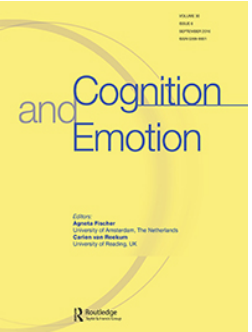

Cognition and Emotion

ISSN: 0269-9931 (Print) 1464-0600 (Online) Journal homepage: https://www.tandfonline.com/loi/pcem20

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COGNITION AND EMOTION, 2016
Vol. 30, No. 6, 1081–1106, http://dx.doi.org/10.1080/02699931.2015.1049124

Perceptual and affective mechanisms in facial expression recognition: An integrative review

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(Received 8 May 2014; accepted 2 May 2015)

Facial expressions of emotion involve a physical component of morphological changes in a face and an affective component conveying information about the expresser's internal feelings. It remains unresolved how much recognition and discrimination of expressions rely on the perception of morphological patterns or the processing of affective content. This review of research on the role of visual and emotional factors in expression recognition reached three major conclusions. First, behavioral, neurophysiological, and computational measures indicate that basic expressions are reliably recognized and discriminated from one another, albeit the effect may be inflated by the use of prototypical expression stimuli and forced-choice responses. Second, affective content along the dimensions of valence and arousal is extracted early from facial expressions, although this coarse affective representation contributes minimally to categorical recognition of specific expressions. Third, the physical configuration and visual saliency of facial features contribute significantly to expression recognition, with "emotionless" computational models being able to reproduce some of the basic phenomena demonstrated in human observers. We conclude that facial expression recognition, as it has been investigated in conventional laboratory tasks, depends to a greater extent on perceptual than affective information and mechanisms.

Keywords: Facial expression; Recognition; Emotion; Affective priming; Perception.

Theoretical issues and research questions

Emotional facial expressions consist of morphological changes in a face, such as frowning, widening the eyes, pulling lip corners up-and-backwards, lip stretching or tightening, nose wrinkling or opening the mouth, among others (Ekman, Friesen, & Hager, 2002). These expressive changes are assumed to reflect a person's internal feelings and emotions, motives and needs, intentions and action tendencies (Ekman, 1992). For expressions to fulfil a communicative and adaptive function in social interaction, they should convey reliable information about the expressers' internal states, so that these can be "read out" from the face by observers. But what information of facial expressions allows viewers to identify them and makes some expressions more recognisable than others? There are two major aspects in this question: the nature of the

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information that is encoded when people observe facial expressions and the contribution of such information to expression recognition. In this review, we will focus on the functional mechanisms of facial expression recognition and aim to provide answers to the following questions:

1. *Are facial expressions recognised as distinct categories?* To answer this question, we first review the relevant evidence of expression recognition, as indexed by behavioural and neurophysiological measures. Next, we discuss how different methodological aspects may influence the findings and address whether categorical face perception is dependent on cultural context.
2. *Is affective (appetitive versus aversive) value automatically extracted from facial expressions in non-sensory systems, and is such affective processing functional for expression recognition?* To answer this question, we review data from behavioural studies using explicit and implicit measures of affective processing and relate them to chronometric information stemming from neurophysiological work on event-related potentials (ERPs).
3. *What visual information is critical for expression recognition, and how perceptual processes contribute to expression recognition?* To answer this question, we review the evidence obtained with computational models of expression processing and discuss the role of characteristics such as visual saliency or the frequency of perceptual exposure to facial expression features.

From an information-processing perspective, there are two major components of emotional expressions: the physical facial features and configuration and the affect they are assumed to convey. Processing of the physical facial features in the inferior and superior temporal cortices can lead to visual recognition and assignment of category labels such as "anger" or "fear" to a facial configuration (e.g., Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2000). This process is coined as expression recognition. Yet, the affective information reflecting the appetitive or aversive properties of faces is coded to a significant extent outside the sensory cortices, such as the amygdala and the mesolimbic reward circuit (Haber & Knutson, 2010; LeDoux & Phelps, 2008; Vuilleumier, 2009). Thus, only the *physical* facial features are initially available to visual perception, and *affective* encoding of faces requires non-sensory processing of the visual input. Consequently, a critical issue in facial expression recognition is the degree to, and order in, which it relies on perceptual versus affective information. In a general sense, this relates to the affective versus semantic primacy debate (e.g., Nummenmaa, Hyönä, & Calvo, 2010; Storbeck, Robinson, & McCourt, 2006; Zajonc, 1980), as applied to facial expression processing.

Understanding expression recognition from categorical and dimensional viewpoints

Explicit expression recognition in categorisation tasks is typically operationalised as the assignment of a facial stimulus to an emotion or expression category. In such tasks, "recognition" involves observers' matching their responses with predefined categories. Expression categorisation and discrimination are thus cognitive processes whereby some properties in a facial configuration are perceived as being or not being shared by other configurations, and therefore the various stimuli are classified into the same or a different category. Which of such properties are encoded and used by observers as a criterion for expression categorisation and discrimination? And what is the contribution of properties involving visual information relative to those involving affective information?

These issues can be addressed within the general context of the categorical versus dimensional conceptualisations of emotional facial expressions. According to the *categorical* view (Ekman, 1992; Ekman & Cordaro, 2011; Izard, 1994; Levenson, 2011; Panksepp & Watt, 2011), viewers readily perceive discrete basic emotions from particular physiognomic changes in the facial musculature. For example, a happy expression is characterised by a smile with mouth corners pulled up and backwards, cheek raising, wrinkles around the eyes, or anger is characterised by frowning, lid tightening and lip tightening/pressing, etc. (Ekman et al., 2002). Proponents of the categorical view typically consider six basic expressions: happiness, anger, sadness, fear, disgust and surprise, which are assumed to be culturally universal and rooted in biological adaptive functions. In contrast, the *dimensional* (Russell, 1994) and *constructionist* (which originates from the dimensional account; e.g., Barrett, 2006; Lindquist & Gendron, 2013) views question the existence of basic expressions and the correspondence between facial muscle configurations and discrete emotion expression and perception. Rather, all expressions would be initially processed along an affective continuum on two orthogonal dimensions: valence (pleasantness versus unpleasantness) and arousal (calmness versus tension). Expression category would subsequently be "constructed" by interpreting visual patterns as a function of contextual information, and by selecting an available verbal and conceptual label for the facial configuration.

These models deal with our major issues (i.e., what information is encoded and functional for expression recognition) differently. For the *categorical* approach, the morphological changes in faces would be critical for the recognition of expressions, as each expression is presumably associated with a characteristic perceptual configuration. Such visual properties would automatically convey affect-specific information about internal states of the expresser, which would also be encoded. Given that this conceptualisation assumes a direct link between specific patterns of expressive changes and specific emotional states, it does not strictly separate the relative contribution of perceptual and affective information to expression recognition. In contrast, for the *dimensional* approach, lower-order affective dimensions (valence and arousal) are assumed to be automatically encoded. However, this information would not correspond directly with specific morphological changes in the face. Accordingly, expression recognition would constitute a strategic process: the perceptual and the affective information are interpreted by means of semantic knowledge and contextual information, which would make the greatest contribution to the categorisation of specific expressions. Thus, neither the visual features nor affect alone would be sufficient for expression recognition. In the following sections we will review the evidence obtained with different paradigms that is relevant to these conceptualisations and to answer our basic questions.[1]

ARE FACIAL EXPRESSIONS RECOGNISED AS DISCRETE CATEGORIES?

