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What Are Emotion Expressions For?

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Abstract

Although research on the nonverbal expression of emotion has played a prominent role throughout psychology during the past two decades—including an instrumental role in the development of contemporary evolutionary psychology—little research has focused on the evolutionary origins and functions of the emotional expressions themselves. However, recent findings from psychophysical, comparative, social, and cross-cultural psychology are converging to produce a compelling functionalist account, suggesting that emotional expressions serve critical adaptive purposes. Most of these studies have narrowly focused on single emotions—an approach that has been very useful for providing new insights about specific expressions but not for developing a broader understanding of *why* humans universally display and recognize distinct emotions. Here we unify these disparate findings in order to illuminate this fundamental form of social communication.

Keywords

emotion expressions, nonverbal displays, evolutionary psychology, adaptation, signal

Darwin's (1872) *The Expression of Emotions in Man and Animals* (*EEMA*) began as half of a single chapter devoted to humankind in his massive manuscript on the evolution of plants and animals. Ultimately that manuscript expanded into four books, beginning with *On the Origin of Species* in 1859 and concluding with *EEMA* in 1872. Despite being the last chapter of this groundbreaking series, *EEMA* marked the first chapter in a long-standing naturalist investigation into nonverbal expressions of emotions.[1] In it, Darwin broke with established perspectives, controversially proposing innate, evolved, and survival-related functions for features of emotion expressions, which, he argued, are rooted in our shared evolutionary heritage with other animals. The theoretical depth and testable hypotheses laid out in *EEMA* cemented Darwin's role not just as a progenitor of contemporary emotion-expression research but also as the first evolutionary psychologist.

If *EEMA* is the "first chapter" of research on the evolution of emotion expressions, one could consider the second chapter to be the vast 1960s–1970s cross-cultural exploration of emotion recognition led by Ekman, Izard, and colleagues. These researchers conducted the first major empirical test of Darwin's hypotheses by examining whether individuals from disparate cultures could reliably identify the emotions conveyed by certain expressions (see Ekman, 1992). Their discovery, that a handful of emotions are cross-culturally recognized, was a major breakthrough in research on psychological universals. Indeed, cited as some of the strongest evidence supporting an underlying "human nature," Ekman's and Izard's findings laid critical groundwork for the eventual development of an evolution-informed psychology addressing the ultimate origins and functions of psychological phenomena. Within emotion research, these findings paved the way for new lines of research addressing questions about the functions these expressions may have evolved to serve. That is, having established that certain emotion expressions are universally recognized, this "second chapter" prompted the question, "Why?"

The Third Chapter: Evolved Functions of Emotion Expressions

That question is now being addressed by several streams of research that are coalescing into what could be considered the third chapter in this long history. Darwin (1872) proposed that emotion expressions evolved to serve two classes of functions: (a) preparing the organism to respond adaptively to environmentally recurrent stimuli and (b) communicating critical social information. Subsequent researchers (e.g., Chapman, Kim, Susskind, & Anderson, 2009; Eibl-Eibesfeldt, 1989; Ekman, 1992) further developed this account, arguing that internal physiological regulation was likely the original adaptive function of emotion expressions, which later evolved to serve communicative functions. Here we review emerging evidence for this "two-stage model" of emotion-expression evolution.

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Adaptation: Emotion expressions for physiological regulation

From a functionalist perspective, emotions are generalized and (theoretically) coordinated suites of behavioral, physiological, cognitive, and affective processes selected to promote automatic, adaptive responses to recurrent environmental events that pose fitness challenges.

Fear provides a useful illustration. Detection of potentially threatening stimuli elicits a cascade of responses including heavier breathing, the redistribution of blood in preparation for rapid movement, and a marshaling of attentive resources to promote hypervigilance. These responses facilitate the animal's ability to escape a predator or other threat. From the Darwinian perspective, the facial muscle movements that together constitute a fear expression originally emerged as part of this adaptive behavioral "macro."

Indeed, recent studies by Anderson and colleagues support this suggestion. The widened eyes of individuals instructed to pose a fearful facial expression were found to increase the scope of their visual field and the speed of their eye movements, allowing expressers to better identify (potentially threatening) objects in their periphery (Susskind et al., 2008). Components of the fear expression thus may be as much a part of the adaptive emotional response as the frightened affect and quickened heart rate.

