as *evolutionary* and *ontogenetic* perspectives, common intuition would predict greater expertise in decoding dynamic compared to static emotional face signals (Richoz et al., 2024).

Relatively few studies have investigated the question of whether there is a dynamic advantage for facial expression recognition and, to date, the findings have been equivocal (for a review, see Krumhuber, Kappas, & Manstead, 2013). Behavioural studies have found a dynamic advantage for expression recognition in suboptimal viewing conditions (for a review, see Dobs, Bulthoff, & Schultz, 2018), complex stimuli (Namba, Kabir, Miyatani, & Nakao, 2018; Zloteanu, Krumhuber, & Richardson, 2018), and in both clinical (e.g., Atkinson, Dittrich, Gemmell, & Young, 2004; Schaefer, Baumann, Rich, Luckenbaugh, & Zarate, 2010) and neuropsychological populations (Adolphs, Tranel, & Damasio, 2003; Humphreys, Donnelly, & Riddoch, 1993; Richoz et al., 2015; Yitzhak, Gilaie-Dotan, & Aviezer, 2018). Other behavioural studies have found that any dynamic advantage is minimal (e.g., Gold et al., 2013) or inexistent (e.g., Christie & Bruce, 1998; Fiorentini & Viviani, 2011). However, recently it has been demonstrated that when visual information is limited, dynamic signals are more effective and sensitive than static ones in decoding facial expressions of emotion (Richoz et al., 2024). This advantage cannot be accounted for by low-level properties because spatial frequency, contrast, and the total energy transmitted over time were comparable across modalities.

Also, few studies have investigated how recognition of static and dynamic facial expression recognition evolves throughout the lifespan. Findings from developmental studies that have compared static and dynamic facial expression recognition have shown ambiguous results; none have found a dynamic advantage and two studies found higher performance with static stimuli (Nelson & Russell, 2011; Widen & Russell, 2015). Similarly, only very few studies of ageing adults have compared performance for static versus dynamic facial expressions (e.g., Grainger, Henry, Phillips, Vanman, & Allen, 2015). Of these studies, findings have tended to show a dynamic advantage, but the study designs were largely limited to a subset of facial expressions or participants were not tested across both conditions, which precludes firm conclusions being made about a dynamic advantage in the elderly population. In a large lifespan study of static and dynamic expression recognition of the six basic emotions, children and elderly adults showed better recognition of dynamic compared to static expressions (Richoz et al., 2018). However, elderly participants' recognition of static expressions was poor, which prompted the greater difference in recognition rates, as opposed to an increased ability to recognise dynamic facial expressions (see also Ruffman, Kong, Lim, Du, & Tiainen, 2023). These findings therefore invite caution when drawing conclusions from the sole use of static face images with elderly populations.

Dynamic cues provide noticeable improvement in facial expression recognition for people with neuropsychological and clinical conditions. The additional cues that dynamic faces provide may enhance motor simulations and indicate to participants where shifts in attention to different facial features are required. In this way, attention might more easily be diverted towards the diagnostic information of an expression in a bottom-up fashion (i.e., the mouth for surprise), whereas static images might incline participants to move towards such information based on top-down internal representations. Findings from patients with brain damage have shown higher performance for dynamic facial expressions of emotion (e.g., Humphreys et al., 1993; Yitzhak et al., 2018). A recent study of a patient, PS, with acquired prosopagnosia and an impaired performance for static facial expressions,

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found that – with the exception of fear – her performance was within the normal range for recognition of all other emotions when they were presented dynamically. Her impaired performance for static facial expressions therefore suggests that her information use with static faces is suboptimal, as she focuses on the lower part of the face (Fiset et al., 2017), whereas with dynamic faces, she extracts information from all facial features (Richoz et al., 2015). This finding, combined with the location of her lesions, provides evidence for distinct cortical pathways in the processing of static and dynamic face information (Bernstein & Yovel, 2015; Duchaine & Yovel, 2015). PS's advantage for the recognition of dynamic facial expressions might rely on an intact functional cortical pathway directly connecting the early visual cortex to the pSTS, and subsequent processing in the aSTS (see Figure 9.4).