The majority of prior studies on expression recognition have used categorisation paradigms in which viewers must choose a verbal label (the expression category) best fitting with a face stimulus, generally in forced-choice tasks with a limited number of pre-specified labels (e.g., "anger", "fear", etc.). The criterion to determine whether expressions are recognised as distinct entities thus involves response agreement across observers. Kayyal and Russell (2013) have proposed five standards against which endorsement of the predicted label in an expression categorisation task can be tested. The most basic standard (level 1) requires that endorsement of the predicted label exceeds what is expected by chance. The highest standard (level 5) requires that the predicted label be modal and assigned more frequently than any other label. With a strict criterion, Haidt and Keltner (1999)

[1] The term expression "recognition" fits well within the categorical view, as it implies that there exists a discrete, "correct" emotion category with which a currently seen expression can be matched. In contrast, from the perspective of the dimensional-constructivist view, this process could be labelled expression "interpretation", as there would be no fixed facial configurations for expressions, and emotion categories would be fuzzy. Rather than "accurate" recognition (categorical view), the process could thus be conceptualised as degree of "agreement" on an interpretation (dimensional-constructivist view). Nevertheless, for the sake of keeping a widely shared term, such as expression recognition, we will continue to use it, although keeping in mind the possible interpretive nature of the process.

proposed that recognition rates should be in the 70–90% range.

Recognising prototypical facial expressions

Most expression recognition research in cognitive and social psychology and neuroscience has been conducted under the categorical conceptualisation assumptions and the corresponding methodological approach. These studies have used face stimuli with posed prototypical expressions that viewers must classify into predefined emotion categories.

Laboratory studies: Basic findings

In a number of laboratory experiments, recognition performance has been compared for all six basic facial expressions (Calder, Young, Keane, & Dean, 2000; Calvo & Lundqvist, 2008; Calvo & Nummenmaa, 2009; Elfenbein & Ambady, 2003; Palermo & Coltheart, 2004; Recio, Schacht, & Sommer, 2013; Tottenham et al., 2009). Accuracy scores were above chance level and also above 50% for all the expressions, and were generally above 70%, except for disgust and fear (Recio et al., 2013; with computer-morphed faces), and for sadness, disgust and fear (Palermo & Coltheart, 2004; with genuine photographic faces). In addition, responses were typically more accurate and faster for happy versus all the other faces, followed by surprised, angry, sad and disgusted faces, with the poorest accuracy and longest latencies for fearful faces. Such a recognition pattern holds across different response systems: manual (e.g., Calder, Young et al., 2000; Calvo & Lundqvist, 2008; Elfenbein & Ambady, 2003), verbal (Palermo & Coltheart, 2004) and saccadic (Calvo & Nummenmaa, 2009). Results are also consistent across different databases, including the Pictures of Facial Affect (POFA; Ekman & Friesen, 1976), the Karolinska Directed Emotional Faces (KDEF; Lundqvist, Flykt, & Öhman, 1998), the NimStim Stimulus Set (Tottenham, Borscheid, Ellertsen, Marcus, & Nelson, 2002) and others. This strengthens the reliability of recognition differences among facial expressions as separable categories.

Facial expressions can also be recognised as distinct from one another under constrained visual conditions. Expression recognition can be accomplished above chance level even when the face stimuli are displayed less than 50 ms and/or the face is pre- and post-masked (Calvo & Lundqvist, 2008; Milders, Sahraie, & Logan, 2008; Svärd, Wiens, & Fischer, 2012; Sweeny, Suzuki, Grabowecky, & Paller, 2013), when faces are presented in parafoveal or peripheral vision (Bayle, Schoendorff, Henaff, & Krolak-Salmon, 2011; Calvo, Fernández-Martín, & Nummenmaa, 2014; Goren & Wilson, 2006), and also when blurred or with their major expressive sources (eyes and mouth) scrambled (Bombari et al., 2013). This indicates that facial expressions are easily accessible to the visual system, as they can be identified and discriminated even when the visual signal is significantly reduced.

Laboratory studies: Dynamic expressions

Most prior studies have considered only recognition of static faces, yet facial behaviour in real life is dynamic. In general, dynamic information improves coherence in the identification of facial affect, particularly for degraded, lower-intensity and subtle stimuli, leads to enhanced judgements of emotional intensity and helps to differentiate between genuine and fake expressions (Krumhuber, Kappas, & Manstead, 2013). Dynamic expressions are also discriminated from one another more accurately than static expressions (but see Fiorentini & Viviani, 2011). Kinetic information presumably boosts recognition because motion captures and focuses attention on the relevant diagnostic facial features changing from neutral to emotional. As a result, enhanced attention facilitates early perceptual processing and expression recognition (Jiang et al., 2014; Recio, Sommer, & Schacht, 2011). Consistent with this, neuroimaging studies have found stronger haemodynamic responses in regions involved in the processing of social (superior temporal sulcus; STS) and emotional (amygdala) information for dynamic versus static expressions (Arsalidou, Morris, & Taylor, 2011). Similarly, ERPs to dynamic versus static expressions show larger amplitudes in temporo-occipital areas involved in early visual processing and centro-parietal areas responsible for categorisation (Recio et al., 2011).

The recognition accuracy scores in studies using all six basic expressions are of particular interest here. With 1-s duration video clips and computer-morphed faces starting with a neutral expression and developing to a full emotional expression for 900 ms, Recio et al. (2013) found that performance accuracy was above 50% for the six basic expressions, and it was above 70% for all of them except disgust and fear. Similarly, with real faces and 600-ms video clips, Recio, Schacht, and Sommer (2014) reported accuracy scores above 70% for all six basic expressions when they were developed to full intensity, and even at moderate and lower intensities, except for fear. Importantly, the relative order of recognition accuracy across expressions was similar for dynamic and static displays, with happy faces identified most accurately, and disgusted and fearful faces least accurately (Recio et al., 2013, 2014).

Laboratory studies: Type of confusions

A subset of the laboratory studies investigating recognition of all six basic expressions has also analysed confusions, as an index of expression discrimination (Calvo & Lundqvist, 2008; Palermo & Coltheart, 2004; Tottenham et al., 2009). A clear pattern has emerged. Fear is frequently confused with surprise (31%: Palermo & Coltheart, 2004; 19% with open-mouth faces and 29% with closed-mouth faces: Tottenham et al., 2009; 10%: Calvo & Lundqvist, 2008), and surprise is confused with fear (18% with closed-mouth faces and 14% with open-mouth faces: Tottenham et al., 2009; 10%: Calvo & Lundqvist, 2008). Disgust tends to be confused with anger (12%: Palermo & Coltheart, 2004; 13% with closed-mouth faces: Tottenham et al., 2009) and sadness (10%: Palermo & Coltheart, 2004). Sadness is confused with disgust (15% with open-mouth faces: Tottenham et al., 2009), and also with neutral expressions (17%: Palermo & Coltheart, 2004; 12% with closed-mouth faces: Tottenham et al., 2009). Relatedly, with computer-morphed expressions, Recio et al. (2013) found fear to be confused with surprise (37%), disgust with anger (42%) and sadness with fear (16%).

Altogether, these confusions indicate that the boundaries between some basic expressions—particularly those between surprise and fear, and anger and disgust—are not well defined. Interestingly, with a totally different method involving the combination of perceptual expectation modelling, information theory and Bayesian classifiers, Jack, Garrod, and Schyns (2014) obtained results that are consistent with those emerging from the confusion data. They found evidence of four basic expressions, namely, happy, sad, fear/surprise and disgust/anger, instead of six. Fear and surprise, on the one hand, and disgust and anger, on the other hand, would share processing and representation codes, at least at early processing stages. This corresponds with the reported patterns of major recognition confusions in categorisation tasks.

Section summary: Basic expressions are discriminated from one another

The six basic emotional expressions can be readily identified and discriminated from one another. However, this conclusion is constrained by the nature of the stimuli and the type of response format. Typically, studies have used posed, prototypical and full-blown expressions with exaggerated features, which may have amplified expression recognition. Also, studies have mostly used a forced-choice response procedure, with a limited number of predetermined verbal labels, which probably funnels a variety of interpretations of expressions into one-word categories.

