Review

The Human Face as a Dynamic Tool for Social Communication

Rachael E. Jack[1,2] and Philippe G. Schyns[1,2]
[1]School of Psychology, University of Glasgow, Scotland G12 8QB, UK
[2]Institute of Neuroscience and Psychology, University of Glasgow, Scotland G12 8QB, UK
Correspondence: Rachael.Jack@glasgow.ac.uk (R.E.J.), Philippe.Schyns@glasgow.ac.uk (P.G.S.)
http://dx.doi.org/10.1016/j.cub.2015.05.052

As a highly social species, humans frequently exchange social information to support almost all facets of life. One of the richest and most powerful tools in social communication is the face, from which observers can quickly and easily make a number of inferences — about identity, gender, sex, age, race, ethnicity, sexual orientation, physical health, attractiveness, emotional state, personality traits, pain or physical pleasure, deception, and even social status. With the advent of the digital economy, increasing globalization and cultural integration, understanding precisely which face information supports social communication and which produces misunderstanding is central to the evolving needs of modern society (for example, in the design of socially interactive digital avatars and companion robots). Doing so is challenging, however, because the face can be thought of as comprising a high-dimensional, dynamic information space, and this impacts cognitive science and neuroimaging, and their broader applications in the digital economy. New opportunities to address this challenge are arising from the development of new methods and technologies, coupled with the emergence of a modern scientific culture that embraces cross-disciplinary approaches. Here, we briefly review one such approach that combines state-of-the-art computer graphics, psychophysics and vision science, cultural psychology and social cognition, and highlight the main knowledge advances it has generated. In the light of current developments, we provide a vision of the future directions in the field of human facial communication within and across cultures.

Introduction

As a highly social species [1], humans frequently engage in complex interactions to support the functioning of almost every facet of life — personal, familial or professional. Social interactions involve dynamically exchanging specific patterns of information to achieve a mutual understanding between two or more individuals, allowing each to adjust their cognitions and behaviors for adaptive action within a given culture or context. For example, successfully communicating threat, aggression or submission (agonistic behavior) typically prevents potentially harmful encounters, thereby benefitting all engaging in the interaction [2]. In contrast, a breakdown in communication — for example, difficulty in showing or identifying signs of emotion — can significantly impair social relations, resulting in an increased risk of social isolation [3–5], or even physical or mental harm. With subsequent migration across the world, increasing cognitive complexity [6] and cultural diversification, systems of social communication, much like languages [7], are both highly sophisticated and variable.

One of the richest and most powerful tools in social communication is the face. A brief look at any face demonstrates the numerous inferences observers can make about an individual — identity [8–12], gender/sex [13–15], age [16,17], race/ethnicity [18–20], sexual orientation [21–23], physical health [24,25], attractiveness [26,27], emotions [28–32], personality traits [33–35], pain [36] or physical pleasure [37], deception [38–40] and even social status (for example, in pigmentocracies [41]). Although humans quickly, and apparently effortlessly, perform such a variety of social categorizations on a daily basis [21,33,42], understanding the precise

nature of this process — which specific face information subtends the perception of each category — remains challenging, because the face, as a transmitter of multiple and complex social categories, comprises a high-dimensional, dynamic information space (see also [43]).

Historically, attempts to understand the face as a social communication tool have stimulated nature *versus* nurture debates, from Darwin's groundbreaking theory of the evolutionary origins of facial expressions of emotion [28], to the Zeitgeist of cultural relativism (for example [44–49]), the more recent wave of cross-cultural recognition studies pioneered by Ekman (for example [50]; see [51–53] for reviews) and ontological theoretical developments [29–32,54–56] (see [57] for a review). Yet, whether facial expressions are biologically hardwired or socially learned, or their recognition is based on two (for example, valence and arousal [58]) or many (for example, value, novelty, pleasantness or legitimacy [59–61]) appraisal dimensions, understanding the face as a social communication tool requires identifying which specific face information elicits the perception of a specific social category, such as 'happy', 'female', 'white Caucasian' or 'attractive'.

To address these questions, traditional approaches have typically used theoretical knowledge or naturalistic observation to first select and test small sections of the high-dimensional face information space. A classic example is the universal facial expressions of emotion — 'happy', 'surprise', 'fear', 'disgust', 'anger' and 'sad' — which correspond to a small set of theoretically derived facial expressions that elicit above chance accuracy across cultures [50,62–68]. Although widely considered the gold
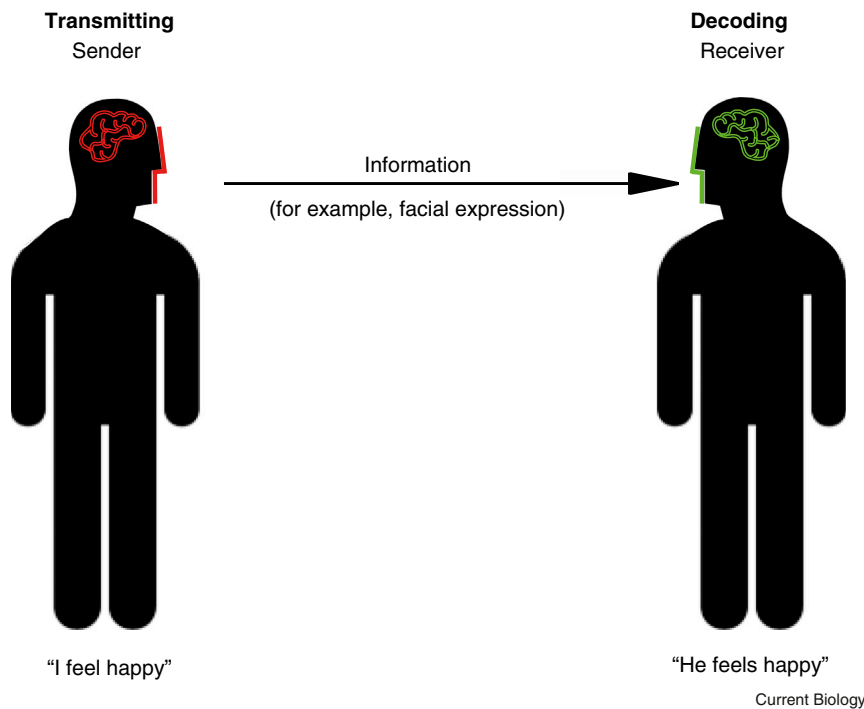
Transmitting
Sender

Decoding
Receiver

Information

(for example, facial expression)

"I feel happy"

"He feels happy"

Current Biology

Figure 1. Information transmission and decoding framework.
Facial expressions, whether innate or learned, form part of a dynamical system of information transmission and decoding. Transmission: the sender encodes a message (here, 'I feel happy') as a form of information (for example, a facial expression, body movement, vocalization) and transmits it across a communication channel to the receiver (for example, a visual or auditory system). Decoding: to decode the incoming information, the receiver uses their prior knowledge (mental representation of category information) to extract task-relevant (diagnostic) features and perform an interpretation (categorical perception), typically resulting in a sufficiently accurate reconstruction of the message (here, 'he feels happy'). Adapted from [53] with permission from the publisher (Taylor & Francis Ltd, http://www.tandfonline.com).

standard in research [69–85], implicit acceptance of these (static) facial expressions not only curtails progress in characterizing the dynamic patterns of facial expressions (see [86] for a review), but also in broadening knowledge of more intricate social categories — for example, 'irritated', 'delighted', 'confused', 'skeptical' — that support our complex everyday social interactions. Consequently, and in contrast to detailed knowledge we have gained of social communication in other species — for example, the alarm calls of the vervet monkey [87] or the waggle dance of the honeybee [88] — a precise characterization of the face as a social communication tool remains to be addressed.

With advances in digital technologies and experimental methods, and the broadening of a scientific culture that embraces cross-disciplinary approaches, exploring the complexities of the face as a dynamic transmitter of social information is now an empirical reality. To mark this new chapter and build a vision of the future directions in the field of facial communication, our review has the following aims. First, to illustrate the challenges of understanding the face (a complex dynamical system) as a tool for social communication. Second, to demonstrate new interdisciplinary approaches that combine methods imported from traditionally distinct fields — for example, psychophysics, vision science, dynamic computer graphics, information theory, social cognition and cultural psychology — to overcome these challenges. And third, to review recent work that has used such methods to advance understanding in facial communication. Finally, we consider future directions by highlighting new and remaining key questions.

A Dynamic System for Transmitting and Decoding Information

To illustrate the challenge of understanding the face as a dynamic tool in social interaction, it is useful first to consider the

process of social communication. At an abstract level, social communication is, like many other communication systems in humans (for example, telephone, television, satellites), other animals (for example [89]), plants (for example [90]) or bacteria (for example [91]), a dynamic system involving the transmission and decoding of information. Figure 1 illustrates the main components of such a general communication system.

As discussed in behavioral ethology [2,92], psychology [93] and engineering [94], *communication* is the act of *information transfer*, in which one individual sends information that modulates the behavior of another, thereby reducing uncertainty. Specifically, as shown in Figure 1, the sender encodes the message (here, 'I feel happy') as a form of information — for example, a facial expression, body movement or vocalization — and transmits it across a communication channel to a receiver. To decode the incoming information, the receiver must use their prior knowledge (their mental representations of category information) to extract relevant (diagnostic) features (for example, [95]) and perform an interpretation (categorical perception). When communication is successful, the receiver reconstructs the message with sufficient accuracy and extracts a meaning, in this case, 'he feels happy'. Understanding a system of communication therefore requires precisely identifying which transmitted information elicits a particular response in the receiver.

Importantly, the act of communication — providing information about the environment (but see [96] for deception) — depends on a number of conditions. Firstly, the information transmitted must be detectable by the receiver; for example, the retinal receptor density of the human eye allows detection of detailed visual information only at relatively short distances. Therefore, increasing distances between sender and receiver would diminish the detectability of relevant face information, such as that conveyed by the sclera, and the recognition of an associated social category — in the case of the sclera, 'fear' [83]. Such receiver characteristics force communication to rely on other sources to transmit detectable information

across longer distances, for example, voice or body movements [97].

