Trends in Cognitive Sciences

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Opinion

Facial Displays Are Tools for Social Influence

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Based on modern theories of signal evolution and animal communication, the behavioral ecology view of facial displays (BECV) reconceives our 'facial expressions of emotion' as social tools that serve as lead signs to contingent action in social negotiation. BECV offers an externalist, functionalist view of facial displays that is not bound to Western conceptions about either expressions or emotions. It easily accommodates recent findings of diversity in facial displays, their public context-dependency, and the curious but common occurrence of solitary facial behavior. Finally, BECV restores continuity of human facial behavior research with modern functional accounts of non-human communication, and provides a non-mentalistic account of facial displays well-suited to new developments in artificial intelligence and social robotics.

Highlights

Like non-human animal signals, human facial displays are an important way that we regulate our social interactions, whether they are in public or in private, and whether our 'interactants' are real or fantasied people, non-human animals, virtual agents, or even inanimate objects toward which we attribute agency.

Facial displays are not fixed, semantic read-outs of internal states such as emotions or intentions, but flexible tools for social influence. Facial displays are not about us, but about changing the behavior of those around us.

The behavioral ecology view of facial displays (BECV) is an externalist and functionalist approach to facial behavior that reconceives it as signaling contingent social action.

Facial Displays and Emotions

The field of human facial expressions is riven by two contrasting views of what our expressions mean and how to study them. The traditional view (the origins of which trace back to at least the Hellenic age) is that each of a small number of categorical 'passions' are universally conveyed by matching a facial expression; thus, 'fear' is expressed by a 'fear face,' 'anger' by an 'anger face,' and so on. This historical account, known as basic emotions theory (BET), holds that internal essences ('emotions') are externalized via our different facial expressions. Consequently, for BET the face is the 'royal road to the emotions' [1–3].

Problems with this longstanding view led to a newer alternative, the behavioral ecology view of facial displays (BECV) [4,5]. This perspective, rooted in animal **communication** (see Glossary) and modern evolutionary biology, suggests that our facial expressions, like many non-human displays, are not 'expressions' of anything. They have no intrinsic meaning tied to their morphologies, nor are they contingent upon any specific internal state [6]. Within BECV, our faces are 'social tools' that, like many animal displays, are used as lead signs of contingent action in social negotiation, and how they function depends upon the context of the current social interaction, the interactants, and their interaction histories.

In the present paper, we note the limitations of approaches that conceive of facial displays as outward expressions of internal emotions. Then, we outline an alternative that is functional, externalist, and fundamentally social: the BECV. Finally, we show how the perspective of BECV has been advantageous for grappling with the complexity of our facial displays, forging stronger links between these and non-human displays, and developing useful modes of simulating them in embodied computerized agents and other forms of artificial intelligence (AI).

An Essentialist View of Faces and Emotions

The roots of BET are distinctly Western, with early approaches by Aristotle, but they owe especially to Descartes's continuation of the Hellenic view of emotion as set against reason [7]. Descartes's 'passions' were categorical entities that perturbed the 'animal spirits' in the corporeal body, and could become sufficiently intense to compromise rationality and foment

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incivility. The passions were first tied to the face by artist Charles LeBrun, who prescribed the anatomically correct and appropriately nuanced facial configuration for each Cartesian passion [8]. These links became lore, passed down and eventually incorporated into personality theorist Silvan Tomkins's sprawling, quasi-cybernetic affect theory, which, *mutatis mutandis*, became the most popular and researched BET variant: Ekman's neurocultural theory [1].

BET is considered canonical in much of cognitive science, due in part to its origin as received wisdom from Descartes and LeBrun. A recent poll of hundreds of prominent emotion researchers found that 80% supported the view that certain facial displays are universal 'expressions of emotion' [9]. For instance, the 'gasping face' is commonly used in amygdala studies to indicate fear [10]. The putative, categorical 'facial expressions of emotions' have also found convenient use in many applied areas, such as in AI avatar and social-robotics algorithms [11].

Despite its popularity, the assumptions and prescriptions of BET are meeting unprecedented challenges. BET and related views are essentialist theories [12]. As we shall see, their **essentialism** constrains their ability to incorporate real-world data which fall outside their prescriptions.

Challenges to the Essentialist View of Faces and Emotions: New Evidence from Small-Scale, Indigenous Societies

The historical BET approach to facial expressions can be illustrated by an example from an indigenous, small-scale society. The Trobrianders of Papua New Guinea are subsistence horticulturalists and fishermen for whom the involvement of magic is pervasive in nearly all aspects of daily life [13]. Trobrianders believe that supernatural beings such as ghosts, evil spirits, or flying witches exert influence over them and can even cause misery and death [14]. These spirits can emerge from the bushes at night, perch atop yam houses, or hide within the studs of a house. Notably, those studs are called kokola, which means 'fear' in the Trobrianders' language [15]. Thus, a Trobriand intruder intent on harming others or stealing their yams could be rejected by concealment magic (kaigau) or by the magic of the mwamwala (a spirit), either of which can provoke sickness or death (Figure 1).

For BET, the interloper will likely feel fear (kokola) when approaching a yam house and facing the mwamwala. This fear, once triggered, releases a cascade of neurologically programmed changes (the 'facial affect program') that includes a prewired, universal 'expression' of the instigating emotion; for fear, it's the gasping face [1,16]. Iconic designated facial actions like the gasping face comprise the BET 'facial expressions of emotions,' which BET contends are generated and understood pan-culturally [2]. This assumption about how Trobrianders must react to such sorcery, by having fear, and therefore expressing a 'fear face,' would constitute a piece of fieldwork consistent with the BET **universality thesis**. This thesis predicates that, once they are triggered by environmental elicitors sharing common themes across cultures, then universal, separable, numerable emotions inside will be expressed in universal, prototypical ways outside.