Other expressions function similarly. The prototypic disgust expression, characterized by a scrunched nose and mouth, results in constriction of these orifices, thereby reducing air intake (Chapman et al., 2009). Since the primary adaptive functions of disgust are to alert an organism to, and protect an organism from, potentially noxious stimuli, the disgust expression's feature of reducing the inhalation of airborne particles can be seen as a part of the larger adaptive disgust response.

These novel findings and ongoing follow-up work are revealing the original functional legacy of emotion expressions. However, the physiological functions of distinct expressions are unlikely to be the only reason for their retention within the human repertoire; if they were, there would be little need for expressions to be displayed in exaggerated, highly prototypic, and visually obvious ways during evolutionarily recurrent situations that, in some cases, seem unrelated to those of their original physiological function (e.g., disgust shown in response to morally reprehensible acts; Chapman et al., 2009; Rozin, Lowery, & Ebert, 1994). Indeed, Darwin noted that expressions also serve as potent sources of information about internal states or intended actions. Although the findings reviewed above suggest that at least some physiological functions have been retained, the primary purpose of emotion expressions in contemporary human life, and humans' primary preoccupation with them, may have more to do with their capacity to quickly and nonverbally communicate socially significant information.

Exaptation: Emotion expressions for social communication

Evolutionary biologists make an important distinction between *cues* and *signals*. A cue provides information gleaned as a by-product of something that serves an alternate adaptive purpose; for example, chewing is a reliable cue that someone is eating, but it did not evolve to communicate that information. On the other hand, signals evolved specifically for the purpose of communication; for example, peacock plumage evolved as a hard-to-fake signal of mate quality (Hasson, 1997). In the two-stage model, it is hypothesized that emotion expressions began as cues—providing information about internal states but not existing for that reason—but eventually transformed, in both form and function, to become signals. In other words, in the course of evolutionary history, the function of expressions itself evolved. Over time, as recognizing the internal states of other animals yielded fitness-positive consequences, the facial and bodily behavioral components of certain emotions came to cue those emotional states to observers. As social interaction became more possible and even vital for many species, the adaptive value of these expressions may have shifted toward communication. As a result, the nonverbal behaviors associated with distinct emotions likely underwent *ritualization*: a process of change well researched in evolutionary zoology whereby an animal's nonverbal displays become exaggerated, more visible, distinctive, and/or prototypic in order to function as reliable and effective signals (Eibl-Eibesfeldt, 1989).[2] For emotion expressions, this shift from cue to signal can be thought of as their second stage of evolution—a paradigmatic example of exaptation, the common evolutionary process whereby a feature that evolved for one reason gradually morphs to serve a secondary adaptive function.

As a result of ritualization, emotion expressions have become the highly recognizable displays that characterize daily life. Indeed, the ability to quickly and accurately recognize these expressions appears to be a human universal and even generalizes to certain Great Apes (e.g. Parr, 2003), suggesting that understanding others' emotions is adaptive. What the third chapter of emotion expression research is revealing is *why* emotion communication—reliably displaying and identifying emotion expressions—increases fitness.

Among the best examples of such research are studies that have demonstrated an evolved preparedness in monkeys for automatically responding to, and learning from, the fear expressions of their conspecifics. Lab-reared rhesus monkeys previously unafraid of snakes were found to rapidly develop this historically adaptive fear after seeing wild rhesus monkeys display fear expressions in the presence of snakes (but, importantly, not in the presence of flowers, see Ohman & Mineka, 2001). Hence, monkeys not only "recognize" fear expressions but also respond to the meaning behind these expressions in an adaptive manner. Similar findings have emerged in human infants, who by 12 months seem to respond

adaptively to parents' fear expressions, using them to guide decisions about whether to cross a visual cliff (Sorce, Emde, Campos, & Klinnert, 1985).

Thus, a number of primates seem to have evolved two complementary psychological abilities—one to automatically display ritualized expressions in prototypic, evolutionarily recurrent situations and another to automatically interpret and respond to the meaning behind these expressions when they are displayed by others (see Fig. 1). In the case of fear, this means that the reason the expression is universally displayed and recognized is not only that expressers benefit physiologically from widening their eyes in response to fear-eliciting stimuli but also because both expressers and observers benefit from a rapidly communicated nonverbal signal of danger.