Secondly, for communication to succeed, the receiver must associate the detected information pattern, for example, the sclera, with a perceptual category — prior knowledge, whether acquired or hard-wired, here 'fear' — and its associated meaning in a given culture or context. Communication tends to breakdown when the transmitted information is unknown to the receiver — for example, only certain medical professionals associate specific facial movements with underlying neurological conditions [98] — or where sender and receiver do not share the same meaning associated with the information pattern. For example, the 'thumbs up' gesture means 'OK' in Western countries, but is a phallic insult in the Middle East (see [48,49,99] for more examples of cross-cultural confusions and mismatching). Thus, understanding the characteristics of the receiver's mechanism (see also [100] for environmental factors) — detection capabilities, stored information patterns and their associated meanings — can inform the patterns of information it is designed to capture to support social communication (but see also superstimuli [101]). In recognizing the fundamental link between information production and perception, Darwin used the receiver's perceptual response (emotion categorization) to investigate the universality of facial expressions of emotion, an approach that would dominate the field for over a century.

Thirdly, communication largely depends on the reliability (honesty) of the information transmitted and sender/receiver advantages. For example, sending information that reliably manipulates the behavior of others, or receiving reliable predictions about the environment, both support adaptive action. However, the transmission of dishonest information and sender/receiver disadvantages is regularly observed in communication [102]. Thus, communication comprises three distinct forms: *signalling*, such as reliable fearful facial expressions [103,104]; *cueing*, such as when skin color indicates caste/social status; and *coercion*, such as the mimicry of genuine Duchenne smiles. Such distinctions, applicable to both animal and human communication, highlight the intricacies of understanding the phylogenetic and ontogenetic evolutionary bases (within a culture) and communicatory function (veridical, deceptive or involuntary) of transferred information.

Finally, the act of communication — sending information to modulate another's behavior — can be deliberate, such as a greeting smile, or unintentional, as in blushing, which indicate uncontrolled anxiety. Identifying which specific aspects of the face — morphology, complexion, dynamics — can be used to intentionally manipulate others' behavior, and which produces involuntary, fixed, and possibly inconcealable information, is central to understanding *how* the face is used to optimize success within an ecological niche. For example, a specific facial expression such a smile (voluntarily produced information) could dampen the negative social impressions from an untrustworthy looking facial morphology (involuntarily produced information).

In all such cases — honesty or deception, volitional or forced, advantageous or detrimental — identifying the specific face information that subtends the perception of specific social categories is essential to understanding the system of social communication. However, a major challenge to this endeavor is that the face is a high-dimensional, dynamic information space.

A High-dimensional Dynamic Information Space

There are three main dimensions of facial variation: dynamics, morphology and complexion. Firstly, the human face is equipped with a large number of independent striated muscles, under voluntary control [105], each of which can be combined and activated at different levels of intensity over time. Consequently, the face is capable of generating a high number of complex dynamic facial expression patterns. Secondly, facial morphology (shape and structure) varies across multiple dimensions, including face width, height, brow ridge and cheek-bone prominence, jaw width, inter-eye distance, mouth width, lip thickness, forehead height, and so on [106,107]. Thirdly, complexion — comprising color, for example, pigmentation [108] or pallor/redness, and texture, for example, wrinkles, scarring, cutaneous conditions, adiposity — provides yet another potential source of information.

Another salient platform for social communication is provided by facial adornments: cosmetics/painting, tattooing, piercing, jewelry, hair, clothing and teeth sharpening/blackening are widely used to indicate social status or group alliances, or accentuate beauty (by enhancing or camouflaging morphological or textural face features [109]). As a result of these variations, every one of the 106 billion humans [110] that has ever walked the earth has possessed a unique face (and one that has changes across his or her lifetime), a point that brings home the high level of objective information the face can transmit.

To advance the science of social communication and inform socially intelligent and culturally aware avatars and companion robots with precise knowledge of social information [111–117], it is necessary to objectively identify the low-dimensional face information, for example, facial expression patterns, that subtends different social judgments, and we shall consider how this may be done in the next section.

Theoretical and Empirical Approaches to Social Communication

As mentioned above, classic approaches to understanding the face as a communication tool typically used theoretical knowledge or naturalistic observations to select and test a very small portion of the high-dimensional face information space. Although undoubtedly influential, such approaches can cast a relatively narrow light on the question, as we will now illustrate (see also [51,53,118] for further discussion).

Most notably, based on Darwin's groundbreaking theory of the biological and evolutionary origins of facial expressions of emotion (see also [103,119]), pioneering work by Ekman proposed a specific set of facial expressions as universally communicating six basic emotions across all cultures. Each of these facial expressions comprised a theoretically derived facial movement pattern (see [120] for prototypes and major variants) described according to the Facial Action Coding System (FACS) [121] — an objective system that comprehensively describes all visible facial movements called Action Units (AUs) [122]. For example, 'happy' comprises AU6 (Cheek Raiser) and AU12 (Lip Corner Puller), whereas 'sad' comprises AU1 (Inner Brow Raiser), AU4 (Brow Lowerer) and AU15 (Lip Corner Depressor). In a series of cross-cultural recognition studies (for example [29,50,63,65,68,123]), these specific facial expressions, the AU patterns, consistently elicited above chance recognition performance across different cultures.

Subsequently, the field largely concluded that these specific AU patterns universally communicate six basic emotions across all cultures (see [69] for a review) with resulting stimulus sets (for example [124–129]) fast becoming the gold standard across broad fields including cultural (for example [69–71]), clinical (for example [72,73]), developmental (for example [74]) and health psychology (for example [75]), neuroscience (for example [76–81]), perception and visual cognition (for example [82–84]) and computational modelling (for example [85]).

However, in addition to a criterion (>16% recognition accuracy) that does not reflect reliable communication and potentially masks cultural differences (for example AU patterns for 'fear' and 'disgust' consistently elicit significantly lower recognition accuracy in non-Western cultures [50,62–68]; see [130] for a review), the conclusions provided little impetus to consider or test other AU patterns for basic emotion communication. Consequently, knowledge of facial expressions of emotion remained restricted to a small set of static AU patterns that communicate only six emotions mostly in Western culture (a small proportion of the human population, see [131]). Yet, to precisely identify the dynamic AU patterns that communicate emotions, or other relevant social categories such as personality traits or mental states, within and between cultures requires a thorough exploration of the high combinatorics of dynamic AUs — a major empirical challenge that requires a systematic data-driven approach.

Psychophysical Laws of Social Perception

One way of addressing this challenge is to import the successful methods and knowledge of psychophysics, a field that aims to characterize the relationship between objectively measurable information in the external environment (physical stimuli) and its interpretation by an observer (subjective perception). Thus, by deriving psychophysical laws (for example [132–134]), psychophysical methods typically simplify complex, high-dimensional stimulus information to the few dimensions that subtend perception: they perform a dimensionality reduction. For example, a model observer performing the low-level visual task of discriminating left from right oriented Gabor patches near contrast threshold will require information about three parameters: input orientation, contrast and spatial frequency. A parametric design examining these three dimensions would produce a thorough understanding of how the model observer's visual system resolves the task, with the contribution of each dimension to perceptual decisions modeled within the framework of statistical decision theory [135,136].

As indicated above, however, psychophysically probing the receptive fields of social face perception (high level vision) immediately presents a considerable challenge [137,138]. Relative to the dimensions of simple Gabor patches, however, conjecturing which dimensions of complex, natural face information — dynamics, morphology, complexion or a combination of the three — to probe is disproportionately more complicated, with each dimension constituting an explicit hypothesis about the nature of the categorization task. Because the theoretical and empirical stakes are high when selecting and exploring dimension(s) of face information, combining theoretical and empirical knowledge of social face communication can help guide experimental design.

To illustrate this, consider judgments of physical attractiveness, which could relate to judgments of mating or parenting potential. Mating potential relies on identifying a healthy opposite sex individual, communicated by genetically determined, and thus relatively fixed, aspects of the face, such as symmetry and complexion [25,139], and sex differences in morphology, such as jaw and brow ridge prominence [140]. In contrast, parenting potential might depend more on judgments of behavioral intentions such as trustworthiness or warmth, as communicated by more transient and voluntarily controlled face information such as facial expressions (for example [141]). Thus, psychophysics could be used to sample information from each potentially relevant dimension of the face — complexion and dynamics - and measure the receiver's subjective response, thereby deriving the psychophysical laws of social perception, in this case, of long-term partnering or one night stand potential [142,143].

To directly illustrate the successful application of psychophysics to exploring dimensions of face information, we will return to our previous example of facial expressions of emotion (dynamics). Consider that we aim to identify which facial expressions communicate 'rapid danger' and 'distant danger' in a largely unknown culture (for example, the Sentinelese people). With no a priori knowledge, or assumptions, of these facial expressions, psychophysical methods can be used to sample the dynamic dimension of the face (their dynamic AU patterns) and measure the receiver's subjective response (categorical perception).

Figure 2 illustrates such an approach using an example trial. On each experimental trial, a computer graphics Generative Face Grammar (GFG) platform [144] randomly samples from the relevant face dimension — the dynamic AU information space. In this illustrative trial, a biologically plausible combination of three AUs is randomly selected from a core set of 42 AUs (AU5 — Upper Lid Raiser color-coded in red, AU9 — Nose Wrinkler in green and AU12 — Lip Corner Puller in blue). The GFG then assigns a random movement to each AU by selecting random values for each of six temporal parameters (onset, acceleration, peak amplitude, peak latency, deceleration and offset; see color-coded curves). The dynamic AUs are then combined to produce a photo-realistic random facial movement, illustrated here with four snapshots (see Movie S1 in the Supplemental Information). The naïve receiver categorizes the stimulus as meaningful (here, 'rapid danger') at a given level of intensity (here, 'strong') if the synchronies of random face movements correlate with their perceptual expectations (mental representation) of 'rapid danger' at 'strong' intensity; if the pattern does not correspond to either category, 'rapid danger' or 'distant danger', the receiver selects 'other'.