The tests that lent initial support to this universality thesis were conducted among peoples similar to the Trobrianders, in small-scale, indigenous societies that were sufficiently isolated to permit pan-cultural claims. These studies, originally heralded as proving universality, are now in dispute, because of both serious methodological problems and countervailing data emerging from new studies [17]. While the impact of the replication movement was beginning to confront psychology [18], two independent multidisciplinary research labs conducted new tests among three indigenous peoples, one Melanesian (the Trobrianders of Papua New Guinea) and two African (the Himba of Namibia and the Mwani of Mozambique) [19–22] (Box 1). The data

Glossary

Active appearance model: a computer vision approach in which a set of model parameters (e.g., from a prototype image) is tuned to achieve a statistical best fit to a new image.
Adaptive radiation: the evolutionary diversification of a single lineage into a series of forms adapted to different niches (e.g., Darwin's observations of variation among the finches across the Galápagos).
Communication: the reduction of uncertainty for receivers provided by prognostic movements of signalers [4]. The prognostic value of these movements is typically probabilistic; see 'ecology of signaling'.
Cultural evolution: changes in societal practices due to cultural variation, selection, and inheritance, analogous to the biological processes operative in evolution by natural selection [37,39].
Ecology of signaling: a coevolutionary process whereby receivers discern lead signs to others' behavior, and the producers of those lead signs learn to deploy them to influence receivers. This signaling ecology is probabilistic. Displayers may emit bluffs and false alarms, and because so-called 'honest' displays are readily mimicked, receivers develop necessary skepticism. Essentialist, moral concepts like 'honesty' or 'authenticity' are actually indices of signal reliability, good matches of lead signs to behaviors, with receiver judgments constituted of moving averages of reliability estimates derived from past interaction histories and current interaction contexts.
Epigenetic marking: changes ('marks') to genes that silence or activate certain gene sequences but do not change the genes themselves. These changes occur within the lifespan, are stable and heritable, and they alter the 'functional genome' without changing the 'structural genome'.
Essentialism: the doctrine that every object has properties that grant it a particular form or 'essence'. Basic emotion theory is essentialist in declaring that there are separable, numerable emotions with intrinsic qualities that define each.

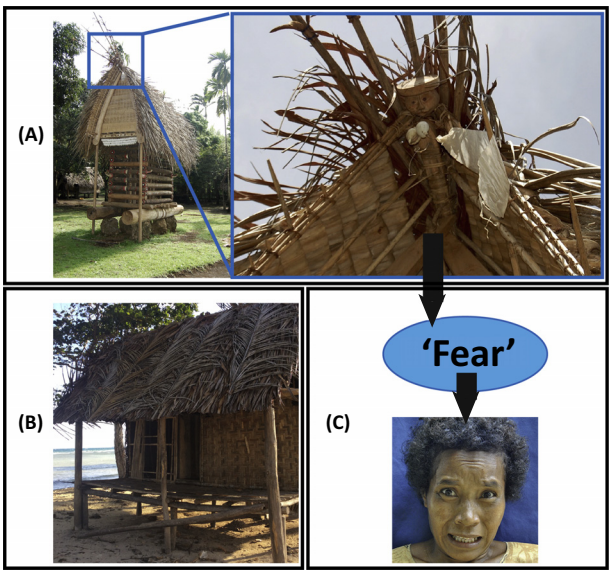

Figure 1. Magic, Evil Spirits, and Fear in a Melanesian Small-Scale Society. (A) One mwamwala sits on top of the yam house (liku) to protect the harvested yams with its magic. A mwamwala is considered a spirit (tokwai) (Jarillo de la Torre, S., PhD thesis, University of Cambridge, 2013). (B) A tokwai lives in rocks and trees (e.g., as found in the studs of a Trobriand house). Tokwai can be used by sorcerers' magic to protect gardens and houses from human, animal, and supernatural intruders [92]. (C) The production of 'fear' gasping faces from an essentialist view of faces and emotions. The spirit inside the mwamwala triggers fear in thieves approaching the yam house; the fear, in turn, results in its expression as the gasping face. The stipulation that the gasping face expresses fear does not hold for these Trobrianders, who regard it as a threat display.

gathered in the past 5 years by the two teams are inconsistent with the universality thesis. These results were obtained using a variety of methods (e.g., free-labeling, forced-choice, emotional antecedents, sorting). Moreover, these new studies involved tests of several competing theories and explanatory frameworks (e.g., core affect theory, action-identification theory, behavioral ecology) [23]. Special attention was also paid to ethnographic issues sidestepped in the early BET studies but now obligatory for internal and external validity: conducting prior extensive fieldwork to build a much-needed descriptive base [24,25], speaking the local languages, and designing and testing the hypotheses based on those in-field findings [26].

The universality thesis was challenged most powerfully by a convergence of experimental tests using **'recognition' studies** [23], material culture such as carvings [26], and observational ethological data [27]. All three sources of evidence controvert the BET prescription for the 'gasping face.' Trobrianders understand it not as a 'fear' face, but a threat display. First, recognition studies conducted in the Trobriand Islands showed that this understanding was commonplace within and across different islands of the archipelago, regardless of the assessment method (e.g., label-facial display matching, story-facial display matching). Second, carvings depicting Trobriand flying witches (yoyowa) using the gasping face to threaten villagers extend back more than a century. Finally, observational data show that the gasping face is used as a threat display not just among one 'exotic' group of people, but also in several African, Amazonian, and Pacific small-scale, indigenous societies.

Facial Displays as a Flexible System to Negotiate Interactions

The growing evidence on cognitive diversity shows how culture influences basic psychological phenomena [28–30], and research on facial expressions shows a similar trend. Traditionally, essentialist emotion theories such as BET conceive facial displays within a system bounded by Western preconceptions about both 'emotion' and 'expression' (i.e., interior emotions are expressed on faces to inform others of those emotions). Deviations from predictions (e.g., when fear does not produce the predicted gasping face, or when people smile when they say they are not happy) are considered veneers of inauthenticity [31], reflecting the operation of learned

Founder effect: a very few atypical 'founders' establish an offshoot population.
Genetic drift: the change in frequency of alleles in a population due to non-randomness in the seed population. It is most common in smaller populations and it can produce phenotypic diversity even in neighboring populations. The extreme of genetic drift is the founder effect.
Recognition studies: experimental tasks in which observers commonly are asked to match one stimulus to a response option (e.g., facial displays, emotion labels and antecedents, valence and arousal, behavioral repertoire), or to produce a response freely after being showed one stimulus.
SNP: a variation in a single DNA nucleotide (e.g., cytosine replaced by thymine), occurring roughly once in every 300 nucleotides. They are the most common type of genetic variation in humans, and they allow genetic identifications of diverse cultures, and mappings ('haplotype maps') of dominant maternity or paternity in ethnic and/or geographic groups.
Universality thesis: the assumption that certain facial actions ('facial expressions of emotion') convey categorical, numerable, subpersonal basic emotions such as happiness, sadness, anger, fear, or disgust, with the expression and recognition of these facial expressions being pancultural and phylogenetic.