Brain-imaging studies have further shown that dynamic facial expressions of emotion elicit larger activations in brain areas crucial for processing social and emotional information. In comparison to static emotional faces, dynamic faces show greater responses in the fusiform gyrus (e.g., Kessler et al., 2011; Trautmann, Domínguez-Borràs, Escera, Herrmann, & Fehr, 2013), the STS (e.g., Kessler et al.,

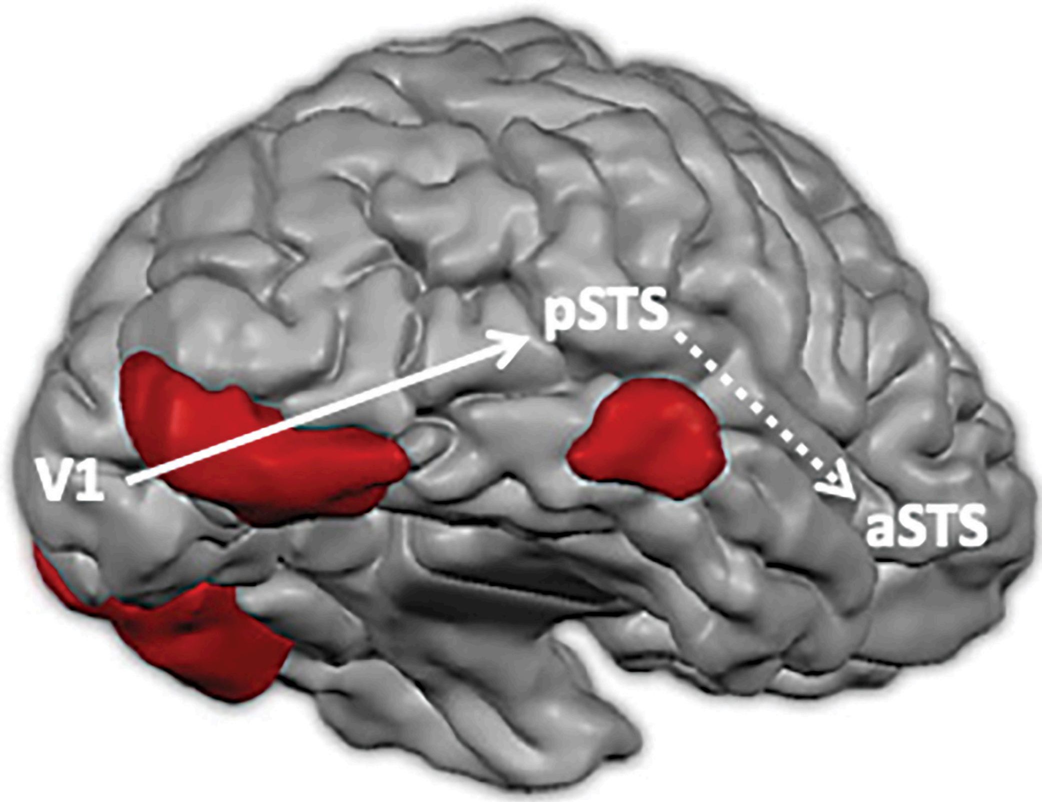

Figure 9.4 Ventrolateral view of PS's lesions visualized on 3D cortex reconstructions following the segmentation of the grey matter boundary. The lesioned regions are displayed in red. Richoz et al.'s (2015) results point towards the existence of a direct and functionally distinct cortical pathway connecting the early visual cortex to the pSTS. This neural pathway would not require structural information from the right inferior occipital gyrus to decode expressions effectively because this region is damaged in patient PS. This advantage for directly processing dynamic visual inputs seems to be specific to facial expressions, as patient PS cannot recover identity through dynamic visual information in everyday life. Adapted from Sorger, Goebel, Schiltz, and Rossion (2007).

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2011), the IFG (e.g., Trautmann, Fehr, & Herrmann, 2009), and the visual motion area, V5, in the occipitotemporal lobe (e.g., Johnston, Mayes, Hughes, & Young, 2013). Increased activity for dynamic information in the STS and in the visual motion area supports findings from previous studies evidencing involvement of these regions in processing biological motion (Peelen, Wiggett, & Downing, 2006; Puce & Perrett, 2003). Interestingly, a very recent fMRI study using multivoxel pattern analysis revealed that dynamic facial expressions of emotion elicit increased activation in face-selective regions (OFA, FFA, pSTS) and motion-selective areas, as well as higher categorisation accuracies compared with static facial expressions of emotion (Liang et al., 2017).

Critically, previous findings from PS, the patient with prosopagnosia and a bilateral lesion encompassing the right OFA (Richoz et al., 2015), showed a clear dissociation between the impaired decoding of static and preserved decoding of dynamic facial expressions of emotion, as well as the existence of a direct pathway between the early visual cortex to the pSTS. However, future studies are necessary to further clarify the neural bases of dynamic facial expression processing and potentially promote movement towards the more ecological use of dynamic faces in the study of facial expression recognition.