Over many such trials, we obtain a distribution of the relationships between specific dynamic AU patterns — segments of the high-dimensional information space called the categorization manifold — and the receiver's perceptual response. Statistical analysis of these relationships, broadly referred to as reverse correlation [145], can reveal the dynamic AU patterns that reliably communicate to the receiver 'rapid danger' and 'distant danger' at different levels of intensity. In doing so, we can derive the psychophysical laws of high-level constructs as they relate to the physical aspects of the face. Repeating the same experiment
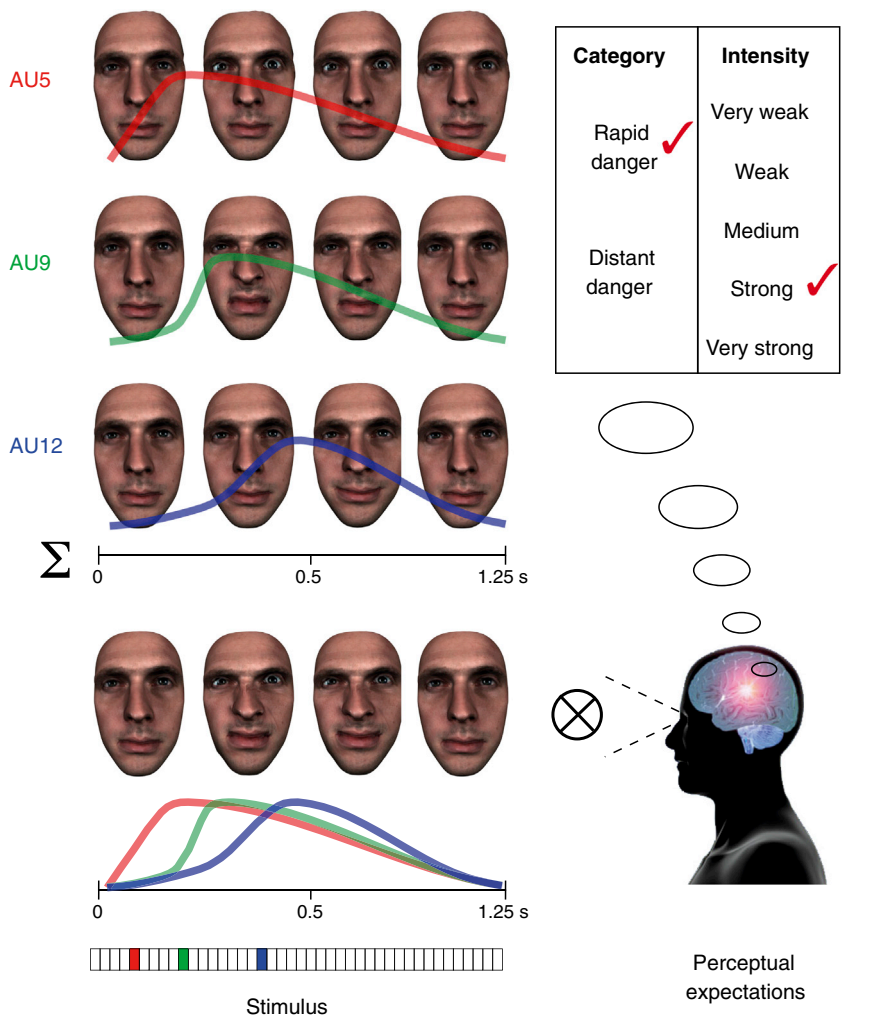
chronies of information such as AU conjunctions over time and structure the diagnostic dimensions of the categorization manifold. Consequently, deriving the psychophysical laws of social perception can provide both the syntax of dynamic information, which could also constrain the algorithms (computational procedure) subtending human and artificial perception of different social categories, for example, by informing the specific temporal order for the coding and integration of the components of information for each social category.

We will now briefly consider recent work that has used psychophysical methods to explore two dimensions of face information, dynamics and morphology, to identify the dynamic facial expressions that communicate the key social categories of emotions and social traits.

in different cultures (Western and East Asian, or different socio-economic classes, or age groups) could then reveal whether the dynamic facial expressions are similar or different, and if so, how.

Whether applied to the individual dimensions of dynamics, complexion or morphology, or their combination, the strength and broad potential of psychophysics is that it can, in principle, model any face information that communicates perceptual categories. This could include basic or complex emotions such as 'happy', 'contempt', 'panic' or 'fury' [146,147], social traits such as 'competent', 'dominant', 'attractive' or 'trustworthy' [141,148,149], mental states such as 'thinking', 'bored', 'confused' or 'doubtful' [150–152], genuine and fake happiness, sadness, or guilt, masculinity and femininity, pain and pleasure, sick and healthy [153,154], young and old [17], individual identity, and so forth (and including parameters of intensity, when applicable).

Such statistical relationships between dimensions of the face information space and the receiver's perceptual judgment can be univariate, thereby reducing the high-dimensional information space to those that communicate a specific meaning (for example, 'rapid danger'), or multivariate, which can capture syn-

Cultural Specificities in Dynamic Facial Expressions of Emotion

Facial expressions provide visually salient dynamic patterns of information to communicate emotions (see also [155,156] for information from voice and [157] for information from body posture). With biological and evolutionary origins [103,119], the six basic facial expressions of emotion have largely been considered universal. Yet, differences in recognition accuracy across cultures [50,62–68] and proposed culture-specific accents/dialects [49,158,159] question the true extent of universality (see also [51,160] for reviews). Although cultural specificities in facial expressions of emotion are widely discussed [29,161–163], knowledge of which facial expressions communicate emotions within and across cultures is largely limited to static (typically posed) facial expressions [124,127,128,159] that are recognized primarily in Western culture (see [62–64,67]).

To address this knowledge gap, we used the GFG (Figure 2) to psychophysically model the dynamic facial expressions of the six classic emotions in Western Caucasian and East Asian
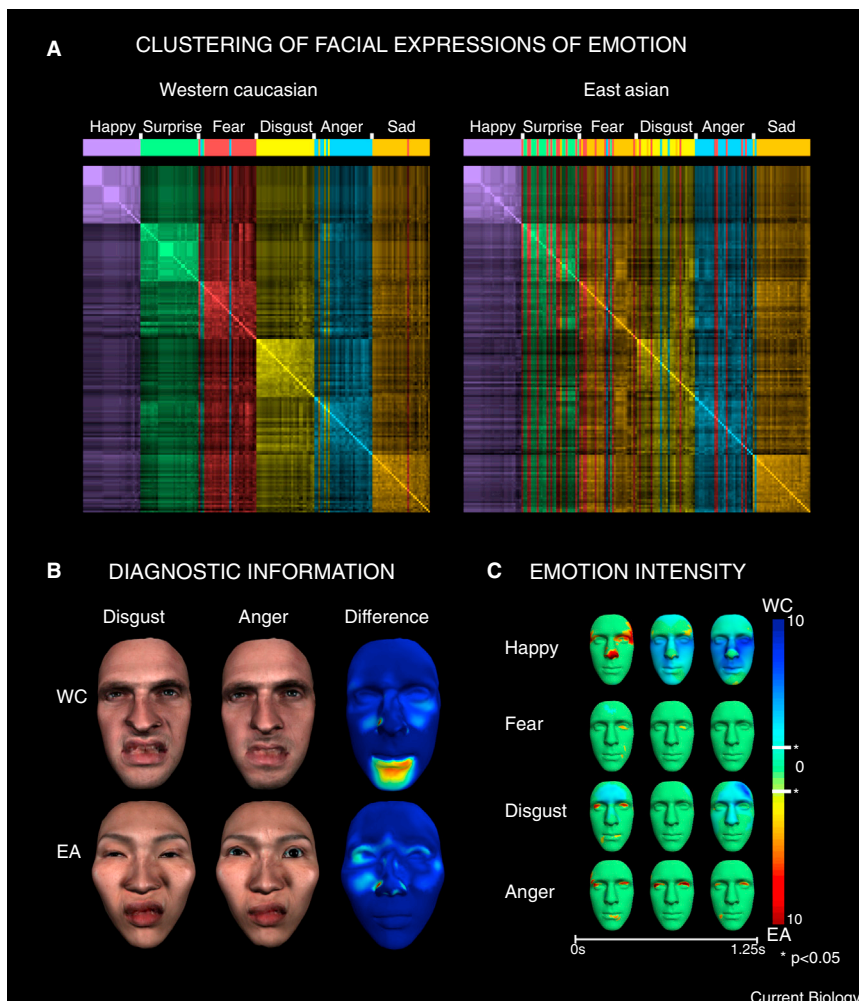
Figure 3. Cultural specificities in dynamic facial expressions of emotion.
(A) Clustering of facial expressions of emotion. For each culture, Western Caucasian (WC) and East Asian (EA), vertical color coded bars show the cluster membership of each facial expression model (represented as a 42 x 1 dimensional vector detailing the AU pattern) as labeled — 'happy', 'surprise', 'fear', 'disgust', 'anger' and 'sad' (30 models per emotion category and culture). The underlying gray-scale similarity matrix shows the similarity between model pairs, where lighter squares indicate high similarity, darker squares low similarity. Note in the WC group, lighter squares along the diagonal indicate higher model similarity within each of the six emotion categories compared with the EA models. Correspondingly, k-means cluster analysis shows that the WC models form six emotionally homogenous clusters (for example, all 30 'happy' WC facial expression models comprise a single cluster, color-coded in purple). In contrast, the EA facial expression models show overlap between emotion categories, particularly for 'surprise', 'fear', 'disgust', 'anger', and 'sad' (note their heterogeneous color coding). (B) Diagnostic information. WC and EA models show that different face regions distinguish certain emotions (here, 'disgust' and 'anger'). In WC models (top row), the mouth is more informative to distinguish 'disgust' and 'anger' (note the difference in the mouth region of the face identity maps, and the corresponding color-coded difference map). In EA models (bottom row), the eyes are more informative — note the narrowing of the eyes in 'disgust' compared to the salient eye whites in 'anger' (see also corresponding face identity and difference map). (C) Emotion intensity. For four emotions, color-coded face maps at three time points show the spatio-temporal location of expressive features conveying emotional intensity. Blue indicates WC-specific dynamic face patterns; red indicates EA-specific dynamic face patterns where values represent the t-statistic ($p < 0.05$). Note for the EA models (red colored regions), emotional intensity is communicated with early eye region activity. Adapted with permission from [147].

culture, revealing three main differences [147], with the results shown in Figure 3.

Panel A of Figure 3 shows the clustering of facial expressions of emotion: using a combination of k-means cluster analysis and Mutual Information [164], Western Caucasian models form six distinct and emotionally homogeneous clusters — high *within*-category facial expression similarity and low *between*-category facial expression similarity (for example, all 30 Western Caucasian 'happy' facial expression models comprise a single cluster, color-coded purple) — revealing a distinct and culturally shared representation of each emotion. In contrast, East Asian models tend to overlap between certain emotion categories (note the heterogeneous color-coding of the facial expression models of 'surprise', 'fear', 'disgust' and 'anger'), reflecting a culture-specific departure from the common view that human emotion communication is comprised of six universally represented basic categories (for example [165]).