Box 1. Diversity, Not Uniformity: Evidence from Small-Scale Indigenous Societies

Prior support for the universality thesis rested mostly on using null hypothesis significance testing in matching-to-sample experiments, using posed face photos and emotion labels or stories. Although the few tests of the thesis reported overall matching scores of roughly 50%, the results have been touted consistently as proving universality [17]. Excluding chance in the way participants responded to the tasks (i.e., rejecting the null hypothesis) became the standard criterion for claiming universality, regardless of the magnitude of the effect [23]. Ironically, the much higher 90% rate of right-handedness worldwide, known since Galton's observations in the 1880's, never led to a claim of 'universality of dexterity.' Mismatches on those original face studies were always attributed to thin cultural, rule-governed overlays. Those deviations, like the new evidence found in African and Melanesian populations [19–22], may indicate fundamental human diversity, just as the approximate 10% global rate of sinistrality and ambidexterity constitutes acknowledged, stable, congenital variation.

These new studies showed that in many emotion categories considered 'basic' (e.g., anger, fear, disgust), respondents fared poorly by BET expectations. Indigenous respondents attributed disparate meanings to facial displays when isolated from context. For example, although Western participants clearly believe that a smiling face reflects happiness, Trobrianders instead associate smiling with behaviors (laughing), Trobriand emotions (mwamwasila; magic of attraction, radiance), or dimensional affective properties such as valence (kalalumkola bwena, feeling good) [22].

Studies of facial displays and emotions have typically conflated four questions: (i) what accounts for the faces we make and see? (ii) How do we describe the faces we make and see? (iii) How do we describe the faces that others make? and (iv) How do people respond to the faces we make and see? Nearly all essentialist theories of facial displays focus on questions (ii) and (iii). Namely, researchers ascribe face causation to emotions or appraisals (question ii). They typically present face stimuli (usually photographed poses) to participants, and lead the participants either to generate ascriptions for them, like emotions, intentions, or goals, or match them to experimenter-provided ascriptions (question iii). Investigations into questions (ii) and (iii) tend toward self-confirmation, perhaps because the historical BET framework is part of early childhood education across cultures, via curricula that incorporate classroom wall posters showing arrays of iconic faces with prescribed emotion labels underneath.

BECV focuses instead on questions (i) and (iv). It posits that the production and behavioral consequences of our facial displays are intertwined, co-evolved products of both biological and cultural phylogenies, and suggests that they can be understood only using a functional analysis of social interaction.

display rules [2,32]. The concept of display rules is highly problematic on both methodological and conceptual grounds [5,33,34]. Thus, data that depart from uniformity toward cultural diversity are explained, *ad hoc* and *post hoc*, by recourse to culture-specific learning that supervenes on the stipulated phylogenetic 'universal facial expressions of emotion.' Note, however, that BET researchers invoke display rules only to explain deviations from uniformity; never for findings favoring communality. This is a restricted understanding of culture's range of influence: cultural diversity may be explained just as well by different subpopulation genetics, and cultural similarities may owe to convergent **cultural evolution**.

Nowadays, within the cognitive sciences, the process-uniformity versus content-diversity dichotomy is considered outdated [35,36]. By contrast, in affective science, the fallacious twin notions that uniformity implies phylogenesis, whereas diversity implies rule-governance, are explicit and are generally accepted [1–3]. It is inconsistent with modern theories of natural and cultural selection to sustain this dichotomy, and flipping the questions indicates the possibilities. Might phylogeny account for diversity, and 'culture-specific learning' for uniformity? [37–39]. True, some expression diversity may result from culture-specific learning, but it may also arise from biological phenomena like **adaptive radiation**, **founder effects**, **genetic drift**, random mutation, or **epigenetic marking**. Indeed, ethnicities differ not only by their languages and traditions, but also by the **SNPs** among their genomes [40]. Uniformity may result from common descent, but also from convergent genetic evolution ensuing after different initial paths of descent, and, as mentioned earlier, from convergent cultural evolution.

As an example of the latter, the Darwin-Hecker hypothesis (i.e., a proposed link of tickling with laughter and humor advocated by Charles Darwin and Ewald Hecker) suggests that, in

probably every culture, parents tickle their babies to get them laughing and smiling. This early interaction establishes a context by which physical tickling of the passive infant may be supplanted first by more elaborate interactive games involving tickling, and then by psychological 'tickling' (i.e., humor) as the child matures and becomes capable of language and abstraction [41]. Thus, social smiling and laughter, originally elicited reflexively through tickling, may, in part, arise anew in each society with every generation, with nearly all cultures co-opting and 'emancipating' these responses for later affiliation, play, and humor.

The presumptions of BET, which have not yet incorporated the varied mechanisms at work in biological and cultural evolution, thereby render the universality thesis and its derived predictions resistant to falsification. For instance, both high and low matching levels on recognition and production studies can be, and have been, explained *ad hoc* as well as *post hoc* by the baseline assumption of phylogenesis and the selective invocation of cultural display rules for any unexpected variation [42].

Reliance on these presumptions has had unfortunate effects. First, BET made its foundational thesis binary (whether or not there is 'universality') and stipulated what would explain the answer. In so doing, it preempted determination of the extent of both display communality and diversity, and the relative contributions of the many mechanisms that can account for either. Second, the presumptions of BET have also been too restrictive to allow unbiased inquiry into how members of different cultures actually use their facial displays. BET foreordained what certain facial expressions signified, and researchers in the BET tradition searched largely for agreement with its predictions.

More recent investigations have started from the outset to consider our facial displays as tools of a flexible, pragmatic system by which humans navigate their social terrain. This flexible system implies no natural semantic code by which members of all cultures share universal understandings of certain facial movements. Moreover, a flexible system to regulate interactions should not be circumscribed to the face. Classic functional, microsociological accounts rightly focused on gestures, postures, proxemics, and proximal context to understand how we operate within the social world [43,44]. Understanding how our displays function in everyday life requires a more powerful and open descriptive approach that focuses on situational relevance rather than iconic meaning, and on the trajectories of the interactants in their social context [45]. Pragmatic [46] and ecological [47] approaches to facial displays have shown how evidence from other disciplines such as linguistics, environmental psychology, and animal communication contributes to our appreciation of similarities and differences among diverse human groups. We next detail such an ecological, functional view of facial displays.

Getting Real about Faces: The Behavioral Ecology View of Facial Displays

The roots of the BECV of facial displays are solidly biological, and stem from modern conceptions of animal signaling (Box 2). BECV is not another expressive theory, and although some as yet uncertain brain processes certainly intermediate the path from external events to a facial display, no 'essence' or mentalistic state is assumed to be 'expressed,' 'read out,' or 'communicated' by any display. A display may have arisen adventitiously and become ritualized (dramatized and stereotyped) via natural selection, or similarly 'conventionalized' by cultural selection [48]. Exaptation (co-option) from a related functional response is always a possible origin (e.g., ear-retraction during alerting may have been an exaptation for current human brow-flashing; grimacing may have arisen from the orofacial conformation required to screech or hiss [5]). Nor does BECV assume display uniformity. It is agnostic on the issue but well-grounded in contemporary views of the evolutionary and cultural forces at play.