Discrete neural signatures for facial expressions

Studies reviewed above used behavioural measures of explicit recognition of facial expressions, to determine whether they are perceived as distinct categories. A more direct approach involves assessing whether different expressions trigger discernible neural signatures in specific brain regions, by means of functional magnetic resonance imaging (fMRI). The amygdala plays an important role as a general-purpose emotion processing unit, assigning affective significance to sensory events (LeDoux & Phelps, 2008; Vuilleumier, 2009), whereas the posterior areas of the STS (pSTS) play a critical role in encoding changeable aspects of faces (Calder & Young, 2005; Engell & Haxby, 2007). Expression-specific neural responses in these regions could thus reveal whether each expression is associated with a different emotional (amygdala) versus higher-order visual (pSTS) signature. Human amygdala responds reliably to all six basic facial expressions (Whalen et al., 2013). Similarly, the pSTS responds more strongly to all basic facial expressions than to neutral faces, and is sensitive to changes in expressive intensity irrespective of the actual emotion category (Harris, Young, & Andrews, 2012). Although this suggests that the different expressions share similar neural underpinnings, recent work has revealed significant differences among expressions.

First, in a narrative review of brain imaging studies, Matsumoto, Keltner, Shiota, O'Sullivan, and Frank (2008) reported differential activation patterns for basic expressions: fearful faces activate regions in the left amygdala; sad faces, the left amygdala and right temporal lobe; angry faces, the right orbito-frontal cortex and cingulate cortex; disgusted faces, the basal ganglia, anterior insula and frontal lobes; and happy faces with Duchenne smiles, the left side of the lateral frontal, mid-frontal, anterior temporal and central anterior scalp regions. In a subsequent quantitative meta-analysis, Vytal and Hamann (2010) found that each of the five basic expressions (excluding surprise) was associated with unique and distributed patterns of neural activation: happiness was consistently associated with activation of rostral anterior cingulate cortex; fear, with the amygdala; disgust, with the insula; sadness, with medial prefrontal cortex; and anger, with orbitofrontal cortex. This reveals distinct patterns of activation across brain regions when perceiving different facial expressions.

Second, recent studies employing spatially more accurate multivariate pattern recognition (MVPA) analysis of fMRI data suggest that different emotions (Saarimäki et al., in press) and facial expressions reliably elicit separable brain activity even within specific brain regions (see Kragel & LaBar, 2014). Using targeted high-resolution fMRI of the temporal cortex, Said, Moore, Engell, Todorov, and Haxby (2010) showed that responses to seven categories of dynamic facial expressions can be decoded from the posterior STS (pSTS) and anterior STS (aSTS). Critically, the neural similarity structure of facial expression-evoked activity was significantly correlated with the perceptual similarity structure of the expressions. This confirms that the STS holds perceptual rather than emotion-based codes of facial expression categories (see also the section on *Visual and structural similarities and differences: computational modelling*, below). Nevertheless, complete differentiation of neural signatures for each expression within a region is probably not possible because all expressions are processed by a network of interacting sub-cortical and cortical structures with which the amygdala and the STS are connected (Skelly & Decety, 2012; see also Hamann, 2012).

Section summary: Basic expressions have discrete neural signatures

Neuroimaging literature suggests that different facial expressions have statistically discernible neural signatures, both within specific regions (e.g., pSTS) and in distributed cerebral circuits, supporting the categorical representation of facial expressions in the brain. However, the relative importance or temporal primacy of visual versus affective processing cannot be readily inferred from the fMRI data.

Does reliance on prototypical expressions and forced-choice response format inflate categorical perception of expressions?

The use of prototypical expressions coupled with forced-choice response formats in most prior studies may have inflated the impression that there is recognition of six differentiated emotional categories. Accordingly, a more realistic approach to facial expression recognition—yet within the discipline of experimental research—requires using face stimuli that are representative of those occurring in the everyday natural environment, with spontaneous, subtle and blended expressions. In addition, task conditions should allow for the collection of open categorisation responses that can reveal the observers' unbiased interpretations of the expressions.

Spontaneous versus posed expressions

A number of studies have assessed recognition of spontaneous emotional expressions (see Kayyal & Russell, 2013). The percentage of observers matching the face to the predicted emotion was generally low, both when the expressions were static (26%: Motley & Camden, 1988; 38%: Yik, Meng, & Russell, 1998; and 32%: Naab & Russell, 2007) and dynamic (63%: Hess & Blairy, 2001; 15%: Wagner, 1990; and 22%: Wagner, MacDonald, & Manstead, 1986). In the Matsumoto, Olide, Schug, Willingham, and Callan (2009) study, agreement was also low, with a median of 28% across different expressions, and it varied significantly with culture of the observers. These scores are noticeably lower than those reported for posed expressions (see above; generally > 70%). In the Kayyal and Russell (2013) study, observers endorsed the predicted emotion moderately often (44–65%), but also denied it often (35–56%), and they normally assigned more than one label for each facial expression. Consistently, studies in naturalistic settings (presumably, with spontaneous expressions) have yielded weak correlations between the actual felt emotions and the corresponding facial expressions (Fernández-Dols & Crivelli, 2013). Spontaneous expressions do not involve fixed signals of basic emotions, and thus their recognition is open to interpretations that need to rely on social knowledge and context, beyond the facial muscle configuration (Hassin, Aviezer, & Bentin, 2013; Parkinson, 2013).

Blended versus prototypical expressions

Rather than having a uniform configuration, facial behaviour in daily life shows a great deal of individual idiosyncrasy and variability. In fact, ambiguous and blended expressions are encountered very often (Calvo, Gutiérrez-García, Fernández-Martín, & Nummenmaa, 2014; Carroll & Russell, 1997; Scherer & Ellgring, 2007). A number of non-basic facial emotions were proposed by Ekman (1994) to be common across cultures: amusement, excitement, embarrassment, awe, contempt, contentment, guilt, interest, pride, relief, satisfaction, sensory pleasure and shame. Even finer nuances exist for blended expressions in which facial configurations of two or more basic expressions are combined (Du, Tao, & Martinez, 2014). For blended expressions, the prototypical facial configurations disappear, thus making recognition unreliable, unless contextual information and social knowledge is used. When this information is not available, as is often the case in laboratory settings with isolated photographs, viewers tend to rely on the most distinctive facial cue to categorise expressions (Calvo & Fernández-Martín, 2013; Fiorentini & Viviani, 2009; Tanaka, Kaiser, Butler, & Le Grand, 2012). In this case, categorisation agreement drops as blends move farther away from the prototype (Young et al., 1997). This often leads to misperceptions, as is the case for smiling faces with non-happy (neutral, sad, etc.) eyes, which are frequently seen as happy, as shown by explicit judgement (Calvo, Fernández-Martín, & Nummenmaa, 2013) and ERP (Calvo, Marrero, & Beltrán, 2013) measures.

Full-blown versus subtle expressions

In everyday life, social norms often restrict the magnitude of emotional response in many situations. As a consequence, the explicit expressive changes frequently entail low-intensity signals in the face. The recognition of subtle expressions has been investigated by means of morphing, whereby linear intensity levels are established in the transition between a neutral and a prototypical emotional expression of the same individual (e.g., Calder, Rowland et al., 2000; see Matsumoto

& Hwang, 2014, for a different measure of signal intensity). For static expressions, a positive relationship has been found between intensity or degree of morphing and (1) the participants' emotional intensity ratings (Calder, Rowland et al., 2000) and (2) the actual expression recognition accuracy (Hess, Blairy, & Kleck, 1997). With dynamic expressions, to our knowledge, no systematic variations of multiple intensity levels have been investigated, although full-intensity expressions are recognised better than subtle ones (Ambadar, Schooler, & Cohn, 2005; Bould, Morris, & Wink, 2008; Recio et al., 2014). Recio et al. (2014) found that the recognition accuracy of all six basic expressions was above 70% (except fear: 62.5%) already at a 60% intensity level. In a recent study (Calvo, Avero, Fernández-Martín, & Recio, 2015), intensity levels were morphed from 20% to 100%. Measures of discrimination (*A'*) established recognition thresholds: 20% of intensity for happiness; 40% for sadness, surprise, anger and disgust; 50–60% for fear, similarly for dynamic and static expressions. Thus expression recognition operates consistently even at low signal-to-noise ratios.