Panel B of Figure 3 shows diagnostic information: Western Caucasian (top row) and East Asian (bottom row) facial expressions show that different face movements distinguish certain emotions (here, 'disgust' and 'anger'). As shown across the individual texture maps, and corresponding color-coded difference

maps, the mouth is more informative in the Western Caucasian facial expressions of 'disgust' and 'anger', whereas the eyes are more informative in the same East Asian facial expressions (note the narrowing of the eyes in 'disgust' compared to the salient eye whites in 'anger' (see also [67,166,167] for culture-specific use of the eyes and mouth).

Panel C of Figure 3 shows emotion intensity: Western Caucasian and East Asian facial expressions also show differences in the dynamic communication of emotional intensity. Illustrated here with four facial expressions of emotion — 'happy', 'fear', 'disgust', and 'anger' — color-coded face maps show the culture-specific face features that convey emotional intensity across time. For example, early red colored areas show that East Asian individuals primarily use early eye region activity to convey emotional intensity, a finding that is mirrored by East Asian emoticons, where (^.^) represents happy and (>.<) represents angry.

By mapping the relationship between the dynamic AU information space and the perception of the six classic emotion categories in different cultures, we precisely characterized cultural specificities in facial expressions of emotion, questioning notions of universality. Given that the complexities of human emotion
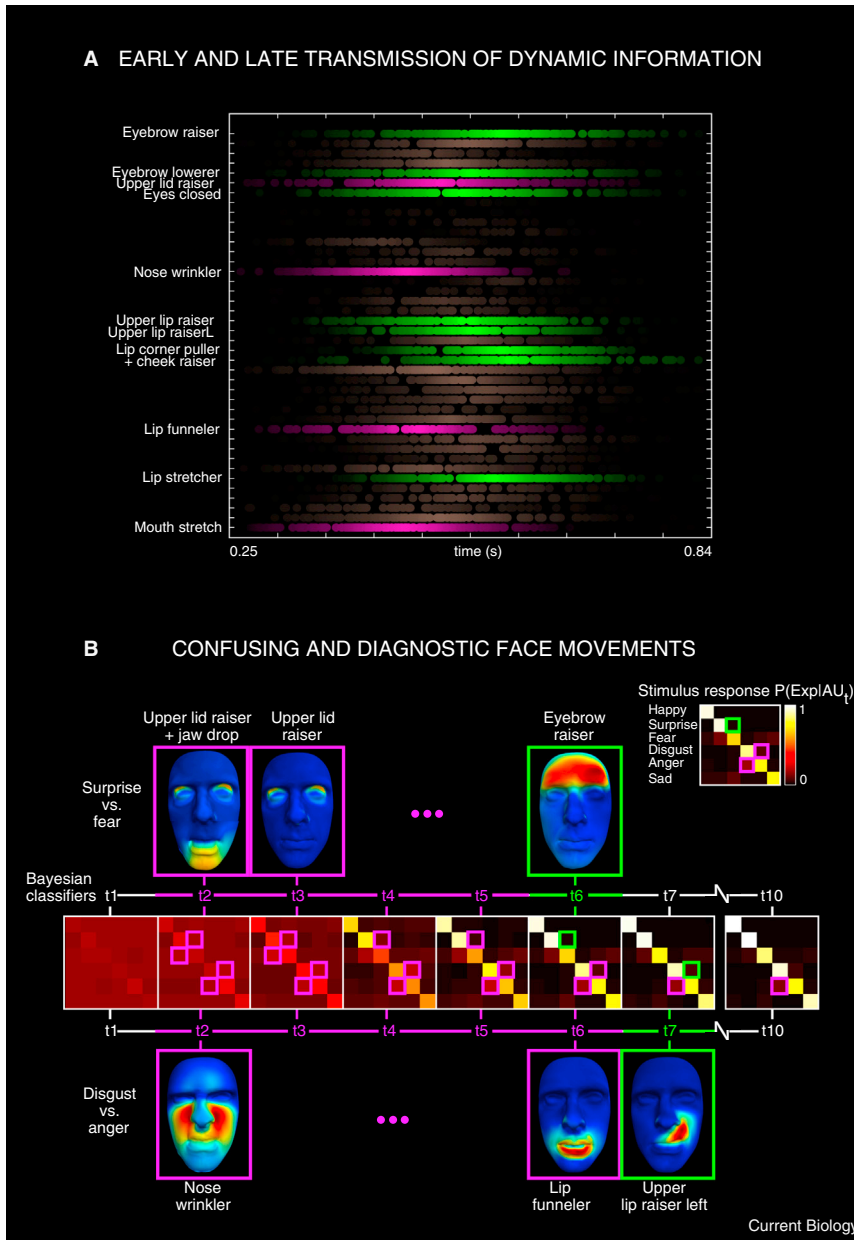
Figure 4. Hierarchical transmission of dynamic face information over time.
(A) Early and late transmission of dynamic information. In each row, color-coded circles show the distribution of peak latencies for each AU (see labels on left) for all facial expression models (120 models per emotion category). Brightness indicates distance to the median peak latency (weighted by the proportion of models with that AU). Facial expressions of emotion are characterized by the early transmission of few biologically rooted AUs, color-coded in magenta (for example, Upper Lid Raiser, Nose Wrinkler; $p < 0.05$), followed by the later transmission of AUs typically diagnostic for the six classic emotions, color-coded in green (for example, Brow Raiser, Upper Lip Raiser; $p < 0.05$). (B) Confusing and diagnostic face movements. Bayesian classifiers applied to dynamic facial expression models across time (t1–10) show that early confusions (see magenta squares in confusion matrices) are due to the common transmission of certain AUs, such as Upper Lid Raiser in Surprise *versus* Fear (see color-coded deviation maps outlined in magenta from t2–t5), and Nose Wrinkler in Disgust *versus* Anger, from t2–t6. Later transmissions of diagnostic AUs support the categorization of all six emotions (for example, 'surprise' transmits Brow Raiser (t6) distinguishing it from 'fear'; 'disgust' is discriminated from 'anger' due to the transmission of Upper Lip Raiser Left (t7). See also Movie S2 in the Supplemental Information. Adapted with permission from [168].

tory function. For example, whereas eye widening and nostril flaring, typical of fear facial expressions, facilitate the flight response, for example, by identifying escape routes and optimizing muscle function, wrinkling the nose and narrowing the eyes, typical of disgust facial expressions, provide an effective strategy for protecting against the entry of pathogens. As adaptive behaviors that benefit the expresser [103], these biologically-rooted face movements probably evolved as rapid movements to enhance their physiological function. Consequently, the facial expressions used by modern man to support social communication could comprise an embedded set of early, elemental face movements on which social and culture specific information is later grafted to refine meaning. Analysis of dynamic models of the six classic facial expressions of emotion indeed shows an intriguing hierarchical transmission of information over time, reflecting a more complex communication system that supports a series of successive and increasingly refined categorizations [168]. The data are illustrated in Figure 4.

Panel A of Figure 4 shows early and late transmission of dynamic information: In each row, color-coded circles show the distribution of peak latencies for each AU over time for all facial expression models. The early transmission of dynamic face information is characterized by few, biologically rooted AUs (for example Nose Wrinkler and Upper Lid Raiser, color-coded in

communication require a number of nuanced emotion categories, for example, 'fury', 'delighted', 'contempt' or 'panic', extending the range of dynamic facial expressions of emotion across cultures [146] could further refine the characterization of cultural commonalities and differences in emotion communication.

Hierarchical Transmission of Dynamic Face Information Over Time
Rather than comprising all-or-nothing displays, facial expressions are orchestrated dynamic patterns that unfold over time. Because facial expressions of emotion are largely evolved signals, adapted from their original biological function to serve social communication [28,103,119], understanding how and why specific face information is transmitted over time, their syntactical 'design', could reveal further knowledge of their communica-

magenta) [103], whereas later transmissions (color-coded in green) comprise AUs typically diagnostic for the six classic emotions (for example, Brow Raiser and Upper Lip Raiser) [84].

Panel B shows confusing and diagnostic face movements: Using Bayesian classifiers applied to the dynamic facial expressions over time, the early transmission of certain AUs supports the categorization of fewer emotion categories. For example, both 'surprise' and 'fear' transmit Upper Lid Raiser early in the dynamics, resulting in their early confusion. Later in the dynamics, the transmission of diagnostic AUs results in the discrimination of all six emotion categories. For example, 'surprise' transmits the Brow Raiser later, which distinguishes it from 'fear' (see also Movie S2 in the Supplemental Information for a similar pattern with 'disgust' and 'anger').

Analysis of the syntax of dynamic face patterns shows that facial expressions of emotion are perceptually segmented across time and follow a hierarchical evolution from biologically basic to socially specific, thereby questioning the view that human emotion communication comprises six basic, psychologically irreducible categories. In line with biological signalling predictions, early face movements also show characteristics of detectability, such as the sudden appearance of the high contrast eye whites (a feature unique to humans [169]) and nose wrinkling typical of danger signals [170], each of which could act as salient 'attention grabbers' [171,172] to facilitate the perceptual processing of socially relevant information (for example, see [104] for eye gaze). Thus, precisely examining the unfolding of dynamic facial expressions across time reveals that early and late facial information could perform functionally different roles in social communication.

Psychophysical methods can thus be used to precisely characterize the syntactical design of dynamic facial expressions of emotion, which could be broadened to examine other more subtle emotions, for example, 'irritation', 'delighted' or 'shame', or other forms of dynamic social communication, such as genuine and fake smiles [39], social traits, such as trustworthiness or dominance, or mental states, such as 'confusion', 'doubt' or 'interest', in a culturally sensitive manner. Modelling the perceptual expectations of individual observers of different cultures, for example, in clinical and typical populations, could also inform the sources of communication breakdown, for example, where expectations of temporal order are violated, and inform the development of therapeutic interventions.

Dynamic Face Information Transiently Camouflages Social Trait Impressions From Facial Morphology

Successfully negotiating social situations involves communicating not only transient emotional states, but also stable traits such as trustworthiness, dominance or attractiveness, with important consequences for individuals. This can be important, for example, in mate choice [27,173], occupational [174] or educational opportunities [175], sentencing decisions [176,177], and the behavior of groups (for example, voting preference [42,178]). Across the animal kingdom, specific facial displays are used to strategically alter the perceptions and subsequent behaviors of others, for example, subordinates, prey, or predators, thereby increasing one's chances of success within an ecological niche. As an example, high status rhesus monkeys display specific facial expressions to communicate their rank to

subordinates in the animal hierarchy [179]. Although certain human face morphologies are strongly associated with specific social traits such as attractiveness, dominance and trustworthiness [149,180], specific patterns of face movements can strategically camouflage these default social impressions, thereby manipulating the social judgments of others.