Box 2. Origins of the Behavioral Ecology View of Facial Displays

By the 1970s, animals were no longer the hapless creatures run by tripwire mechanisms portrayed by early ethologists. Those same creatures were now recognized as skilled negotiators and context-dependent communicators [4,48]. It became obvious that animals were signaling more flexibly and contextually than BET theorists were granting for humans. Indeed, this gap widens further with recent discoveries of exquisitely flexible, contextual signal systems among non-human primates [6,93–95]. Animal communication was reconceived as an '**ecology of signaling'** based on the interests of signal displayers and receivers who have interaction histories and who must negotiate for advantage within a behavioral niche. This insight readily suggested the possibility that human facial displays might be studied similarly, as part of the growing field of human behavioral ecology, which had traditionally concerned topics such as reproduction and resource production and distribution [96].

The behavioral ecology view of facial displays (BECV) of facial displays reconciled the growing evidence about animal signaling with the study of human facial displays and social influence [5,97,98]. BECV provided an open yet parsimonious approach to facial displays, without recourse to any intermediating subpersonal constructs (e.g., emotions, appraisals) in the *explanans*. To the contrary, the BECV approach was externalist. Facial displays were signals of contingent social action (i.e., they were lead signs of one's incipient interaction trajectory), a position that led to predictions about the functionality of facial displays among interactants, rather than ascriptions of mental causation in 'expressors' [49]. Although BECV and BET both emerged from Western thought, BECV is more 'Baconian,' (i.e., it relies on induction following observation). By contrast, BET is more 'Kantian,' having originally drawn its links of faces to emotions from received philosophical and aesthetic wisdom. It then made *post hoc ergo prompter hoc* presumptions about what innate, categorical facial expressions and perceptions of them evolution and culture must have wrought.

Thus, for BECV, facial displays are tools for social influence, and these signals, like all behavior, are always ramifications of both biological and cultural phylogenies [49], in addition to more proximal influences such as the identities of the interactants, their interaction history, and the immediate context of their interaction. Thus, the use of the gasping face as a threat display is counter-theoretical within BET and escaped previous notice by BET researchers because it was preordained as expressing 'fear.' From the BECV standpoint, its use was readily discerned, from multiple sources of evidence, as influencing interactants to submit (especially in agonistic face-to-face interactions), as previously observed not only in the Trobriand Islands but also in other African, Pacific, and Amazonian small-scale societies [27].

The emphasis in BECV is on what facial behavior does within the interaction. Our facial displays are not about us, or what is inside us; they are about you. They are about signaling our contingent next move in order to alter yours. We alter the trajectory of our interaction toward a certain outcome, with this outcome often a negotiated settlement carrying mutual advantages. Table 1 (Key Table) shows BECV provides a functional and externalist reframing of some sample facial displays which BET regards as prototypical. In no case should it be interpreted as a simple rewording of BET predictions or ratification of its expressions.

BECV is a young theory. Because its understanding of *in vivo* facial displays is based on a knowledge of the interactants, their history, and their current interaction context, research following from the BECV approach is more demanding than that required by BET, with its prototype expressions and prescribed meanings for each. Indeed, most BET research has been conducted using still photos [34] and written checklists, outside of fMRI tubes and within them, consistent with a problematic trend in fields like social psychology that have seen such 'paper-and-pencil' responses become accepted substitutes for real-world social behavior [50]. Nonetheless, BECV has already had a major influence in two research areas: the sociality hypothesis [51] and implicit audience effects [52].

The Sociality Hypothesis

The sociality hypothesis states that behaviors such as gestures and facial displays serve to influence a target audience, so that the issuance of those displays should be highly dependent

Key Table

Table 1. Two Approaches to Sample Facial Behaviors: Expressions of Internal States versus Functional Social Tools[a]

Sample facial behavior	State expressed (BET)	Social use (BECV)[b]
Smiling	Happiness	Influence interactant to play or affiliate
Pouting	Sadness	Recruit interactant's succor or protection
Scowling	Anger	Influence interactant to submit
Gasping	Fear	Deflect interactant's attack via one's own submission or incipient retreat
Nose scrunching	Disgust	Reject current interaction trajectory
Neutral	'Suppressed emotion' (poker face) or no emotion	Lead the interactant nowhere in interaction trajectory
'Micromomentary' or 'compound' expressions	'Leaked' or 'blended' emotion	Conflict between displayer's interactional tactics

[a]Abbreviations: BET, Basic emotions theory; BECV, behavioral ecology view of facial displays.
[b]Possible facial tool usage, as indicated by behavioral consequence. Display morphologies and usages in BECV are dependent on interactants, their histories, and their social context.

on the presence and positioning of that audience. The earliest evidence on the hypothesis was provided by an observational study which found that bowlers smiled not when they made strikes (their moments of triumph) but rather when they pivoted in their lanes to see their fellow bowlers [53]. A succession of studies points to the same outcome: facial displays are not 'deployed' when BET would predict that emotion peaks, but when an audience is most available [54–56]. In a recent study conducted with observations gathered on junior and senior judo fighters, roughly 20% of medal match winners displayed the predicted 'happy' smile. Of those judo fighters who smiled at match completion, it was engaging in social interaction with the audience, not winning a medal match, that predicted the issuance of smiles [57]. Developmental studies have also shown that facial displays such as smiles mainly occur when an audience is present, irrespective of the presumed emotional state of the child [58,59].

BECV does not privilege smiling among facial displays. Smiles, however, have been studied most, for several reasons: (i) naturalistically, they are frequent and distinctive human facial displays and thus conspicuous; (ii) methodologically, they are produced reliably in the laboratory, whereas other BET 'prototype' faces are rarely seen, given that typical facial activity is subtle and shifting; and (iii) ethically, eliciting smiles is the least fraught.

There are notable exceptions. Expressions labeled 'surprise' in BET were greater among laboratory participants with friends than those paired with strangers, or who participated alone. The displays were captured the moment participants left the lab to find a bright green adjacent room with furniture, rather than the stark corridor by which they had entered. The increase in 'surprise' displays was unaccompanied by differing self-reports of 'surprise' [60]. Similar sociality effects occurred for facial displays held by BET univocally to signify happiness, sadness, anger, and fear, following imagery inductions using BET-prototypical situations for each. Greater facial activity, measured via electromyography, accompanied imagery of social than solitary contexts, and these differences remained after self-reports of emotion were controlled statistically [5].