Response format and semantic context

In the standard, forced-choice response format, participants must select a single emotion word from a predetermined list, rather than making up their own label. This format creates a semantic context that biases viewers to pick *one* basic expression category per face (see Fugate, 2013; Gendron, Roberson, van der Vyver, & Barrett, 2014). Yet, in the absence of such verbal and conceptual constraints, viewers could actually perceive an emotion not included in the list, or even various emotions for the same facial expression. In contrast with this approach, Kayyal and Russell (2013) and Gendron et al. (2014) used open response formats, with a wide list of feeling labels beyond the six basic emotion words or simply no cue words (free responding). In such conditions, viewers perceived multiple emotions in the same face. This is not consistent with the hypothesis of discrete emotional categories with specific facial signals. One conclusion from these studies is that categorical perception of discrete expressions is shaped by the semantic context created by emotion words, an effect that would be enhanced in the forced-choice format. Words create emotion categories or augment the categorical perception of expressions.

Section summary: Realistic expressions can be categorised moderately consistently, albeit constrained by forced-choice response format

Understandably, discrimination accuracy is lower for spontaneous, blended and subtle expressions, relative to posed, prototypical and full-blown expressions. Yet such expressions can still be categorised reliably under conditions with reduced signal intensity or quality. Nevertheless, a critical issue affecting the majority of studies in all conditions continues to be the constraint imposed by forced-choice response formats. The available—limited and conceptually restricted—response options do not provide a realistic representation of the variety of interpretations that viewers make of the facial expressions, beyond discrete and basic categories.

Is categorical expression recognition consistent across cultures?

If facial expressions reflect activation of culturally universal and biologically driven affect programmes, recognition of facial expressions should be consistent across different cultures. Nelson and Russell (2013) reviewed 21 cross-cultural judgement studies published between the years 1992 and 2010, providing 39 sets of data of Western (20) and non-Western (18) literate samples of observers and illiterate samples (1). The 39 datasets used at least four of the hypothesised six basic emotions, posed facial expressions, a forced-choice response format and a within-subjects design. In all the studies, endorsement of the predicted label was above chance. For the whole group of studies, the mean recognition agreement scores across expressions ranged between 52.4% and 90.8% for Western samples, between 45.4%

and 82.2% for non-Western samples and 50% for illiterate samples. Across studies, scores ranged between 64.7% (disgust) and 88.6% (happiness) for Western samples; between 46.3% (fear) and 90.7% (happiness) for non-Western samples; and between 30.0% (fear) and 84.0% (happiness) for illiterate samples. The average agreement scores for studies conducted before 1994 (reviewed by Russell, 1994) were generally above (between 2% and 9%) those in the 1992–2010 period.[2]

These results imply that the lowest (1) Kayyal and Russell (2013) standard of expression recognition was clearly exceeded. Also, the fact that scores were generally well above 50% suggests that even the highest (5) standard was fulfilled for most of the expressions. Moreover, some of them (happiness, anger, sadness and surprise, for Western samples; happiness and surprise, for non-Western samples; and happiness, for illiterate samples) were even within the 70–90% range proposed by Haidt and Keltner (1999). Nevertheless, a statistical analysis conducted by Nelson and Russell (2013) revealed that matching scores varied significantly as a function of culture for three out of the six basic expressions: while happiness, surprise and sadness were recognised similarly across cultures, Western observers' matching scores were higher than were non-Western observers' scores for anger, fear and disgust. This indicates that despite high agreement rates, there are *quantitative* differences in how much people in different cultures perceive expressions as distinct, even though some expressions seem to be culturally universal.

Two additional approaches show also *qualitative* differences. A key observation for the dialect theory of expressions (Elfenbein, 2013; Elfenbein & Ambady, 2002) is that viewers are more accurate when judging them from their own cultural group versus foreign groups (i.e., the in-group advantage effect). Individuals tend to judge other people's facial cues based on their own culture styles. Research findings obtained by Jack and colleagues (Blais, Jack, Scheepers, Fiset, & Caldara, 2008; Jack, Blais, Scheepers, Schyns, & Caldara, 2009; Jack, Caldara, & Schyns, 2012; Jack, Garrod, Yu, Caldara, & Schyns, 2012) are consistent with this view. Western Caucasian (WC) and East Asian (EA) observers associate different facial movement patterns with different expressions. These authors modelled the internal representation of each expression by reverse correlating random facial movements with the emotion category (e.g., "happy") that the participants associated with the movements. In addition, eye fixations were measured while participants viewed the faces. Whereas WC representations predominantly featured both the eyebrows and mouth, EA representations relied mainly on information in the eye region, including changes of gaze direction. Second, rather than distributing their fixations evenly across the face as WC do, EA observers persistently fixate the eye region. This reveals cultural specificity in expression recognition in two respects: how facial emotions are perceived using culture-specific facial signals in the observer's representation of the expressions, and the specific way such signals are strategically fixated in the expresser's face.

Section summary: There is consistency in cross-cultural expression recognition

Recognition of facial expressions is consistent across cultures, but there are both qualitative and quantitative differences. This suggests that the facial expression recognition system is supported by a biologically driven, innate mechanism, which, nevertheless, has significant capacity to adjust to different environmental demands. Future studies,

[2]We conducted a statistical analysis (ANOVA followed by Bonferroni-corrected multiple post hoc comparisons) of the average matching scores, i.e., recognition agreement or "accuracy" across observers, reported in the Nelson and Russell (2013) review, with each set of data treated as a single case. The 17 cross-cultural judgement studies published between the years 1992 and 2010 were chosen, which provided 38 sets of data of Western (20) and non-Western (18) literate samples of observers. Statistically significant differences as function of expression emerged: scores were higher for happy faces (89%) than for all the other basic expressions, followed by surprise (83%), which were higher than for sadness and anger (71% and 68%, respectively), followed by disgust and fear (65% and 59%, respectively, which were similar to each other).

however, need to establish how consistent cross-cultural recognition of blended and subtle expressions are, and how much the cross-cultural consistency observed in prior studies is influenced by the use of prototypical expressions and the forced-choice response format.

AFFECTIVE PROCESSING AND FACIAL EXPRESSION RECOGNITION

As their name implies, emotional expressions are assumed to convey affect. But do viewers encode their affective significance spontaneously and non-intentionally? And, most importantly, when does this occur during the categorisation process, so that affect can (or cannot) influence expression recognition? Relatedly, is affect extracted more likely or earlier for some expressions than for others, such that it can account for the typical recognition differences among them? Or, alternatively, is affective encoding unrelated to recognition, while non-affective factors play a major role?

Is affect extracted automatically from facial expressions?

Valence and arousal: Explicit ratings and affective similarity judgements

The dimensional model of facial expressions (Russell, 1994, 2003) assumes that core affect is extracted early, with expressions being initially perceived on a continuum along the orthogonal dimensions of affective valence and arousal. Such a coarse affective processing would occur earlier than categorisation of specific expressions (e.g., happy, angry, etc.), which would arise from a cognitive interpretation of the valence and arousal sensations later. Valence and arousal have been measured by means of explicit ratings of the un/pleasantness and tension conveyed by facial expressions. Valence ratings are generally consistent: Happy faces are judged as more pleasant than any other expression or neutral faces, which are rated as more pleasant than the negatively valenced basic expressions. This pattern has been obtained with various face databases (POFA: Lipp, Price, & Tellegen, 2009, and Russell & Bullock, 1985; KDEF: Calvo, Gutiérrez-García, Avero, & Lundqvist, 2013, and Eisenbarth, Alpers, Segré, Calogero, & Angrilli, 2008; or both KDEF and NimStim: Adolph & Alpers, 2010). For arousal ratings, the pattern is much less consistent: happy faces are more arousing than neutral or other emotional faces (Eisenbarth et al., 2008), or equally arousing as angry faces (Calvo, Gutiérrez-García et al., 2013; Lipp et al., 2009, Experiment 2), or equally arousing as angry and fearful faces (Adolph & Alpers, 2010), or less arousing than angry and fearful faces (Russell & Bullock, 1985; Lipp et al., 2009, Experiment 3).