Using psychophysical methods, we have shown that facial expressions trump morphology in the perception of social traits. Figure 5 demonstrates the results using two social traits, dominance and trustworthiness, as illustrative examples. Each color-coded face map shows the dynamic AU patterns associated with the perception of each social trait (dominance and trustworthiness). We then applied each dynamic mask to different face morphologies that were previously rated as the opposite social trait; for example, we applied a dominant dynamic mask to submissive face morphologies. Social trait judgments of the resulting faces showed that the dynamic masks transiently camouflage the default social trait impressions conveyed by phenotypic facial morphology. For example, a face previously judged as highly submissive produced a rating of highly dominant when displaying a dominant facial expression [141].

An intriguing source of inequality is also shown: whereas dynamic masks of dominance and trustworthiness easily override the effects of our genes (for example, the actor Anthony Hopkins can convincingly portray either a psychopathic cannibal or a loyal butler), attractiveness, where phenotype dominates, is the most difficult to camouflage with dynamic masks, which is why fashion/beauty models comprise a niche group. Thus, while individuals can display specific facial expressions to flexibly manipulate social perceptions of trustworthiness and dominance to their advantage, regardless of their inherited facial morphology, perceptions of attractiveness, a relevant factor for mating potential and gene transmission, remain relatively robust to dynamic mask camouflaging.

In this review we have explained how psychophysical methods can be applied to understanding how different dimensions of face information, dynamics and morphology, each contribute to social perception, providing new opportunities to address key questions. For example, to elicit judgments of trustworthiness, must out-group members, indicated, for example, by skin color, display more intense facial expressions of trustworthiness than in-group members? How does voluntary face information such as facial expressions (a potential tool for deception) and involuntary, fixed and inconcealable face information such as skin color contribute to social judgments? Modelling the contribution of different dimensions of face information in relation to the receiver's internal knowledge, including perceptual biases such as racial stereotyping [148] and theory of mind, can therefore further reveal the complexities of social communication within and between different groups.

Conclusions

We have illustrated the challenges to understanding the human face as a dynamic transmitter of social information, presented psychophysical methods designed to address this challenge — parametric sampling of face information coupled with subjective perception to derive the psychophysical laws of social perception — and recent work demonstrating the strengths of this approach. Earlier models of face recognition
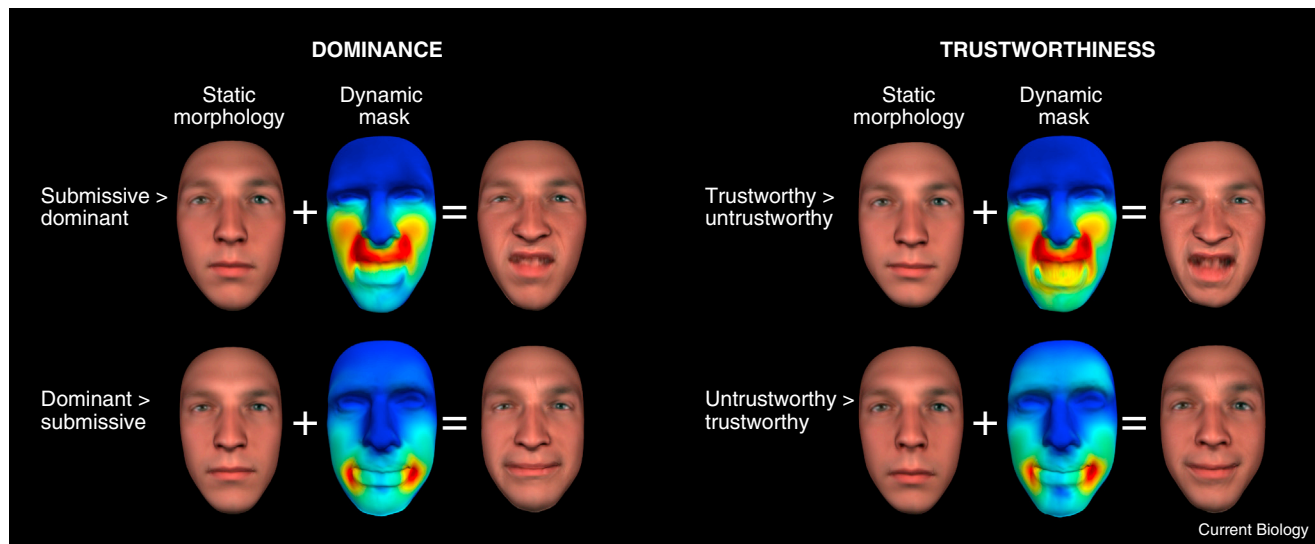
Figure 5. Dynamic face information transiently camouflages social trait impressions from facial morphology.
Here, we use two social traits, dominance and trustworthiness, as examples to illustrate the perceptual effect of applying a dynamic social mask to different face morphologies. Dominance: the Static Morphology represents an average of male identities judged as highly submissive (–ve dominance). The color-coded Dynamic Mask shows the face movements associated with judgments of high dominance. When added to the Static Morphology, the Dynamic Mask transforms the social judgments of the face from submissive to dominant. As shown in Dominant > Submissive, the same transformation occurs when a submissive Dynamic Mask is added to a dominant Static Morphology. Trustworthiness: the Static Morphology represents an average of male identities judged as highly trustworthy. The color-coded Dynamic Mask shows the face movements associated with judgments of low trustworthiness. When added to the Static Morphology, the Dynamic Mask transforms social judgments of the face from trustworthy to untrustworthy. As shown in Untrustworthy > Trustworthy, the same transformation occurs when a trustworthy Dynamic Mask is added to an untrustworthy Static Morphology.

[181] considered that different social categorizations such as identity, expression, gender, and ethnicity rely on separate information processing streams. Now, current knowledge shows that complex interactions between different dimensions of face information, for example, dynamics, morphology and/or complexion, subtend social perception. For example, while certain face morphologies are strongly associated with certain social traits such as trustworthiness or dominance, specific facial expressions can be used to camouflage this information, thereby manipulating social trait impressions.

Using the face to transmit information for social communication is typically achieved within specific contexts, where the same face information (for example, tightly squeezed eyes, bared teeth) can have different meanings (winning, losing, pleasure or pain) when combined with additional sources of information such as body movements, vocalizations, clothing or scenery (see [182–184] for reviews). As with exploring the high-dimensional information space of the face, precisely identifying which contextual information — vocalizations, body posture, movements or shape, clothing and hairstyles, in and outdoor scenes, weather, season or time of day, buildings, occasion, culture and so on — contributes to different social categorizations presents an additional, much greater challenge. Because social communication (and perception generally) can involve the integration of information from multiple high-dimensional information spaces, exploring this hyperspace of multi-sensory information presents a genuinely ambitious feat. To begin to address this challenge, we have demonstrated the strengths and potential of psychophysics to parametrically manipulate and combine different information sources to derive the psychophysical laws of social perception.

With the emergence of a new digital economy, it is increasingly important to equip new technologies — for example, web-based facilities designed for cross-cultural communication, socially interactive avatars and companion robots — with detailed knowledge of human social communication. Using objective methods to derive such knowledge — for example, which facial expressions communicate the same meaning across cultures, and those that generate confusion — can be installed and used for the accurate recognition and adaptive display of culture-appropriate or universally understood social information. Web-based facilities for human communication could analyze the face of each participant, identify potentially confusing face movements — for example, using the eyes to show emotional intensity in East Asian culture [147] — and provide real time on-screen translations for other-culture participants where necessary. Similarly, companion robots could adjust their facial structure, complexion and dynamics to suit a specific role or context, such as displaying more signs of trustworthiness when greeting guests, or dominance when guarding a property.

Finally, although the nature *versus* nurture debate has provided substantial empirical and theoretical impetus (particularly in emotion communication), modern research now aims to understand the symbiotic relationship between biology and environment: "genes are expressed *through* the environment, and not independently of it" [185]. Thus, understanding social communication within an ecological (cultural) niche also requires examination of how different physical environments — for example, mountainous or flat landscapes, differing light exposure — have shaped sender and receiver apparatus (the face and visual system), which could reveal the extent and impact

of genetic differences on social communication (the nature component). On the other hand, visual perception remains a fundamentally subjective experience that is realized and shaped by acquired conceptual knowledge. For example, cultural differences in learning specific 'feature vocabularies' corresponding to a given perceptual category (concept) could facilitate or hinder learning of new culture-specific categories [186,187]. By identifying the feature vocabularies that subtend social communication over the lifespan and in different cultures could further inform how the transmission and decoding of information is achieved (or challenged) across cultural boundaries.

To embrace the true complexity of the task, one thing is certain: understanding the system of human social communication — the dynamic transmission of information using rich and complex sources (face, body, voice, scenes), and decoding based on biologically constrained apparatus (the eye, visual brain) coupled with prior knowledge (whether acquired or hardwired) — relies on the strategic interdisciplinary convergence of knowledge from broader fields including vision science and psychophysics, cognitive psychology, cultural and social psychology, anthropology, biology, information theory and engineering. With the emergence of a new scientific culture that embraces such interdisciplinary approaches, the field of human social communication is poised to experience a new chapter of progress and exciting discoveries.

SUPPLEMENTAL INFORMATION

Supplemental Information includes two movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.05.052.

REFERENCES

1. Wilson, E.O. (2012). The Social Conquest of Earth, First Edition. (New York, NY: WW Norton & Company).

2. Dukas, R. (1998). Cognitive Ecology: the Evolutionary Ecology of Information Processing and Decision Making, First Edition. (Chicago: University of Chicago Press).

3. Hawkley, L.C., and Cacioppo, J.T. (2007). Aging and loneliness: downhill quickly? Curr. Dir. Psychol. Sci. 16, 187–191.

4. Baron-Cohen, S., Leslie, A.M., and Frith, U. (1985). Does the autistic child have a "theory of mind"? Cognition 21, 37–46.

5. LeMoult, J., Joormann, J., Sherdell, L., Wright, Y., and Gotlib, I.H. (2009). Identification of emotional facial expressions following recovery from depression. J. Abnorm. Psychol. 118, 828–833.

6. Dunbar, R.I. (1993). Coevolution of neocortical size, group size and language in humans. Behav. Brain Sci. 16, 681–693.