Implicit Audience Effects

People make faces in many kinds of private situations (e.g., scowling at defiant pets, praying to God, sexually self-pleasuring, and the crying out of infants when their caretakers have slipped out of sight). And it need not be a pet or deity or missing person who is 'in mind,' it could be a nonliving agent (e.g., we make faces at computers that crash precipitously, or soda machines that defiantly will not return change) or even ourselves (e.g., we make faces as we mutter to ourselves, *sotto voce* or not, on our triumphs or our failures).

Could all these 'private' faces be implicitly social? BET theorists argued that, 'facial expressions do occur when people are alone . . . and contradict the theoretical proposals of those who view expressions solely as social signals' [61]. But did being alone physically imply that we were alone 'psychologically'? Soon, studies appeared which documented variations in facial behavior that depended upon the presence of observers, with audiences that were both explicit (physically present), or with solitary participants whose audiences were merely implicit, that is, present 'in the heads' of the participants via imagery instructions, or located elsewhere but ostensibly coviewing the experimental stimuli [52,62,63]. More studies replicated such implicit audience effects, expanding the findings to infants, beyond smiling, and to augmenting versus decrementing effects of friends versus strangers [64–66].

So why do we make faces when we are alone? For BECV, the answer is simple: although we may be alone physically, we are never alone psychologically. When solitary infants, or injured adults, cry out and make plangent cry-faces, they are broadcasting signals to recruit care. Such broadcasts are commonplace. Among our ancestors, juveniles who did not call out would have perished sooner or more frequently than those who did. For that reason, alarm calls are ubiquitous among animals capable of vocalization. These and other examples lead to one conclusion: when people are not physically near, we repopulate our world with whatever is salient. Our cast of interactants may include fantasied humans, real non-humans, humans who are not proximal, or any nearby objects. Regardless of our casting choices, we treat them as social interactants, and use words and faces that suit the occasion.

Future Directions

New lines of research using diverse methods, research teams, and populations are being developed in different areas of the cognitive sciences [26,67], but, unfortunately, the scope of human diversity still awaits a satisfactory treatment [68]. Studying the manifold strategies whereby we use our facial displays to shape our social interactions, and how these strategies may differ across and within diverse cultures, is one antidote to past limitations of narrow sampling. It also offers relief from methodological traditions and operationalizations that limit context variation and generalization [69].

Psychophysical methods, such as reverse correlations, permit sampling of stimulus parameters (e.g., facial movements) agnostically. Minimizing *a priori* assumptions suggests that we use our facial displays in ways more flexible and diverse than presupposed by theory-driven approaches [70,71]. Individual and cultural contexts powerfully mediate the social impact of facial displays. Because such psychophysical methods are theoretically agnostic, they will be key to understanding how facial displays shape social interactions. Such data-driven methods are proving to be valuable complements to traditional approaches to facial displays; they provide individual and aggregated models of the associations between our mental representations of facial displays and their behavioral consequences [72]. Additionally, observational studies can account for the proximal situational cues operating during a particular interaction, which may allow determining the plausible sets of interaction trajectories for a given display in that context.

These are promissory notes, but in the meantime, BECV has lent insights to research on facial displays and persuasion [73], power and dominance [74,75], smiling in pain [76], and evolutionary theories of pain [77], and responses to social media [78], as well as studies with rats [79] and chimpanzees [80]. The early contributions of BECV were within the areas of social psychology and nonverbal communication, as an alternative to the longstanding BET approach. We now point to two areas in which it has made distinctive, new, interdisciplinary contributions: primatology and AI.

The Behavioral Ecology View of Facial Displays and Primatology

BECV was based in great part on contemporary views of animal signaling, and one hope was always to regain a common framework for understanding both non-human and human displays. Primatologists have noted limitations of the 'emotional model,' particularly for comparative research. Both by the assumptions and linguistic conventions of the BET framework, comparative researchers are led to presumptions about emotions and 'expressions of emotion' that may not generalize phyletically. Specifically, they have noted that: (i) many human facial displays have no non-human counterparts; (ii) the overall co-operative nature of human societies probably engendered different selection pressures on display behavior than those non-human societies that are predominantly competitive; (iii) attributing human emotion to non-humans limits the objective study of their displays; and (iv) the emphasis on displayers' behavior within BET minimizes the reciprocal influence of receivers on displayers [81]. For instance, the function of the silent bared-teeth display in rhesus macaques, once considered clearly affinitive and homologous with human smiling [82], turns out to depend on contextual cues (e.g., the sex of the producer and receiver, affinitive or aggressive situations) [83]. In sum, primatologists now endorsing BECV are using a framework that strips hypotheses about non-human displays of unproven ties to human emotion, and allows the unconstrained study of their predictive functions in social interaction.

The Behavioral Ecology View of Facial Displays and Artificial Intelligence

Researchers in AI and social robotics are tasked with facilitating human–computer interaction, in part by developing methods both to understand human facial displays, and to produce reasonable facsimiles of them in embodied computerized agents. As early as 2000, it was recognized that the dominant approach of multivariate pattern classification (matching BET-designated prototypic posed faces to their foreordained matching emotion labels) would be insufficient to capture: (i) the wide range of common facial displays that escape the prototypes, (ii) their all-important contexts of issuance, and (iii) their time-courses [84]. The field of social robotics realized the need for an ecological approach [85].

By 2015, one influential review specifically called the challenge of BECV to the assumed linkage between emotion and facial displays in BET a 'fundamental question' in how virtual humans are designed and implemented [86]. One proposed resolution was to distend the 'emotion' concept to include social appraisals that lead computationally to social judgments and assessments of the personal significance of events, which then produce 'emotional responses that [will] thereby influence external behavior' [87]. Although this kind of reconciliation is always welcome, the causal path from emotion to action is left unspecified. This leaves it subject to the ready objection that, like its roots in BET, it makes emotion causal when there are no agreed-upon inclusion and exclusion criteria for determining when 'it' (emotion, or a specific emotion) begins and ends [88].

Addressing these longstanding concerns led to the development of a successful AI system for the adaptive, context-dependent facial classification of dynamic facial displays, using optical

flow measurement, and hidden Markov models, conditioned on a context variable, that makes no prior assumptions about the facial displays people use or the meanings of those displays. This AI system was directly inspired by BECV [89].