Valence and arousal processing have also been assessed by means of affective similarity judgements (Bimler & Paramei, 2006; Gerber et al., 2008; Russell & Bullock, 1985; see Posner, Russell, & Peterson, 2005). Multidimensional scaling (MDS) of the responses has typically produced a similarity structure that is represented as a circumplex model. This model reflects how similar or different various expressions are in terms of the perceived emotions. The basic expressions appear distributed in a circular space along the two bipolar dimensions of valence and arousal: sadness is high in unpleasantness but relatively low in arousal, whereas happiness is high in pleasantness and relatively high in arousal; fear, anger and disgust are unpleasant, but fear is higher in arousal than anger, which is more arousing than disgust; and surprise is located high in the arousal axis, but in the middle of the un/pleasantness axis, between fear and happiness.

Affective priming of facial expressions

Both valence and arousal ratings and the affective similarity judgements reflect strategic affective processing. Alternative measures are thus required to determine whether affect is extracted *automatically* from facial expressions. One such method is the affective priming paradigm, whereby an emotional face is briefly presented as a prime followed by an emotional probe word or visual scene. The viewer is asked to ignore the prime and to judge the probe as pleasant or unpleasant. Thus, the face is task-irrelevant, as probe categorisation does not require explicit recognition of the prime. If the prime face activates affective information, reaction times will be faster when the prime and the probe are affectively congruent (both pleasant or unpleasant) than when they are incongruent or unrelated (a neutral prime). To determine the time course of affective processing, the prime–probe stimulus onset asynchrony can further be manipulated to estimate when the potential priming effect peaks.

Priming studies suggest that affective information along the valence dimension is obtained automatically from facial expressions (Aguado, García-Gutiérrez, Castañeda, & Saugar, 2007; Calvo, Fernández-Martín, & Nummenmaa, 2012; Calvo, Nummenmaa, & Avero, 2010; Carroll & Young, 2005; Lipp et al., 2009; McLellan, Johnston, Dalrymple-Alford, & Porter, 2010; Sassi, Campoy, Castillo, Inuggi, & Fuentes, 2014). Although some studies did not analyse the effects separately for each basic expression (Aguado et al., 2007; Carroll & Young, 2005), Lipp et al. (2009) reported affective priming for happy, angry, fearful and sad faces, at 300-ms prime–probe onset asynchrony (SOA): affective evaluation of pleasant probe words was faster after happy than after angry, sad and fearful faces, whereas evaluation of unpleasant probes was slower after happy faces. Also, McLellan et al. (2010) found priming effects at 100-ms SOA: Participants responded faster to positive words following genuine rather than posed displays of happiness, and were faster to respond to negative words following genuine displays of fear. Priming effects were absent for sad faces. Using visual scenes as probes, affective priming was observed at 550-ms SOA or later for happy (Calvo et al., 2010; Calvo et al., 2012), but not for sad faces or those with a smile but non-happy eyes (Calvo et al., 2012). Altogether, these findings reveal automatic (in the sense of being non-intentional and fast) encoding of facial affect along the pleasantness–unpleasantness dimension. The priming effects are more consistent for happy expressions than for the others. There are, nevertheless, discrepancies about the time course of such affective processing.

Neural timing of implicit expression processing

ERP amplitudes triggered by different expressions provide another implicit measure of affective processing. Given their high temporal resolution, ERPs potentially allow assessment of the time course of facial expression-processing stages. Viewing emotional versus neutral facial expressions modulates multiple ERP components. Following an initial stage (100–150 ms from stimulus onset) where the P1 and N1 components are mainly sensitive to physical stimulus ("rather than emotional") factors, at a second stage (150–300 ms), the face-sensitive N170 and its positive counterpart vertex positive potential (VPP), as well as the P2, respond with an enhanced amplitude to emotional—mainly, negatively valenced—relative to neutral faces (N170: Williams, Palmer, Liddell, Song, & Gordon, 2006; VPP: Willis, Palermo, Burke, Atkinson, & McArthur, 2010; P2: Calvo, Marrero, & Beltrán, 2013). This suggests that coarse affective processing starts by differentiating emotional and non-emotional expressions, presumably on the basis of arousal. At a third stage (200–350 ms), the N2 and the early posterior negativity (EPN) also show sensitivity to emotion, with N2 (Williams et al., 2006) and EPN (Schupp et al., 2004) responding differently to neutral, positive and negative expressions. This suggests that a more refined discrimination along the positive–negative axis develops as a function of affective valence. Later stages (>300 ms) involving the P3b (Luo, Feng, He, Wang, & Luo, 2010), late positive potential (LPP; Leppänen, Kauppinen, Peltola, & Hietanen, 2007) and slow positive waves (SPWs; Calvo & Beltrán, 2013) are more related to expression categorisation than to affective processing.

ERP data thus reveal enhanced early neural responses to emotional relative to neutral faces, and subsequent discrimination between positive and negative emotions (Luo et al., 2010; Schupp et al., 2004; Willis et al., 2010; Williams et al., 2006). Nevertheless, ERP studies have generally compared only a few emotions. In a review of 45 relevant studies (see Calvo & Beltrán, 2013), only three included the six basic expressions (Balconi & Mazza, 2009; Batty & Taylor, 2003; Eimer, Holmes, & McGlone, 2003), and results were not convergent regarding specific ERP differences among them. Accordingly, the major conclusion that can be drawn from electrocortical research is that, between 150 and 300 ms (i.e., the N170 to EPN latency range), emotional expression is implicitly encoded as different from neutral expression, followed by some discrimination among the emotional faces, albeit no solid and systematic pattern has emerged.

Section summary: Affective significance is extracted automatically from emotional expressions

Explicit affective ratings have shown a two-dimensional valence and arousal space where expressions are distributed. Implicit affective priming measures have confirmed that affective processing of valence occurs automatically, at least in the sense of being involuntary. ERP components assumed to assess affective processing are modulated by facial expressions, with an earlier sensitivity to negatively valenced expressions as a whole, and later to happy expressions, relative to neutral faces. Importantly, the affective measures discriminate among expressions less than the explicit recognition measures do. This likely reflects the fact that different expressions have different neural signatures in overlapping brain regions. Despite this, the implicit measures suggest that affect is processed prior to expression category.

Does affective processing support expression recognition?

ERP findings suggest that affective processing occurs earlier than explicit recognition or categorisation (see also Sweeny et al., 2013, with an alternative paradigm). Yet does affective content contribute to expression recognition, or can expression recognition be undertaken based on visual features only? To answer this question, we should bear in mind the above-reviewed recognition accuracy and speed differences among the various basic expressions in cross-cultural and laboratory studies: happy faces are typically recognised more accurately and faster than all the others, followed by surprised, angry, sad and disgusted faces, with the poorest performance for fearful faces. Are such recognition differences related to affective processing?

Do affective intensity differences explain recognition accuracy variation across expressions?

In some studies, measures of affective intensity (valence and arousal) of target faces were obtained alongside with indices of cognitive processing (e.g., categorisation, affective priming or eye movements). These data can be used to examine whether the valence and arousal extracted from the faces contribute to the recognition differences across expressions. In the Eisenbarth et al. (2008) study, happy faces were recognised most accurately and were also rated as the most pleasant and arousing. Nevertheless, although fearful faces were the poorest to be recognised, they were not the most (or least) unpleasant or the least (or most) arousing expressions. In the Lipp et al. (2009) experiments, happy faces produced more affective priming than the others (angry, sad and fearful, which did not differ from one another) did. Although this was in correspondence with the higher pleasantness of happy faces, the relationship was inconsistent with arousal, as happy faces were equally or less arousing than the others. Finally, Calvo, Gutiérrez-García et al. (2013) found that the higher valence of happy faces was associated with initial attentional orienting to, and later engagement with, the mouth region, while arousal was not related to the pattern of eye movements. Also, differences in valence and arousal among the other expressions (anger, fear, sadness, disgust and surprise) were not consistently associated with any overt attention pattern. Thus, even though positive valence (i.e., pleasantness) may promote recognition of happy faces, different combinations of valence and arousal levels are unlikely to explain recognition performance differences among the facial expressions.