7. Fay, N., Garrod, S., Roberts, L., and Swoboda, N. (2010). The interactive evolution of human communication systems. Cognitive Sci. 34, 351–386.

8. Yin, R.K. (1969). Looking at upside-down faces. J. Exp. Psychol. 81, 141–145.

9. McKone, E., Crookes, K., and Kanwisher, N. (2009). The cognitive and neural development of face recognition in humans. Cognitive Neurosci. 4, 467–482.

10. Haxby, J.V., Hoffman, E.A., and Gobbini, M.I. (2000). The distributed human neural system for face perception. Trends. Cogn. Sci. 4, 223–233.

11. Gauthier, I., Tarr, M.J., Anderson, A.W., Skudlarski, P., and Gore, J.C. (1999). Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. Nat. Neurosci. 2, 568–573.

12. Farah, M.J., Wilson, K.D., Drain, M., and Tanaka, J.N. (1998). What is "special" about face perception. Psychol. Rev. 105, 482–498.

13. O'Toole, A.J., Deffenbacher, K.A., Valentin, D., McKee, K., Huff, D., and Abdi, H. (1998). The perception of face gender: The role of stimulus structure in recognition and classification. Mem. Cognit. 26, 146–160.

14. Little, A.C., Jones, B.C., Waitt, C., Tiddeman, B.P., Feinberg, D.R., Perrett, D.I., Apicella, C.L., and Marlowe, F.W. (2008). Symmetry is related to sexual dimorphism in faces: data across culture and species. PLoS One 3, e2106.

15. Thornhill, R., and Gangestad, S.W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. Evol. Hum. Behav. 27, 131–144.

16. Rhodes, M.G., and Anastasi, J.S. (2012). The own-age bias in face recognition: a meta-analytic and theoretical review. Psychol. Bull. 138, 146–174.

17. van Rijsbergen, N., Jaworska, K., Rousselet, G.A., and Schyns, P.G. (2014). With age comes representational wisdom in social signals. Curr. Biol. 24, 2792–2796.

18. Feingold, G.A. (1914). The influence of environment on identification of persons and things. J. Am. Institution Criminal Law Criminol. 5, 39–51.

19. O'Toole, A.J., Deffenbacher, K.A., Valentin, D., and Abdi, H. (1994). Structural aspects of face recognition and the other-race effect. Mem. Cognit. 22, 208–224.

20. Tanaka, J.W., Kiefer, M., and Bukach, C.M. (2004). A holistic account of the own-race effect in face recognition: evidence from a cross-cultural study. Cognition 93, B1–B9.

21. Rule, N.O., and Ambady, N. (2008). Brief exposures: Male sexual orientation is accurately perceived at 50ms. J. Exp. Soc. Psychol. 44, 1100–1105.

22. Tskhay, K.O., Feriozzo, M.M., and Rule, N.O. (2013). Facial features influence the categorization of female sexual orientation. Perception 42, 1090–1094.

23. Freeman, J.B., Johnson, K.L., Ambady, N., and Rule, N.O. (2010). Sexual orientation perception involves gendered facial cues. Pers. Soc. Psychol. Bull. 36, 1318–1331.

24. Grammer, K., and Thornhill, R. (1994). Human (Homo sapiens) facial attractiveness and sexual selection: The role of symmetry and averageness. J. Comp. Psychol. 108, 233–242.

25. Jones, A.L., Kramer, R.S., and Ward, R. (2012). Signals of personality and health: The contributions of facial shape, skin texture, and viewing angle. J. Exp. Psychol. Hum. Percept. Perform 38, 1353–1361.

26. Perrett, D.I., Lee, K.J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D.M., Henzi, S.P., Castles, D.L., and Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. Nature 394, 884–887.

27. Rhodes, G. (2006). The evolutionary psychology of facial beauty. Annu. Rev. Psychol. 57, 199–226.

28. Darwin, C. (1999/1872). The Expression of the Emotions in Man and Animals, 3rd Edition. (London: Fontana Press).

29. Ekman, P. (1972). Universals and cultural differences in facial expressions of emotion. In Nebraska Symposium on Motivation (University of Nebraska Press).

30. Tomkins, S.S. (1962). Affect, Imagery, and Consciousness, Volume 1: The Positive Emotions. (New York: Springer).

31. Tomkins, S.S. (1963). Affect, Imagery, and Consciousness, Volume 2: The Negative Emotions. (New York: Springer).

32. Ekman, P. (1993). Facial expression and emotion. Am. Psychol. *48*, 384–392.

33. Willis, J., and Todorov, A. (2006). First impressions: making up your mind after a 100-ms exposure to a face. Psychol. Sci. *17*, 592–598.

34. Berry, D.S., and McArthur, L.Z. (1985). Some components and consequences of a babyface. J. Pers. Soc. Psychol. *48*, 312–323.

35. Sutherland, C.A., Oldmeadow, J.A., Santos, I.M., Towler, J., Michael Burt, D., and Young, A.W. (2013). Social inferences from faces: Ambient images generate a three-dimensional model. Cognition *127*, 105–118.

36. Williams, A.C.de C. (2002). Facial expression of pain, empathy, evolution, and social learning. Behav. Brain Sci. *25*, 475–480.

37. Fernández-Dols, J.-M., Carrera, P., and Crivelli, C. (2011). Facial behavior while experiencing sexual excitement. J. Nonverbal Behav. *35*, 63–71.

38. Ekman, P., Friesen, W.V., and O'Sullivan, M. (1988). Smiles when lying. J. Pers. Soc. Psychol. *54*, 414–420.

39. Krumhuber, E., and Kappas, A. (2005). Moving smiles: the role of dynamic components for the perception of the genuineness of smiles. J. Nonverbal Behav. *29*, 3–24.

40. Hill, M.L., and Craig, K.D. (2002). Detecting deception in pain expressions: the structure of genuine and deceptive facial displays. Pain *98*, 135–144.

41. Telles, E. (2014). Pigmentocracies: Ethnicity, Race, and Color in Latin America. (North Carolina: UNC Press Brooks).

42. Ballew, C.C., and Todorov, A. (2007). Predicting political elections from rapid and unreflective face judgments. Proc. Natl. Acad. Sci. USA *104*, 17948–17953.

43. Fernandez-Dols, J.M. (2013). Advances in the study of facial expression: An introduction to the special Section. Emot. Rev. *5*, 3–7.

44. Briggs, J. (1970). Never in Anger: Portrait of an Eskimo Family. (Cambridge, MA: Harvard University Press).

45. Gorer, G. (1935/2004). Africa Dances (London: Eland Books).

46. Hearn, L. (1894/2007). Glimpses of Unfamiliar Japan (Book Jungle).

47. Holt, E.B. (1931). Animal Drive and the Learning Process (New York).

48. Turnbull, J. (1813). A Voyage Round the World in the years 1800, 1801, 1802, 1803, and 1804 in which the Author Visited the Principle Islands in the Pacific Ocean and the English Settlements of Port Jackson and Norfolk Island, Volume 2, (London).

49. Labarre, W. (1947). The cultural basis of emotions and gestures. J. Pers. *16*, 49–68.

50. Ekman, P., Sorenson, E.R., and Friesen, W.V. (1969). Pan-cultural elements in facial displays of emotion. Science *164*, 86–88.

51. Russell, J.A. (1994). Is there universal recognition of emotion from facial expression? A review of the cross-cultural studies. Psychol. Bull. *115*, 102–141.

52. Ekman, P., and Oster, H. (1979). Facial expressions of emotion. Annu. Rev. Psychol. *30*, 527–554.

53. Jack, R.E. (2013). Culture and facial expressions of emotion. Vis. Cogn. *21*, 1248–1286.

54. Ortony, A., and Turner, T.J. (1990). What's basic about basic emotions. Psychol. Rev. *97*, 315–331.

55. Barrett, L.F., Lindquist, K.A., Bliss-Moreau, E., Duncan, S., Gendron, M., Mize, J., and Brennan, L. (2007). Of mice and men: natural kinds of emotions in the mammalian brain? A response to Panksepp and Izard. Perspect. Psychol. Sci. *2*, 297–312.

56. Scherer, K.R. (1999). Appraisal theory. In Handbook of Cognition and Emotion, T. Dalgleish, and M.J. Power, eds. (Chichester, UK: Wiley), pp. 637–663.

57. Tracy, J.L., and Randles, D. (2011). Four models of basic emotions: A review of Ekman and Cordaro, Izard, Levenson, and Panksepp and Watt. Emot. Rev. *3*, 397–405.

58. Russell, J.A. (1980). A circumplex model of affect. J. Pers. Soc. Psychol. *39*, 1161–1178.

59. Frijda, N.H. (1986). The Emotions. (Cambridge University Press).

60. Scherer, K.R. (1984). On the nature and function of emotion: a component process approach. In Approaches to Emotion, K. Scherer, and P. Ekman, eds. (Hillsdale, NJ: Erlbaum), pp. 293–318.

61. Smith, C.A., and Ellsworth, P.C. (1985). Patterns of cognitive appraisal in emotion. J. Pers. Soc. Psychol. *48*, 813–838.

62. Matsumoto, D. (1992). American-Japanese cultural differences in the recognition of universal facial expressions. J. Cross. Cult. Psychol. *23*, 72–84.

63. Matsumoto, D., and Ekman, P. (1989). American-Japanese cultural differences in intensity ratings of facial expressions of emotion. Motiv. Emot. *13*, 143–157.

64. Moriguchi, Y., Ohnishi, T., Kawachi, T., Mori, T., Hirakata, M., Yamada, M., Matsuda, H., and Komaki, G. (2005). Specific brain activation in Japanese and Caucasian people to fearful faces. Neuroreport *16*, 133–136.

65. Biehl, M., Matsumoto, D., Ekman, P., Hearn, V., Heider, K., Kudoh, T., and Ton, V. (1997). Matsumoto and Ekman's Japanese and Caucasian Facial Expressions of Emotion (JACFEE): Reliability data and cross-national differences. J. Nonverbal Behav. *21*, 3–21.

66. Chan, D.W. (1985). Perception and judgment of facial expressions among the Chinese. Int. J. Psychol. *20*, 681–692.

67. Jack, R.E., Blais, C., Scheepers, C., Schyns, P.G., and Caldara, R. (2009). Cultural confusions show that facial expressions are not universal. Curr. Bio. *19*, 1543–1548.