A later BECV-inspired AI project, focused on social robotics, also recognized that the interaction moves common within a particular social context were more important in human–robot interaction than the categorical face-emotion matching paramount for BET. Video segments for analysis were obtained by having human participants teach a robot the names of various objects, while recording the faces made by the humans when the robot made successes or failures at identification. In contrast to most previous attempts, the 'ground truth' of each video sequence of facial displays, head movements, and gaze directions, was not established theoretically, but was defined by the pedagogical interaction situation. **Active appearance models** individualized for each participant enabled the development of highly discriminant feature vectors from subsegments of each video sequence, which were cross-validated and then tested. Accuracy of the system in recognizing 'success' versus 'failure' displays, despite considerable individual and intertrial variation, equaled average human recognition performance [90].

As these bellwether studies indicate, AI and related technologies that are designed to mimic human nonverbal interaction will benefit readily from the functional, externalist approach of BECV; an approach that does not require unnecessary, and in our opinion diversionary, inferences about the internal workings of our android or virtual interactants, or for that matter, ourselves.

Concluding Remarks

In sum, the BECV of facial displays provides an opportunity to advance our understanding of social interaction and influence by providing a context-dependent and functionalist approach that accounts for human diversity in facial behavior (see Outstanding Questions). Notwithstanding this promise, BECV will always be a tough sell, for two reasons. The first is technical. As we indicated earlier, BECV is more demanding experimentally. It requires the systematic and patient mapping of facial displays across a variety of contexts using different methods and populations, and it emphasizes naturalistic observations, whenever possible, over static stimuli and staged laboratory inductions.

The second reason is philosophical. BECV requires shaking off a romanticized view of human nature, intrinsic to essentialist theories, that makes the face a battleground between an interior 'authentic self' and an external, impression-managed 'social self.' The first concept we treasure; the second we concede reluctantly, and the duality goes back at least to Greco-Roman theater and St. Augustine [91]. Within BECV, both 'selves' are illusory. We are unified organisms, and like our words, voices and gestures, our facial displays are part of our plans of action in social commerce.

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References

1. Ekman, P. (1972) Universal and cultural differences in facial expressions of emotion. In *Nebraska Symposium on Motivation, 1971* (Vol. 19) (Cole, J.R., ed.), In pp. 207–283, Nebraska University Press
2. Ekman, P. (2017) Facial expressions. In *The Science of Facial Expression* (Fernández-Dols, J.M. and Russell, J.A., eds), pp. 39–56, Oxford University Press
3. Keltner, D. *et al.* (2016) Expression of emotion. In *The Handbook of Emotions* (4th edn) (Barrett, L.F., ed.), pp. 467–482, Guilford Press
4. Krebs, J.R. and Dawkins, R. (1984) Animal signals: mind-reading and manipulation. In *Behavioral Ecology: An Evolutionary Approach* (2nd edn) (Krebs, J.R. and Davies, N.B., eds), pp. 380–402, Blackwell Scientific

Outstanding Questions

Do findings in Western industrialized societies generalize to small-scale, indigenous societies? For instance, how do implicit audiences vary among more religious (animistic or non-animistic) versus more secular societies? How much might regional variations in the physical aspects of faces (e.g., in coloration of skin and sclera, bony architecture, muscular attachments, adiposity) and climate (average daytime brightness, temperatures requiring facial coverings versus sun exposure that exacerbates skin wrinkling) affect the form and functions of individuals' displays in those regions? How much does regional genetics account for the diversity in facial displays that was always attributed to learned 'display rules'?

Do the facial displays we make differ when we issue them to humans versus non-human or inanimate objects? According to the sociality hypothesis, our facial displays should show more variation and be more sustained when we are socially engaged with another, whose momentary response leads to reciprocal, dynamic adjustments to our displays. Our displays to non-humans should be briefer and show less variation, given that most non-humans have prognathic faces with long snouts that diminish their orofacial mobility, and show briefer bouts of social engagement with us. Inanimate objects should occasion even less variant and sustained displays, because there is no active interactant (excepting computers that may demand constant visual attention). Paradoxically, perhaps our least variable and most sustained displays may occur in broadcasted signals, like the infant's plangent cry with a cry-face for a caretaker, or the lost hiker's plea for rescue.

Will our increasing interaction with embodied computerized agents like on-screen avatars, vocal assistants like 'Hello, Siri', social robots, and sex-bots affect the kinds of facial displays we make to them, and we then make toward each other? How can existing functionalist approaches from linguistics, anthropology, or environmental/ecological psychology be best combined with BECV to develop applications for AI?