Towards Ecologically Valid Experimental Designs

At the beginning of this chapter, we described how the predominant view of facial expression recognition (also referred to as the classical or common view; Barrett, Adolphs, Marsella, Martinez, & Pollack, 2019) – that our faces convey internal emotional states through different facial-muscle configurations, which can be interpreted and recognised as specific emotional expressions – has directed facial expression research and its methods since its inception. Early findings of universally recognised emotional expressions using methods and stimuli available at the time have since undergone robust critiques, including the use of exaggerated stereotypical expressions and forced-choice paradigms (Keltner, Sauter, Tracy, & Cowen, 2019), as more advanced methods and stimuli have been developed. Multiple developments and their combination in the questions and methods used have led the field towards more ecologically valid research. Some of these advances have been discussed over the course of this chapter and will be recapitulated here, along with other advances that will be briefly highlighted to provide an overall summary of the general movement within the field towards more ecologically valid experimental designs.

Developments in the use of dynamic stimuli, discussed in the previous section, have been made, but there is still much to be done as paradigms using dynamic stimuli remain in the minority. The commonalties and specificities across behavioural results, mental representations, and neuronal bases of processing dynamic and static facial expressions of emotion are still unclear and require future work. The developmental section revealed the need to incorporate more studies using age-matched stimuli for children because the majority of studies have used adult-face databases due to their wider availability. Cross-cultural studies have also revealed the importance of using stimuli that accord with a specific culture's mental representations of the emotional expressions being studied, as findings have revealed differences in these mental representations. The field is still lacking standardised ecologically valid stimuli that could optimally probe recognition performance for distinct task manipulations and cultures. Another consideration is the range of expression stimuli used; up until now, most studies have investigated recognition of the six basic emotions, leaving much work still to be done to understand more complex emotion types or how expressions interact with other non-emotional, socially communicative facial signals. The role of

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context has similarly gradually gained consideration, as studies have revealed that the same emotional expressions are categorised differently according to contextual cues (Aviezer et al., 2008), but again this remains limited to select studies. While this chapter's focus is the perception of facial expressions of emotion, it is important to note that there has also been progress in understanding emotional expression signals from other modalities, including the voice (Chapter 11), olfaction (Chapter 13), and the body (Chapter 10). However, the field still has ground to make in the use of multimodal stimuli for a more complete understanding of emotion recognition, which to date has been mainly adopted by computing and AI fields.

Along with diversification in the stimuli being used to investigate facial expression recognition, there has been movement towards the use of methods that sample a wider stimulus space and therefore enable greater correspondence with the mental representations of the emotional expressions of the participants navigating this space. Findings from this movement signify that, as there are individual differences in the mental representations of emotional expressions, there is not a 1:1 correspondence between images of expressions and how they are categorised within relatively similar adult populations (Binetti et al., 2022). These individual differences could also explain differences in recognition performance. Therefore, performance differences could be reflective of differences in the extent to which a stimulus is recognised as an instance of an emotion category, rather than of the mechanisms underlying emotion processing. A recent theoretical perspective, the cultural evolutionary perspective, echoing these findings in individual differences, posits that emotion categories are non-entitative; that there is no consistent 1:1 mapping between specific emotion categories and dedicated biological mechanisms. Instead, emotion categories are conceived of as naming populations of instances, so are inherently heterogeneous (Lindquist et al., 2022).

In sum, current understanding of facial expression processing is largely based on findings from static Western-standardised emotional expressions. More ecologically valid experimental designs simultaneously tracking visual information sampling and use are now necessary to further elucidate our understanding of these idiosyncratic mental representations that are tuned by experience and culture. These experiments should be coupled with ecologically valid, culturally tuned stimuli to probe current research questions in the field.

Outstanding Questions

- Most of the knowledge of facial expression recognition arises from standardised static face images, with posed and exaggerated prototypical expressions. How existing behavioural, computational models, and brain findings generalise to dynamic and multimodal ecological stimuli remains to be determined.
- Most of the knowledge of facial expressions of emotion is based on Western average group results, using static Western Caucasian faces. How the many different human cultures worldwide transmit and decode facial expressions of emotion remains to be determined.
- The role and origins of individual differences in mental representations of facial expressions of emotion and their generalisation to face processing remains to be understood.
- Most of the knowledge of facial expression recognition is based on decontextualised basic facial expressions of emotion. We should increase knowledge on the processing of other more complex emotions, as well as their processing in ecologically contextualised settings.
- The use of recent technological advances in experimental designs (e.g., virtual reality) and statistical analytical tools (e.g., deep learning) should increase knowledge on the transmission and decoding of facial expressions of emotion.

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