68. Ekman, P., Friesen, W.V., O'Sullivan, M., Chan, A., Diacoyanni-Tarlatzis, I., Heider, K., Krause, R., LeCompte, W.A., Pitcairn, T., Ricci-Bitti, P.E., *et al.* (1987). Universals and cultural differences in the judgments of facial expressions of emotion. J. Pers. Soc. Psychol. *53*, 712–717.

69. Izard, C.E. (1994). Innate and universal facial expressions: evidence from developmental and cross-cultural research. Psychol. Bull. *115*, 288–299.

70. Matsumoto, D., and Willingham, B. (2009). Spontaneous facial expressions of emotion of congenitally and noncongenitally blind individuals. J. Pers. Soc. Psychol. *96*, 1–10.

71. Matsumoto, D., and Willingham, B. (2006). The thrill of victory and the agony of defeat: spontaneous expressions of medal winners of the 2004 Athens Olympic Games. J. Pers. Soc. Psychol. *91*, 568–581.

72. Berenbaum, H., and Oltmanns, T.F. (1992). Emotional experience and expression in schizophrenia and depression. J. Abnorm. Psychol. *101*, 37–44.

73. Keltner, D., Moffitt, T.E., and Stouthamer-Loeber, M. (1995). Facial expressions of emotion and psychopathology in adolescent boys. J. Abnorm. Psychol. *104*, 644–652.

74. Matsumoto, D., Haan, N., Yabrove, G., Theodorou, P., and Carney, C.C. (1986). Preschoolers' moral actions and emotions in Prisoner's Dilemma. Dev. Psychol. *22*, 663–670.

75. Rosenberg, E.L., Ekman, P., and Blumenthal, J.A. (1998). Facial expression and the affective component of cynical hostility in male coronary heart disease patients. Health Psychol. *17*, 376–380.

76. Adolphs, R., Spezio, M.L., Parlier, M., and Piven, J. (2008). Distinct face-processing strategies in parents of autistic children. Curr. Biol. *18*, 1090–1093.

77. van Rijsbergen, N.J., and Schyns, P.G. (2009). Dynamics of trimming the content of face representations for categorization in the brain. PLoS Comput. Biol. *5*, e1000561.

78. Furl, N., van Rijsbergen, N.J., Treves, A., Friston, K.J., and Dolan, R.J. (2007). Experience-dependent coding of facial expression in superior temporal sulcus. Proc. Natl. Acad. Sci. USA *104*, 13485–13489.

79. Morris, J.S., Friston, K.J., Buchel, C., Frith, C.D., Young, A.W., Calder, A.J., and Dolan, R.J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. Brain *121*, 47–57.

80. Schyns, P.G., Petro, L.S., and Smith, M.L. (2007). Dynamics of visual information integration in the brain for categorizing facial expressions. Curr. Biol. *17*, 1580–1585.

81. Schyns, P.G., Petro, L.S., and Smith, M.L. (2009). Transmission of facial expressions of emotion co-evolved with their efficient decoding in the brain: behavioral and brain evidence. PLoS One *4*, e5625.

82. Phelps, E.A., Ling, S., and Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. Psychol. Sci. *17*, 292–299.

83. Smith, F.W., and Schyns, P.G. (2009). Smile through your fear and sadness. Psychol. Sci. *20*, 1202–1208.

84. Smith, M.L., Cottrell, G.W., Gosselin, F., and Schyns, P.G. (2005). Transmitting and decoding facial expressions. Psychol. Sci. *16*, 184–189.

85. Dailey, M.N., Joyce, C., Lyons, M.J., Kamachi, M., Ishi, H., Gyoba, J., and Cottrell, G.W. (2010). Evidence and a computational explanation of cultural differences in facial expression recognition. Emotion *10*, 874–893.

86. Krumhuber, E.G., Kappas, A., and Manstead, A.S. (2013). Effects of dynamic aspects of facial expressions: a review. Emot. Rev. *5*, 41–46.

87. Seyfarth, R.M., Cheney, D.L., and Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. Anim. Behav. *28*, 1070–1094.

88. Brines, M.L., and Gould, J.L. (1979). Bees have rules. Science *206*, 571–573.

89. Seyfarth, R.M., and Cheney, D.L. (2003). Signalers and receivers in animal communication. Annu. Rev. Psychol. *54*, 145–173.

90. Heil, M., and Karban, R. (2010). Explaining evolution of plant communication by airborne signals. Trends Ecol. Evol. *25*, 137–144.

91. Bassler, B.L. (2002). Small talk: cell-to-cell communication in bacteria. Cell *109*, 421–424.

92. Slater, P.J., and Halliday, T.R. (1994). Behaviour and Evolution, First Edition. (Cambridge University Press).

93. Scott-Phillips, T.C. (2008). Defining biological communication. J. Evol. Biol. *21*, 387–395.

94. Shannon, C.E. (2001). A mathematical theory of communication. Mob. Comput. Commun. Rev. *5*, 3–55.

95. Schyns, P.G. (1998). Diagnostic recognition: task constraints, object information, and their interactions. Cognition *67*, 147–179.

96. Dawkins, R., and Krebs, J.R. (1978). Animal signals: information or manipulation. In Behavioural Ecology: An Evolutionary Approach, J.R. Krebs, and N.B. Davies, eds. (Oxford: Blackwell Scientific Publications), pp. 282–309.

97. Aviezer, H., Trope, Y., and Todorov, A. (2012). Body cues, not facial expressions, discriminate between intense positive and negative emotions. Science *338*, 1225–1229.

98. Gupta, S.R., and Brumlik, J. (1986). Abnormal facial movements. Guide to differential diagnosis. Postgrad. Med. *79*, 1027–1111.

99. Morris, D. (1979). Gestures, their Origins and Distribution. (New York: Stein and Day).

100. Gerhardt, H. (1983). Communication and the environment. Anim. Behav. *2*, 82–113.

101. Tinbergen, N. (1948). Social releasers and the experimental method required for their study. Wilson Bull, 6–51.

102. Zuckerman, M., DePaulo, B.M., and Rosenthal, R. (1981). Verbal and nonverbal communication of deception. Adv. Exp. Soc. Psychol. *14*, 1–59.

103. Susskind, J.M., Lee, D.H., Cusi, A., Feiman, R., Grabski, W., and Anderson, A.K. (2008). Expressing fear enhances sensory acquisition. Nat. Neurosci. *11*, 843–850.

104. Lee, D.H., Susskind, J.M., and Anderson, A.K. (2013). Social transmission of the sensory benefits of eye widening in fear expressions. Psychol. Sci. *24*, 957–965.

105. Drake, R.L., Vogl, A., and Mitchell, A.W. (2014). Gray's Anatomy for Students. (Philadelphia: Elsevier Health Sciences).

106. Goldstein, A.G. (1979). Race-related variation of facial features: Anthropometric data I. Bull. Psychon. Soc. *13*, 187–190.

107. Goldstein, A.G. (1979). Facial feature variation: Anthropometric data II. Bull. Psychon. Soc. *13*, 191–193.

108. Pathak, M.A., Jimbow, K., Szabo, G., and Fitzpatrick, T.B. (1976). Sunlight and melanin pigmentation. Photochem. Photobiol. Rev. *2*, 211–239.

109. Cohen, M.M. (2006). Perspectives on the Face. (Oxford University Press).

110. Haub, C. (2002). How many people have ever lived on Earth? World *6*, 983–987.

111. Blow, M., Dautenhahn, K., Appleby, A., Nehaniv, C.L., and Lee, D. (2006). The art of designing robot faces: Dimensions for human-robot interaction. In Proceedings of the 1st ACM SIGCHI/SIGART Conference on Human-Robot Interaction. (ACM), pp. 331–332.

112. Rehm, M., Nakano, Y., Koda, T., and Winschiers-Theophilus, H. (2012). Culturally aware agent communication. In Human-Computer Interaction: The Agency Perspective, M. Zacarias, and J. de Oliveira, eds. (Berlin Heidelberg: Springer), pp. 411–436.

113. Koda, T., Ruttkay, Z., Nakagawa, Y., and Tabuchi, K. (2010). Cross-cultural study on facial regions as cues to recognize emotions of virtual agents. In Culture and Computing, T. Ishida, ed. (Berlin Heidelberg: Springer), pp. 16–27.

114. Vinciarelli, A., Pantic, M., and Bourlard, H. (2009). Social signal processing: Survey of an emerging domain. Image Vis. Comput. *27*, 1743–1759.

115. Castellano, G., Leite, I., Pereira, A., Martinho, C., Paiva, A., and McOwan, P.W. (2010). Affect recognition for interactive companions: challenges and design in real world scenarios. J. Multimodal User Interfaces *3*, 89–98.

116. Sandbach, G., Zafeiriou, S., Pantic, M., and Yin, L. (2012). Static and dynamic 3D facial expression recognition: A comprehensive survey. Image Vis. Comput. *30*, 683–697.

117. Pantic, M., and Rothkrantz, L.J.M. (2000). Automatic analysis of facial expressions: The state of the art. IEEE Trans. Pattern Anal. Mach. Intell. *22*, 1424–1445.

118. Elfenbein, H.A., and Ambady, N. (2002). On the universality and cultural specificity of emotion recognition: A meta-analysis. Psychol. Bull. *128*, 203–235.

119. Andrew, R.J. (1963). Evolution of facial expression. Science *142*, 1034–1041.

120. Ekman, P., Friesen, W., and Hagar, J.C. (1978). Facial Action Coding System Investigators Guide. (Salt Lake City: Research Nexus).

121. Ekman, P., and Friesen, W.V. (1976). Measuring facial movement. J. Nonverbal Behav. *1*, 1573–3653.

122. Ekman, P., and Friesen, W. (1978). Facial Action Coding System: A technique for the Measurement of Facial Movement. (Consulting Psychologists Press).

123. Izard, C.E. (1971). The Face of Emotion. (New York: Appleton-Century-Crofts).

124. Matsumoto, D., and Ekman, P. (1988). Japanese and Caucasian Facial Expressions of Emotion (JACFEE) and Neutral Faces (JACNeuF). Human Interaction Laboratory, University of California, San Francisco, 401 Parnassus, San Francisco, CA 94143–0984.

125. Lundqvist, D., Flykt, A., and Öhman, A. (1998). The karolinska directed emotional faces. Department of Clinical Neuroscience, Psychology section, Karolinska Institutet.

126. Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D.H.J., Hawk, S.T., and van Knippenberg, A. (2010). Presentation and validation of the Radboud Faces Database. Cogn. Emot. 24, 1377–1388.