5. Fridlund, A.J. (1994) *Human Facial Expression: An Evolutionary View,* Academic Press
6. Seyfarth, R.M. and Cheney, D.L. (2017) The origin of meaning in animal signals. *Anim. Behav.* 124, 339–346
7. Sihvola, J. and Engberg-Pedersen, T. (1998) *The Emotions in Hellenistic Philosophy,* Springer
8. Browne, J. (1985) Darwin and the expression of the emotions. In *The Darwinian Heritage* (Kohn, D., ed.), pp. 307–326, Princeton University Press
9. Ekman, P. (2016) What scientists who study emotion agree about. *Perspect. Psychol. Sci.* 11, 31–34
10. Marsh, A.A. *et al.* (2016) Neural and cognitive characteristics of extraordinary altruists. *Proc. Natl. Acad. Sci. U. S. A.* 111, 15036–15041
11. Lisetti, C.L. and Schiano, D.J. (2000) Automatic facial expression interpretation: where human-computer interaction, artificial intelligence and cognitive science intersect. *Pragmat. Cogn.* 8, 185–235
12. Barrett, L.F. (2006) Emotions as natural kinds? *Perspect. Psychol. Sci.* 1, 28–58
13. Malinowski, B. (1935/1965) *Coral Gardens and Their Magic: A Study of the Methods of Tilling the Soil and Agricultural Rites in the Trobriand Islands* (Vols. 1 and 2), American Books
14. Mosko, M. (2014) Malinowski's magical puzzles: toward a new theory of magic and procreation in Trobriand society. *HAU* 4, 1–47
15. Senft, G. (1986) *Kilivila: The Language of the Trobriand Islanders,* Mouton de Gruyter
16. Ekman, P. (1993) Facial expression and emotion. *Am. Psychol.* 48, 384–392
17. Nelson, N.L. and Russell, J.A. (2013) Universality revisited. *Emot. Rev.* 5, 8–15
18. Open Science Collaboration (2015) Estimating the reproducibility of psychological science. *Science* 349, aac4716
19. Gendron, M. *et al.* (2014) Perceptions of emotion from facial expressions are not culturally universal: evidence from a remote culture. *Emotion* 14, 251–262
20. Crivelli, C. *et al.* (2016) Reading emotions from faces in two indigenous societies. *J. Exp. Psychol. Gen.* 145, 830–843
21. Crivelli, C. *et al.* (2016) The fear gasping face as a threat display in a Melanesian society. *Proc. Natl. Acad. Sci. U. S. A.* 113, 12403–12407
22. Crivelli, C. *et al.* (2017) Recognizing spontaneous facial expressions of emotion in a small-scale society in Papua New Guinea. *Emotion* 17, 337–347
23. Gendron, M. *et al.* Universality reconsidered: Diversity in making meaning of facial expressions. *Curr. Dir. Psychol. Sci.* https://doi.org/10.1177/096372141774679 (in press)
24. Kagan, J. (2007) *What Is an Emotion? History, Measures, and Meanings,* Yale University Press
25. Rai, T.S. and Fiske, A. (2010) ODD (observation-and description-deprived) psychological research. *Behav. Brain Sci.* 33, 106–107
26. Crivelli, C. *et al.* (2016) A multidisciplinary approach to research in small-scale societies: emotions and facial expressions in the field. *Front. Psychol.* 7, 1073
27. Eibl-Eibesfeldt, I. (1989) *Human Ethology,* Aldine de Gruyter
28. Bender, A. and Beller, S. (2016) Current perspectives on cognitive diversity. *Front. Psychol.* 7, 509
29. Kim, H.S. and Sasaki, J.Y. (2014) Cultural neuroscience: biology of the mind in cultural contexts. *Annu. Rev. Psychol.* 65, 487–514
30. Kitayama, S. and Uskul, S. (2011) Culture, mind, and the brain: current evidence and future directions. *Annu. Rev. Psychol.* 62, 419–449
31. Ekman, P. and Friesen, W.V. (1982) Felt, false, and miserable smiles. *J. Nonverbal Behav.* 6, 238–258
32. Ekman, P. and Friesen, W.V. (1969) The repertoire of nonverbal behavior: categories, origins, usage, and coding. *Semiotica* 1, 49–98
33. Parkinson, B. (2005) Do facial movements express emotions or communicate motives? *Pers. Soc. Psychol. Rev.* 9, 278–331
34. Leys, R. (2017) *The Ascent of Affect: Genealogy and Critique,* University of Chicago Press
35. Bender, A. *et al.* (2010) Anthropology in cognitive science. *Top. Cogn. Sci.* 2, 374–385
36. Ojalehto, B.L. and Medin, D.L. (2015) Perspectives on culture and concepts. *Annu. Rev. Psychol.* 66, 249–275
37. Durham, W.H. (1992) *Coevolution: Genes, Culture, and Human Diversity,* Stanford University Press
38. Mace, R. and Holden, C.J. (2005) A phylogenetic approach to cultural evolution. *Trends Ecol. Evol.* 20, 116–121
39. Rivero, D.G. (2016) Darwinian archaeology and cultural phylogenetics. In *Cultural Phylogenetics* (Mendoza-Straffon, L., ed.), pp. 43–72, Springer
40. Sampson, J. *et al.* (2012) Selecting SNPs to identify ancestry. *Ann. Hum. Genet.* 75, 539–553
41. Fridlund, A.J. and Loftis, J.M. (1990) Relations between tickling and humorous laughter: preliminary support for the Darwin-Hecker hypothesis. *Biol. Psychol.* 30, 141–150
42. Matsumoto, D. (2006) Culture and nonverbal behavior. In *Handbook of Nonverbal Communication* (Manusov, V. and Patterson, M., eds), pp. 219–235, SAGE
43. Goffman, E. (1959) *The Presentation of Self in Everyday Life,* Doubleday Anchor
44. Mehrabian, A. (1968) Relationship of attitude to seated posture, orientation, and distance. *J. Pers. Soc. Psychol.* 10, 26–30
45. Fernández-Dols, J.M. (2017) Natural facial expression: a view from psychological constructionism and pragmatics. In *The Science of Facial Expression* (Fernández-Dols, J.M. and Russell, J. A., eds), pp. 77–92, Oxford University Press
46. Levinson, S.C. (2006) On the human "interaction engine". In *In Roots of Human Sociality: Culture, Cognition, and Interaction* (Enfield, N.J. and Levinson, S.C., eds), pp. 39–69, Berg
47. Patterson, M.L. (2011) *More Than Words: The Power of Nonverbal Communication,* Aresta
48. Smith, W.J. (1977) *The Behavior of Communicating,* Cambridge University Press
49. Fridlund, A.J. (2017) The behavioral ecology view of facial displays, 25 years later. In *The Science of Facial Expression* (Fernández-Dols, J.M. and Russell, J.A., eds), pp. 77–92, Oxford University Press
50. Baumeister, R.F. *et al.* (2007) Psychology as the science of self-reports and finger movements: or whatever happened to actual behavior? *Perspect. Psychol. Sci.* 4, 396–403
51. Fernández-Dols, J.M. and Crivelli, C. (2013) Emotion and expression: naturalistic studies. *Emot. Rev.* 5, 24–29
52. Fridlund, A.J. (1991) Sociality of solitary smiling: potentiation by an implicit audience. *J. Pers. Soc. Psychol.* 60, 229–240
53. Kraut, R.E. and Johnston, R.E. (1979) Social and emotional messages of smiling: an ethological approach. *J. Pers. Soc. Psychol.* 37, 1539–1553
54. Fernández-Dols, J.M. and Ruiz-Belda, M.A. (1995) Are smiles a sign of happiness? Gold medal winners at the Olympic Games. *J. Pers. Soc. Psychol.* 69, 1113–1119
55. Fernández-Dols, J.M. and Ruiz-Belda, M.A. (1997) Spontaneous facial behavior during intense emotional episodes: artistic truth and optical truth. In *The Psychology of Facial Expression* (Russell, J.A. and Fernández-Dols, J.M., eds), pp. 255–274, Cambridge University Press
56. Ruiz-Belda, M.A. *et al.* (2003) Spontaneous facial expressions of happy bowlers and soccer fans. *Cogn. Emot.* 17, 315–326
57. Crivelli, C. *et al.* (2015) Are smiles a sign of happiness? Spontaneous expressions of judo winners. *Evol. Hum. Behav.* 36, 52–58
58. Bainum, C.K. *et al.* (1984) The development of laughing and smiling in nursery school children. *Child Dev.* 55, 1946–1957