Affective uniqueness

In conventional recognition tasks, happy faces are unique in the sense that they are the only ones conveying positive affect, while all the other basic expressions are negative (anger, fear, sadness and disgust) or ambiguous (surprise; amenable to both a positive and a negative interpretation). Affective uniqueness could thus support recognition by making happy faces easily discriminable, whereas the other expressions would be subjected to mutual interference, due to shared negative valence. This could explain the consistent happy face recognition advantage (see a review in Nummenmaa & Calvo, 2015). However, such a valence-based explanation cannot account for recognition accuracy and speed differences among the negative expressions, as, for example, sadness and anger are recognised better than disgust and fear. Also, the affective ambiguity of surprise should impair recognition, according to an affective valence explanation, yet surprise is generally the second most accurately recognised expression (see above). Finally, the happy face advantage occurs even in experimental conditions where *only one* negative expression (disgust: Leppänen & Hietanen, 2004; sadness: Kirita & Endo, 1995; of anger: Calvo & Nummenmaa, 2009) needs to be discriminated from happiness, thus in the absence of within negative valence competition. The fact that affective uniqueness is not sufficient to explain expression recognition differences further suggests that affective encoding is not critical for expression recognition.

Resolving the inconsistency between ERP time course and behavioural recognition performance

Some ERP components related to affective processing (N170, VPP, N2 or EPN) differentiate between neutral and emotional expressions early (150–350 ms; see above). Furthermore, ERPs are sensitive to negatively valenced expressions (especially anger and fear) before positively valenced faces (Calvo, Marrero, & Beltrán, 2013; Frühholz, Fehr, & Herrmann, 2009; Luo et al., 2010; Rellecke, Sommer, & Schacht, 2012; Schupp et al., 2004; Williams et al., 2006; Willis et al., 2010). Thus threat detection, rather than positive affect, seems to be prioritised quickly in neural systems supporting emotion recognition. This is, however, inconsistent with behavioural data showing that happy expressions are explicitly recognised faster than non-happy faces.

Before concluding that early affective processing does not significantly contribute to expression recognition, we must directly examine the relationship between ERP components and explicit expression recognition measures. Most ERP studies have, nevertheless, focused on implicit expression processing, with expression categorisation being task-irrelevant and not being explicitly measured. However, Calvo and Beltrán (2013) recorded ERPs during a categorisation task for happy, angry, fearful, sad and neutral faces. The VPP activity was unrelated to recognition performance accuracy and speed; the enhanced N170 and N2 amplitudes were, actually, related to *slower* recognition; and only a larger EPN was related to faster recognition. This suggests that the early affective processing of expressions does not consistently facilitate explicit recognition, but could, actually, impair it. In contrast, later components involving semantic elaboration (reduced P3b) and response selection (reduced SPW)—rather than affective processing—were significantly correlated with increased recognition accuracy and faster reaction times. Thus the rapidly extracted coarse affective significance (negative versus non-negative followed by negative versus non-emotional versus positive) might simply not provide enough information for successfully identifying specific expressions.

Section summary: Affective processing does not contribute significantly to expression recognition

Although coarse affective processing occurs prior to expression recognition, affect does not contribute significantly to expression recognition. Instead, categorisation requires later, fine-grained discrimination processes. Affective valence—but not arousal—may facilitate categorisation processes to some extent, as shown by the recognition advantage of pleasant (happy) versus non-pleasant faces. However, valence alone is not sufficient to account for expression recognition differences. These findings suggest relative independence of affective processing and expressive categorisation.

PERCEPTUAL PROCESSING DRIVES EXPRESSION RECOGNITION

Thus far we have shown that there are significant differences in the recognition of different facial expressions, with a superior recognition of happy expressions, and less pronounced differences among the non-happy expressions. Affective factors are unlikely to play a critical role in these differences. Next we examine the role of non-affective, perceptual and learning-dependent factors that underlie differences in the relative accuracy and speed of recognising facial expressions.

Perceptual mechanisms constitute the first step in the encoding of any stimulus by the neural and cognitive systems. According to post-attentional models of emotional processing, perceptual analysis is performed and the features of objects must be integrated, and possibly the objects themselves must be identified, prior to affective processing (Cave & Batty, 2006; Lähteenmäki, Hyönä, Koivisto, & Nummenmaa, 2015; Nummenmaa, Hyönä, & Calvo, 2010; Storbeck, Robinson, & McCourt, 2006). In line with this view, perceptual priming has been found to occur earlier (<170 ms) than affective priming (between 340 and 550 ms) in the discrimination of facial expressions (Calvo et al., 2012). Relatedly, perceptual detection of smiles (smile versus no smile) in faces is more accurate and faster than affective judgements (pleasant versus not pleasant) of the corresponding face at 20-, 40- and 80-ms stimulus (pre- and post-masked) displays, with affective judgements becoming equally accurate and fast as perceptual detection later, at 100-ms displays (Calvo et al., 2012). This further implies that perceptual processes precede affective processes.

Altogether, this suggests that perceptual factors devoid of any affective meaning could primarily contribute to facial expression recognition. But are the observed recognition differences, and even the affective circumplex, due to the perception of differences in facial morphology rather than in affect? Is there any salient and distinctive morphological feature available to perception that facilitates recognition of some expressions? And can perceptual expertise in expression recognition be formed over time due to more frequent exposures to particular facial configurations? These questions can be addressed from three perspectives.

Visual and structural similarities and differences: Computational modelling

Computational modelling provides an excellent testing ground for cognitive theories of expression recognition. Neurocomputational models such as EMPATH (Dailey, Cottrell, Padgett, & Adolphs, 2002; Dailey et al., 2010) and support vector machine (SVM)-based techniques (Susskind, Littlewort, Bartlett, Movellan, & Anderson, 2007) simulate face processing and expression recognition in humans (see Cottrell & Hsiao, 2011). In these models, facial expressions are processed on purely perceptual grounds on the basis of physical image properties, and affective processing is not taken into account. This approach serves to estimate whether equivalent expression "recognition" and discrimination can be performed in the absence of affective processing by "emotionless machines", in comparison with the presumed emotional processing systems of human observers.

EMPATH (Dailey et al., 2002, 2010) is a visual pattern classifier, implemented through a neural network that simulates functions of the visual system and particularly the response properties of neurons in the primary visual (V1) and inferotemporal (IT) cortices. The model proceeds through three consecutive stages. At the first, perceptual analysis stage, the image is Gabor filtered to produce a representation that models the spatial responses of complex neurons in the early processing V1 area. At the second, gestalt or object representation stage, the representation is reduced to a lower dimensional pattern by principal components analysis (PCA), mimicking response properties of the IT cortex. At the third, expression categorisation stage, the input is classified into one of six output categories corresponding to the six basic emotions. Through supervised training with paired facial images (input) and emotion labels (output), this network changes its connection strengths to produce the correct response for each face stimulus. If the model activates a wrong output (e.g., respond "happy" when the face is "sad", the training algorithm adjusts the connection strengths between the inputs and the outputs to reduce error. In this way, the model learns to differentiate the facial expressions from one another.

EMPATH (see Cottrell & Hsiao, 2011) and SVM-based models (Susskind et al., 2007) can reproduce several phenomena found with human observers. First, fear is the hardest expression for the models to recognize, and, like humans, they often confuse it with surprise. Second, MDS of the model's output representation produces a similarity structure that is comparable to the circumplex observed in human data. Third, and critically with respect to the categorical models of expression recognition, when presented with morphs between pairs of facial expressions, both EMPATH and human subjects (Young et al., 1997) place similar sharp category boundaries between the prototypes, with assignment to a category dropping smoothly as the morph moves farther away from the prototype. Altogether, these simulations provide support for models assuming that non-affective, visual recognition is *sufficient* for expression recognition. Thus the perceptual structure of facial expressions, in terms of physical similarities and differences, corresponds to the psychological (categorical and emotional) structure.