127. Ekman, P., and Friesen, W.V. (1976). Pictures of Facial Affect, (Palo Alto, CA).

128. Ekman, P., and Friesen, W.V. (1975). Unmasking the Face: a Guide to Recognizing Emotions from Facial Clues. (Englewood Cliffs: Prentice-Hall).

129. Beaupré, M., Cheung, N., and Hess, U. (2000). The Montreal set of facial displays of emotion. Available from Ursula Hess, Department of Psychology, University of Quebec at Montreal, PO Box 8888.

130. Nelson, N.L., and Russell, J.A. (2013). Universality revisited. Emot. Rev. 5, 8–15.

131. Henrich, J., Heine, S.J., and Norenzayan, A. (2010). The weirdest people in the world? Behav. Brain Sci. 33, 61–83, discussion 83–135.

132. Weber, E.H. (1834). De Pulsu, resorptione, auditu et tactu: Annotationes anatomicae et physiologicae. (CF Koehler).

133. Stevens, S.S. (1957). On the psychophysical law. Psychol. Rev. 64, 153–181.

134. Fechner, G.T. (1860). Elemente der Psychophysik. Leipzig, Breitkopf & Härtel 1.

135. Gold, J.I., and Shadlen, M.N. (2007). The neural basis of decision making. Annu. Rev. Neurosci. 30, 535–574.

136. Summerfield, C., and de Lange, F.P. (2014). Expectation in perceptual decision making: neural and computational mechanisms. Nat. Rev. Neurosci. 15, 745–756.

137. Palmer, S.E. (1999). Vision Science: Photons to Phenomenology, Volume 1. (Cambridge, MA: MIT press).

138. Schyns, P.G. (2010). Grand challenges in perception science: modeling the future. Front. Psychol. 1, 1–3.

139. Scheib, J.E., Gangestad, S.W., and Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. Proc. Biol. Sci. 266, 1913–1917.

140. Perrett, D., Lee, K., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D., Henzi, S., Castles, D., and Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. Nature 394, 884–887.

141. Gill, D., Garrod, O.G., Jack, R.E., and Schyns, P.G. (2014). Facial movements strategically camouflage involuntary social signals of face morphology. Psychol. Sci. 25, 1079–1086.

142. Little, A.C., Cohen, D.L., Jones, B.C., and Belsky, J. (2007). Human preferences for facial masculinity change with relationship type and environmental harshness. Behav. Ecol. Sociobiol. 61, 967–973.

143. Boothroyd, L.G., Jones, B.C., Burt, D.M., DeBruine, L.M., and Perrett, D.I. (2008). Facial correlates of sociosexuality. Evol. Hum. Behav. 29, 211–218.

144. Yu, H., Garrod, O.G.B., and Schyns, P.G. (2012). Perception-driven facial expression synthesis. Comput. Graph. 36, 152–162.

145. Ahumada, A., and Lovell, J. (1971). Stimulus features in signal detection. J. Acoust. Soc. Am. 49, 1751–1756.

146. Sun, W., Garrod, O.G.B., Schyns, P.G., and Jack, R.E. (2013). Dynamic mental models of culture-specific emotions. J. Vis. 13, 593–593.

147. Jack, R.E., Garrod, O.G., Yu, H., Caldara, R., and Schyns, P.G. (2012). Facial expressions of emotion are not culturally universal. Proc. Natl. Acad. Sci. USA 109, 7241–7244.

148. Dotsch, R., Wigboldus, D.H., Langner, O., and van Knippenberg, A. (2008). Ethnic out-group faces are biased in the prejudiced mind. Psychol. Sci. 19, 978–980.

149. Oosterhof, N.N., and Todorov, A. (2008). The functional basis of face evaluation. Proc. Natl. Acad. Sci. USA 105, 11087–11092.

150. Ekman, P. (1979). About brows: Emotional and conversational signals. In Human Ethology, J. Aschoff, M. Con Carnach, K. Foppa, W. Lepenies, and D. Plog, eds. (Cambridge University Press), pp. 169–202.

151. Baron-Cohen, S. (1996). Reading the mind in the face: A cross-cultural and developmental study. Vis. Cognit. 3, 39–60.

152. Fridlund, A.J. (1994). Human Facial Expression: An Evolutionary View. (San Diego, CA: Academic Press).

153. Stephen, I.D., Coetzee, V., and Perrett, D.I. (2011). Carotenoid and melanin pigment coloration affect perceived human health. Evol. Hum. Behav. 32, 216–227.

154. Stephen, I.D., Smith, M.J.L., Stirrat, M.R., and Perrett, D.I. (2009). Facial skin coloration affects perceived health of human faces. Int. J. Primatol. 30, 845–857.

155. Belin, P., Fillion-Bilodeau, S., and Gosselin, F. (2008). The Montreal affective voices: a validated set of nonverbal affect bursts for research on auditory affective processing. Behav. Res. Methods 40, 531–539.

156. Sauter, D.A., Eisner, F., Ekman, P., and Scott, S.K. (2010). Cross-cultural recognition of basic emotions through nonverbal emotional vocalizations. Proc. Natl. Acad. Sci. USA 107, 2408–2412.

157. de Gelder, B. (2009). Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. Philos. Trans. R. Soc. B. Biol. Sci. 364, 3475–3484.

158. Marsh, A.A., Elfenbein, H.A., and Ambady, N. (2003). Nonverbal "accents": cultural differences in facial expressions of emotion. Psychol. Sci. 14, 373–376.

159. Elfenbein, H.A., Beaupre, M., Levesque, M., and Hess, U. (2007). Toward a dialect theory: cultural differences in the expression and recognition of posed facial expressions. Emotion 7, 131–146.

160. Elfenbein, and Ambady, N. (2002). Is there an in-group advantage in emotion recognition? Psychol. Bull. 128, 243–249.

161. Elfenbein, H.A. (2013). Nonverbal dialects and accents in facial expressions of emotion. Emot. Rev. 5, 90–96.

162. Mesquita, B., and Frijda, N.H. (1992). Cultural variations in emotions: a review. Psychol. Bull. 112, 179–204.

163. Matsumoto, D., Yoo, S.H., and Fontaine, J. (2008). Mapping expressive differences around the world the relationship between emotional display rules and individualism versus collectivism. J. Cross Cult. Psychol. 39, 55–74.

164. MacQueen, J. (1967). Some methods for classification and analysis of multivariate observations. Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability 1, 281–297.

165. Ekman, P. (1992). An argument for basic emotions. Cogn. Emot. 6, 169–200.

166. Jack, R.E., Caldara, R., and Schyns, P.G. (2011). Internal representations reveal cultural diversity in expectations of facial expressions of emotion. J. Exp. Psychol. Gen. 141, 19–25.

167. Yuki, M., Maddux, W.W., and Masuda, T. (2007). Are the windows to the soul the same in the East and West? Cultural differences in using the eyes and mouth as cues to recognize emotions in Japan and the United States. J. Exp. Soc. Psychol. 43, 303–311.

168. Jack, R.E., Garrod, O.G., and Schyns, P.G. (2014). Dynamic facial expressions of emotion transmit an evolving hierarchy of signals over time. Curr. Biol. 24, 187–192.

169. Kobayashi, H., and Kohshima, S. (1997). Unique morphology of the human eye. Nature 387, 767–768.

170. Cott, H.B. (1940). Adaptive Coloration in Animals. (London: Methuen).

171. Senju, A., and Johnson, M.H. (2010). Is eye contact the key to the social brain? Behav. Brain Sci. 33, 458–459.

172. Niedenthal, P.M., Mermillod, M., Maringer, M., and Hess, U. (2010). The Simulation of Smiles (SIMS) model: Embodied simulation and the meaning of facial expression. Behav. Brain Sci. *33*, 417–433.

173. Little, A.C., Burriss, R.P., Jones, B.C., DeBruine, L.M., and Caldwell, C.A. (2008). Social influence in human face preference: men and women are influenced more for long-term than short-term attractiveness decisions. Evol. Hum. Behav. *29*, 140–146.

174. Johnson, S.K., Podratz, K.E., Dipboye, R.L., and Gibbons, E. (2010). Physical attractiveness biases in ratings of employment suitability: tracking down the "beauty is beastly" effect. J. Soc. Psychol. *150*, 301–318.

175. Ritts, V., Patterson, M.L., and Tubbs, M.E. (1992). Expectations, impressions, and judgments of physically attractive students: A review. Rev. Educ. Res. *62*, 413–426.

176. Eberhardt, J.L., Davies, P.G., Purdie-Vaughns, V.J., and Johnson, S.L. (2006). Looking deathworthy: perceived stereotypicality of Black defendants predicts capital-sentencing outcomes. Psychol. Sci. *17*, 383–386.

177. Blair, I.V., Judd, C.M., and Chapleau, K.M. (2004). The influence of Afrocentric facial features in criminal sentencing. Psychol. Sci. *15*, 674–679.

178. Todorov, A., Mandisodza, A.N., Goren, A., and Hall, C.C. (2005). Inferences of competence from faces predict election outcomes. Science *308*, 1623–1626.

179. de Waal, F., and Luttrell, L.M. (1985). The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. Am. J. Primatol. *9*, 73–85.

180. Todorov, A., Said, C.P., Engell, A.D., and Oosterhof, N.N. (2008). Understanding evaluation of faces on social dimensions. Trends Cogn. Sci. *12*, 455–460.

181. Bruce, V., and Young, A. (1986). Understanding face recognition. Br. J. Psychol. *77*, 305–327.

182. Hassin, R.R., Aviezer, H., and Bentin, S. (2013). Inherently ambiguous: Facial expressions of emotions, in context. Emot. Rev. *5*, 60–65.

183. Parkinson, B. (2013). Contextualizing facial activity. Emot. Rev. *5*, 97–103.

184. Barrett, L.F., Mesquita, B., and Gendron, M. (2011). Context in emotion perception. Curr. Dir. Psychol. Sci. *20*, 286–290.

185. Ladd, D.R., Dediu, D., and Kinsella, A.R. (2008). Languages and genes: Reflections on biolinguistics and the nature-nurture question. Biolinguistics *2*, 114–126.

186. Schyns, P.G., and Rodet, L. (1997). Categorization creates functional features. J. Exp. Psychol. Learn. Mem. Cogn. *23*, 681–696.

187. Schyns, P.G., Goldstone, R.L., and Thibaut, J.P. (1998). The development of features in object concepts. Behav. Brain Sci. *21*, 1–17.