59. Schneider, K. and Josephs, I. (1991) The expressive and communicative functions of preschool children's smiles in an achievement situation. *J. Nonverbal Behav.* 15, 185–198
60. Schützwohl, A. and Reisenzein, R. (2012) Facial expressions in response to a highly surprising event exceeding the field of vision: a test of Darwin's theory of surprise. *Evol. Hum. Behav.* 33, 657–664
61. Ekman, P. *et al.* (1990) The Duchenne smile: emotional expression and brain physiology II. *J. Pers. Soc. Psychol.* 58, 342–353
62. Fridlund, A.J. *et al.* (1990) Social determinants of facial expressions during affective imagery: displaying to the people in your head. *J. Nonverbal Behav.* 14, 113–137
63. Fridlund, A.J. *et al.* (1992) Audience effects in affective imagery: replication and extension to affective imagery. *J. Nonverbal Behav.* 16, 191–212
64. Hess, U. *et al.* (1995) The intensity of facial expression is determined by underlying affective state and social situation. *J. Pers. Soc. Psychol.* 69, 280–288
65. Jones, S.S. *et al.* (1991) An audience effect on smile production in 10-month-old infants. *Psychol. Sci.* 2, 45–49
66. Wagner, H.L. and Smith, J. (1991) Facial expression in the presence of friends and strangers. *J. Nonverbal Behav.* 15, 201–214
67. Jack, R.E. *et al.* (2016) Data-driven methods to diversify knowledge of human psychology. *Trends Cogn. Sci.* 22, 1–5
68. Medin, D.L. (2017) Psychological science as a complex system: report card. *Perspect. Psychol. Sci.* 12, 669–674
69. Medin, D.L. *et al.* (2017) Systems of (non-)diversity. *Nat. Hum. Behav.* 1, 0088
70. Jack, R.E. *et al.* (2012) Facial expressions of emotion are not culturally universal. *Proc. Natl. Acad. Sci. U. S. A.* 109, 7241–7244
71. Jack, R.E. and Schyns, P.G. (2017) Toward a social psychophysics of face communication. *Annu. Rev. Psychol.* 68, 269–297
72. Rychlowska, M. *et al.* (2017) Functional smiles: tools for love, sympathy, and war. *Psych. Sci.* 28, 1259–1270
73. Cesario, J. and Higgins, E.T. (2008) Making message recipients "feel right": how nonverbal cues can increase persuasion. *Psychol. Sci.* 19, 415–420
74. Burgoon, J.K. and Dunbar, N.E. (2006) Nonverbal expressions of dominance and power in human relationships. In *Handbook of Nonverbal Communication* (Manusov, V. and Patterson, M.L., eds), pp. 279–297, SAGE
75. García-Higuera, J.A. *et al.* (2015) Facial expressions during an extremely intense emotional situation: Toreros' lip funnel. *Soc. Sci. Inf.* 54, 349–454
76. Kunz, M. *et al.* (2013) Smiling in pain: explorations of its social motives. *Pain Res. Treat.* 2013, e128093
77. Williams, A.C. (2002) Facial expression of pain: an evolutionary account. *Behav. Brain Sci.* 25, 439–488
78. Litt, E. (2012) Knock, knock. Who's there? The imagined audience. *J. Broadcast. Electron. Media* 56, 330–345
79. Nakashima, S.F. *et al.* (2015) Receiving of emotional signal of pain from conspecifics in laboratory rats. *R. Soc. Open Sci.* 2, 140381
80. Parr, L.A. and Waller, B.M. (2006) Understanding chimpanzee facial expression: insights into the evolution of communication. *Soc. Cogn. Affect. Neurosci.* 1, 221–228
81. Waller, B. *et al.* (2017) Rethinking primate facial expression: a predictive framework. *Neurosci. Biobehav. Rev.* 82, 13–21
82. Van Hooff, J.A. (1972) A comparative approach to the phylogeny of laughter and smiling. In *Nonverbal Communication* (Hinde, R. A., ed.), pp. 209–241, Cambridge University Press
83. Beisner, B.A. and McCowan, B. (2014) Signaling context modulates social function of silent-bared teeth displays in rhesus macaques (*Macaca mulatta*). *Am. J. Primatol.* 76, 111–121
84. 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
85. *Embodied Conversational Agents.* Cassell, J. *et al.*, eds), 2002. MIT Press
86. Lhommet, M.L. and Marsella, S.C. *et al.* (2015) Expressing emotion through posture and gesture. In *Oxford Handbook of Affective Computing* (Calvo, R., ed.), pp. 273–285, Oxford University Press
87. Gratch, J. (2008) True emotion vs. social intentions in nonverbal communication: towards a synthesis for embodied conversational agents. In *Modeling Communication with Robots and Virtual Humans* (Wachmuth, I. and Knoblich, G., eds), pp. 181–197, Springer
88. Fridlund, A.J. and Russell, J.A. (2006) The functions of facial expressions: what's in a face? In *The SAGE Handbook of Nonverbal Communication* (Manusov, V. and Patterson, M., eds), pp. 299–319, SAGE
89. Hoey, J. (2002) Clustering facial displays in context. In *Proceedings of the Fifth IEEE International Conference on Automatic Face and Gesture Recognition*. IEEE
90. Lang, C. *et al.* (2013) Facial communicative signal interpretation in human-robot interaction by discriminative video subsequence selection. In *Proceedings of the IEEE International Conference on Robotics and Automation (ICRA)*, pp. 170–177, IEEE
91. Fridlund, A.J. and Duchaine, B. (1996) "Facial expressions of emotion" and the delusion of the hermetic self. In *The Emotions* (Harré, R. and Parrott, W.G., eds), pp. 259–284, Cambridge University Press
92. Senft, G. (1997) Magical conversation on the Trobriand Islands. *Anthropos* 92, 369–391
93. Arnold, K. and Zuberbühler, K. (2006) Language evolution: semantic combinations in primate calls. *Nature* 441, 303
94. Call, J. and Tomasello, M. (2008) Language evolution: semantic combinations in primate calls. *Trends Cogn. Sci.* 12, 187–192
95. Fischer, J. (2017) *Monkeytalk: Inside the Worlds and Minds of Primates,* University of Chicago Press
96. Nettle, D. *et al.* (2013) Human behavioral ecology: current research and future prospects. *Behav. Ecol.* 24, 1031–1040
97. Fridlund, A.J. (1991) Evolution and facial action in reflex, social motive, and paralanguage. *Biol. Psychol.* 32, 3–100
98. Fridlund, A.J. (1992) The behavioral ecology and sociality of human faces. In *Review of Personality and Social Psychology* (Vol. 13) (Clark, M.S., ed.), In pp. 90–121, SAGE