These findings might lead us to propose that human facial expression recognition and interpretation could be dependent on perceptual discrimination of facial physical features, without any emotional processing required. Before such a conclusion, however, we must make two considerations. First, the purely perceptual account might apply to typical experimental conditions in which decontextualised photographs of otherwise generally prototypical expressions are presented to human observers. In daily life, however, there is a great variety of morphological changes in facial expressions and they appear in a wide variety of contexts. In such conditions, inferences and emotional evaluation of the significance of expressions are probably also important. Second, the computational results do *not disprove* that human observers can extract emotional information, but rather show that perception of facial structure is *sufficient* for accurate expression recognition (Susskind et al., 2007). Instead, the relationship between computational (perceptual) and human (psychological) data suggests that facial expressions and emotional states are not randomly associated, but that expression-to-emotion mappings have evolved in tandem with the need to communicate and detect emotions effectively (Dailey et al., 2002).

Section summary: Perceptual encoding is sufficient for basic expression recognition

Computational models can recognise emotional expressions from facial images, in the absence of affective processing, and such models can reproduce a number of important phenomena obtained with human observers. This suggests that human expression recognition probably relies mainly on the perceptual analysis of visual features rather than emotional meaning or affective dimensions. Nevertheless, while this may be true for photographs of faces in experimental conditions, the role of affective processing is probably more important in daily life conditions.

Saliency and distinctiveness of facial features

The computational models of expression recognition can account for several findings on purely perceptual grounds. However, the highly consistent happy face recognition advantage observed in humans cannot be reproduced with computational models. Both with EMPATH (Dailey et al., 2002) and the SVM-based (Susskind et al., 2007) models, recognition accuracy for happy expressions can reach ceiling (100%), but the same also occurs for surprised and disgusted faces (EMPATH) and for surprised and sad faces (SVM). Given the robustness of the finding with human observers, we propose an additional, perceptually related mechanism involving visual saliency and distinctiveness as an extension of the models.

Expression recognition can be accomplished not only via holistic or configural perception mechanisms, with faces coded as unitary objects, but also by the perceptual analysis of single facial features (Tanaka et al., 2012). These features, such as a frown, wide-open or slit eyes, curved lip corners, etc., vary in visual saliency and distinctiveness. Saliency, i.e., the physical stimulus conspicuousness, enhances sensory gain, thus increasing perceptual accessibility and facilitating selective attentional capture. Distinctiveness, i.e., the degree that a facial feature is uniquely associated with a particular expressive category, reduces ambiguity and thus allows viewers to assign an expression to a specific category with minimal interference. Importantly, due to high visual saliency, the processing of a highly distinctive cue (e.g., a smile) would not be compromised by perceptual competition with other features in the same facial configuration. Accordingly, if the recognition of an expression is driven by the analysis of single features that are conspicuous and distinctive, recognition accuracy and efficiency should increase. A salient and distinctive visual cue could be used as a reliable and quick shortcut for expression recognition. In contrast, the lack of such a cue would require the integration of multiple expressive sources in a face, thus making the recognition process slower or less accurate. Expression recognition is thus expected to be facilitated for expressions with perceptually salient and distinctive facial features.

The smiling mouth of happy faces is salient and distinctive. First, regarding saliency, computational modelling based on a combination of physical image properties such as luminance, contrast and spatial orientation (see Borji & Itti, 2013) has shown that the smiling mouth is more salient than any other region of happy and non-happy faces (Calvo & Nummenmaa, 2008). The smiling mouth remains highly salient even when placed in faces with non-happy (e.g., angry, sad, etc.) eyes (Calvo et al., 2012). Also, the salient smile attracts more overt attention, i.e., eye fixations during expression recognition (Beaudry, Roy-Charland, Perron, Cormier, & Tapp, 2014; Bombari et al., 2013; Calvo & Nummenmaa, 2008) than any other region of basic expressions. Finally, the smile saliency is associated with early attentional capture (90–130 ms post-stimulus onset), as assessed by the N1 ERP component (Calvo, Beltrán, & Fernández-Martín, 2014), and a neural signature that is source-located at the left infero-temporal (IT, MTG) cortex (Beltrán & Calvo, in press).

Second, regarding distinctiveness, the functional value of the smile is corroborated by the fact that happy faces are recognised as accurately and quickly (or even faster) when the mouth region is presented alone as when the whole face is displayed, whereas expression recognition decreases significantly when the eye region is shown alone (Beaudry et al., 2014; Calder et al., 2000; Calvo, Fernández-Martín, & Nummenmaa, 2014). In addition, the smile is the only facial feature that is systematically and uniquely associated with facial happiness, whereas other facial features overlap to some extent across expressions (Calvo & Marrero, 2009; Kohler et al., 2004). Finally, the distinctive smiling mouth region alone enhances the activity of ERP components (P3b) related to semantic categorisation (Calvo & Beltrán, 2014), with a neural signature that is source-located at the right IT (FG) and dorsal cingulate (CC) cortices (Beltrán & Calvo, in press). This suggests that the smile is used as a shortcut for quick recognition of facial happiness.

Section summary: Perceptual processes are critical for expression recognition

Two perceptually related properties of facial expressions—visual saliency and distinctiveness of facial features—predict differences in expression recognition accuracy and speed, particularly the consistent advantage of happy faces. A salient and distinctive smile captures attention early and can be easily used as a shortcut to identify the corresponding expression of facial happiness, without the slower configural integration of different face regions that would be required for expressions with less salient and/or distinctive features. The smile thus represents an illustrative case of how expression recognition critically depends on perceptual processing.

Experience-dependent plasticity of the expression recognition system

The saliency-distinctiveness explanation can account for the consistent recognition advantage of happy faces. However, it cannot totally account for the recognition accuracy and speed differences among the other basic expressions (e.g., surprise and fear, etc.), as these do not clearly differ in saliency and distinctiveness. To explain such recognition differences, we must consider mechanisms that can encompass all the six basic expressions and, ideally, also take daily life experience into consideration, thus extending the laboratory and modelling approaches.

Although the expression recognition system is biologically rooted and universal, data from cross-cultural studies show that the system is still subject to experience-dependent plasticity. Exposure to different expressions *within* one culture could tune the expression recognition system significantly. The frequency with which an expression occurs in everyday social settings provides observers with experience and learning regarding each expressive category. The more frequently a given expression is encountered, the more familiar viewers become with it. The expressions we see more often lead us to construct a more accurate visual template of their facial features and configural structure, which would then facilitate perceptual encoding. Furthermore, frequent exposure to an expression provides observers with more refined information about its significance, due to contextual association. As a consequence, the mental representation of the expression becomes readily accessible and distinctive, and, therefore, new exemplars can be recognised more easily. Expression recognition could thus be driven by the accessibility of a frequency-dependent representation in long-term memory. Various types of data support this hypothesis.

First, in their meta-analysis of data on cross-cultural recognition of emotional expressions, Elfenbein and Ambady (2002; see Elfenbein, 2013) concluded that facial emotions are generally recognised better when posed and judged by members of the same versus a different culture, an effect known as the in-group recognition advantage. Consistently, this advantage decreases for cultures with more exposure to each other. This implies that recognition is dependent on the frequency of exposure to different types and styles of expressions. Second, the in-group advantage can be reproduced with computational models of expression recognition (Dailey et al., 2010). By manipulating the amount of exposure of the computational model to facial expressions of different cultures during training, and the frequency with which the model was exposed to particular categories of facial expressions, Dailey et al. (2010) found corresponding variations in expression recognition. Recognition increased selectively as a function of frequency of exposure to different expression styles and categories.

Additional evidence comes from studies using a correlation approach. First, Somerville and Whalen (2006) obtained retrospective estimates of the frequency with which 1390 participants believed they had encountered each of the six basic expressions in their lifetimes. The expressions were rank-ordered from most to least frequent as follows: happiness, sadness, anger, surprise, disgust and fear. Second, Calvo, Gutiérrez-García et al. (2014) recorded the actual frequency of seen expressions in multiple everyday social contexts along 90 days (2462 samples of seen expressions were collected). Happy faces were observed most frequently (31%), followed by surprised (11.3%), sad (9.3%), angry (8.7%), disgusted (7.2%) and fearful faces (3.4%); non-basic emotional expressions, e.g., pride or shame (29%). The correlation between the online (Calvo, Gutiérrez-García et al., 2014) and the retrospective scores (Somerville & Whalen, 2006) was significant (r = .83). Third, there were significant relationships (generally, rs >

.70) between the observed frequency (Calvo, Gutiérrez-García et al., 2014) and recognition accuracy and/or speed in prior studies (Calder et al., 2000; Calvo & Lundqvist, 2008; Calvo & Nummenmaa, 2009; Elfenbein & Ambady, 2003; Nelson & Russell, 2013; Palermo & Coltheart, 2004): the more frequently an expression occurred, the more accurately and faster it was categorised. These data suggest that frequency of occurrence contributes significantly to recognition and accounts for the recognition differences among facial expressions.

Section summary: Frequency of perceptual exposure is related to expression recognition

Expression recognition and discrimination can be accomplished by processing of perceptual features (e.g., visual similarity, saliency and distinctiveness) without affective processing. Perceptual properties and the corresponding template of each facial configuration may be further tuned by the frequency of encountering each expression. More frequent exposure to particular features that are salient and distinctive of a given expressive category would in this way contribute to recognition and discrimination. The fact that the in-group effect can be computationally simulated suggests that frequency may influence recognition mainly—if not solely—through perceptual mechanisms in the absence of affective experience.

CONCLUSIONS: VISUAL AND EMOTIONAL MECHANISMS OF EXPRESSION RECOGNITION

A major question we aimed to answer with this review was "What information is encoded and functional for the recognition of facial expressions of emotion"? This question can be decomposed into three issues, which we have addressed in three major sections: first, whether facial expressions of emotion are recognised and discriminated as distinct categories; second, whether affective content is extracted from facial expressions and contributes to expression recognition; and, third, the extent to which expression recognition depends on emotionless, purely perceptual processes. We next summarise the certainties as well as the nuances or limitations regarding each of these issues.

Facial expressions are perceived as categories

Explicit recognition studies consistently show that basic expressions are perceived categorically, and that some of them are consistently identified more accurately and faster than others. Happy faces are recognised fastest and most accurately, followed by surprised, sad, angry, disgusted and fearful expressions. Not only is recognition performance for all expressions greater than chance level, but accuracy scores are generally above 70%, with reliable discrimination among the six basic emotions. This supports a categorical view of emotional expression processing. Such results are mainly observed with posed, prototypical and high-intensity expressions as stimuli, whereas discrimination decreases to some extent for spontaneous, blended and subtle expressions.

Nevertheless, in most studies collecting explicit recognition measures, a forced-choice response format has been used, with a reduced number of pre-specified verbal labels available for responding. This limits and biases the response options, as it funnels a variety of potential interpretations into one-word pre-specified categories, thus potentially inflating the discrete nature of the six differentiated facial emotions. However, neuroimaging measures not affected by such methodological constraints have shown specific neural signatures for different facial expressions in the core facial expression recognition system of the brain. This evidence suggests that expressions are processed as relatively separable categories.

Facial affect is automatically processed but does not significantly contribute to expression recognition

Ratings of expression un/pleasantness and emotional intensity, as well as affective similarity judgements, reveal a two-dimensional valence and arousal space where different expressions are distributed. This is consistent with a dimensional conceptualisation of facial expressions processing. In the same vein, both neurophysiological measures and behavioural studies using affective priming techniques reveal that affective information is extracted automatically and quickly from facial expressions. ERP components indexing affective processing are modulated by facial expression, with an early sensitivity to negative, and later also to positive (happy) expressions, relative to neutral faces. Furthermore, affective encoding can occur earlier than explicit expression categorisation.

Nevertheless, the affective measures generally differentiate between expressions less than explicit categorisation measures do. Presumably, this is due to the extracted affective information having a rather coarse and bipolar nature, around the two general dimensions of pleasantness and arousal. As a consequence, affective processing can play only a minor role in expression recognition. The coarse valence encoding along a negative versus non-negative versus positive axis does not contribute significantly to expression recognition because this requires more fine-grained discrimination among multiple specific categories of expressions. Importantly, although affective valence (but not arousal) may be related to recognition accuracy, valence alone is not sufficient to account for expression recognition differences.

Perceptual processes are critical for expression recognition

Non-affective factors including the morphological structure of facial configurations and the visual saliency of distinctive facial cues contribute significantly to expression recognition. These factors drive perceptual mechanisms computing purely visual information in the absence of affective processing. In fact, computational models assessing physical face image properties, and lacking affective-evaluative components, can reliably reproduce expression recognition data obtained with human observers. Consistently, two perceptually related properties of facial expressions, such as visual saliency and distinctiveness, predict the otherwise highly reliable recognition advantage of happy faces. This suggests that human expression recognition relies primarily on the analysis of visual features rather than on emotional meaning or affective dimensions.

Nevertheless, it is possible that such a purely perceptual account may be valid for face stimuli having little emotional relevance for observers, as is normally the case in experimental settings. In contrast, in daily life conditions, facial expressions are likely to be more affectively engaging, for adaptive reasons, and therefore the role of affective processing could be greater. Association between frequency of occurrence of expressions in everyday life and recognition accuracy leaves open the possibility of integrating a perceptual and an emotional account, rather than viewing them as antagonistic: perception of visual configurations and assessment of emotional value could develop—with frequency of exposure—in tandem to facilitate recognition of facial cues that have adaptive relevance.

Summary

Perceptual, categorical (or semantic) and affective information is extracted from facial expressions of emotion at different time points, and they contribute differently to expression recognition. Morphological features and configuration are quickly available for perceptual processing, and thus they drive the early recognition processes. Affective encoding along the valence dimension develops within a few hundred milliseconds later than perceptual encoding, yet earlier than semantic categorisation. However, the coarse and bipolar nature of such an affective representation is not functional for the fine-grained discrimination required for recognition of specific expressions. Consequently, expression recognition in explicit categorisation tasks relies mainly on perceptual rather than affective processes. Nevertheless, to the extent that discrimination of affective significance becomes important for adaptive purposes in real social encounters, affective processing is likely to play a more decisive role.

Future directions

The majority of behavioural and neuroscientific studies on facial expressions have focused on the classic six basic emotions, with prototypical expressions as stimuli. In addition, while several subcategories of negative facial expressions (angry, fearful, etc.) have been regularly used, only one was available for positive expressions (i.e., happy). However, accumulating evidence suggests that there exists a wider array of other non-basic or "social" emotions that also serve adaptive functions and may also be accompanied with specific facial expressions (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Shaw et al., 2005). Yet, the affective and cognitive mechanisms subserving recognition of these blended, nuanced and complex expressions remain unknown and need to be addressed in both laboratory and field studies.

Similarly, most work on facial expression recognition has been conducted with expressions isolated from their wider physical environment, social context and bodily postures, with focus on recognition of facial expressions presented as separate or independent stimuli. Recent evidence strongly suggests an inherent role for context in the processing of facial expressions (see Ambady & Weisbuch, 2011; Hassin et al., 2013). The emotions in facial expressions are made meaningful in context (Lindquist & Gendron, 2013). It thus remains to be uncovered how our proposed model of visual and affective recognition of faces extends to dynamic natural settings, where multiple surrounding cues may modulate the observer's evaluation of the current emotional state, motivations and intentions from other people's facial expressions.

Finally, it has been established that even elementary neural responses are more reliable and/or stronger for naturalistic, complex and dynamic stimuli versus artificial and reduced yet well-controlled laboratory stimuli (Belitski et al., 2008; Yao, Shi, Han, Gao, & Dan, 2007), thus questioning the generalisability of extremely reduced laboratory research of human sensory processes related to expression recognition. Recent developments in brain signal analysis (Huth, Nishimoto, Vu, & Gallant, 2012; Lahnakoski et al., 2012; Nummenmaa et al., 2012) have enabled quantification of stimulus-specific responses even from complex, dynamic and multisensory streams. Consequently, such an approach would allow researchers to quantify the neural dynamics of visual and affective processing of basic, non-basic and blended facial expressions unfolding in natural settings.

Disclosure Statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Spanish Ministerio de Ciencia e Innovación [grant number PSI2009-07245], and Ministerio de Economía y Competitividad [grant number PSI2014-54720-P] to MGC, and Academy of Finland [grant number 265917], and the European Research Council Starting [grant number 313000] to LN.

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