A number of recent, methodologically diverse studies have investigated the signaling properties of emotion expressions in adult humans. For example, research has shown that individuals rapidly react to threat messages sent by expressions of fear and anger; these expressions recruit subcortical neural processing to capture attention and stimulate detailed perceptual processing (Vuilleumier, 2002). Conditioning studies have shown that anger and fear expressions are more easily paired with aversive stimuli than are happiness expressions—suggesting an evolved preparedness to form cognitive associations between threat-signaling expressions and threatening concepts (see Ohman & Mineka, 2001). Others have shown that avoidant, "flight"-oriented motor behaviors are facilitated by viewing fear expressions but not anger expressions, whereas approach, "fight"-oriented motor behaviors are facilitated by anger expressions but not neutral or fear expressions (Wilkowski & Meier, 2010).[3] Together, these findings demonstrate that observers can rapidly read the messages conveyed by fear and anger expressions, not simply to consciously recognize the emotion being expressed but to behaviorally and cognitively respond to evolutionarily recurrent events in the most adaptive way. Indeed, the ability to rapidly prepare for significant environmental events by reading others' nonverbal signals can confer an acute adaptive advantage.

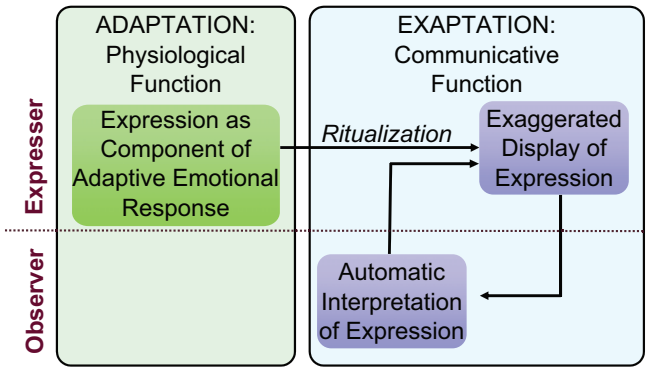

Fig. 1. The two-stage model of the evolution of emotion expressions. Expressions initially evolved as facial components of the overall emotion response. They served to physiologically prepare the body to adaptively respond to emotion-eliciting stimuli. As socially complex animals began to reap fitness benefits from communicating important social information via emotion expressions, two complementary abilities emerged—one for automatically displaying exaggerated forms of original expressions and a second for automatically interpreting the social meaning behind these expressions.

Studies supporting the social-communicative function of emotion expressions have also been conducted on pride and shame, which, as "self-conscious emotions," are thought to have evolved to their present forms relatively recently in order to serve largely social functions (Tracy & Robins, 2004). Indeed, pride and shame's cross-culturally displayed and recognized nonverbal expressions (Tracy & Matsumoto, 2008; Tracy & Robins, 2008) appear to facilitate humans' ability to navigate the social world by efficiently communicating information about social status. As social hierarchies have become increasingly complex in recent hominid history, a facility for rapidly understanding and responding to these complexities has become an essential, and adaptive, skill.

A growing body of evidence supports this account. First, the pride and shame expressions show clear morphological resemblances to dominance and submission displays of other primates (Tracy & Matsumoto, 2008). Second, humans across disparate cultures (including the congenitally blind) have been found to spontaneously display these expressions in status-relevant situations (i.e., success and failure; e.g., Keltner, 1995; Lewis, Alessandri, & Sullivan, 1992; Tracy & Matsumoto, 2008). Third, a series of studies measuring implicit associations demonstrated that individuals *viewing* pride expressions respond by rapidly, automatically, and unavoidably affording higher status to pride-displaying targets than to targets showing a range of other positive and negative displays (Shariff & Tracy, 2009). Furthermore, this effect holds among both Canadian undergraduates and Fijian villagers in a traditional small-scale society with divergent cultural norms about status-seeking behaviors (Tracy, Shariff, Zhao, & Henrich, 2011).

Together, these studies strongly suggest that the automatic communication of social status is an innate, universal, and likely evolved function of the pride and shame expressions. One important question for future research is whether these expressions—and those of other relatively recently evolved emotions—*originated* as signals, to serve these important communicative functions, or whether they too were exapted from other, physiologically adaptive origins.

Future Directions and Conclusion

There are alternative explanations for the ubiquity of distinct emotion expressions in human life, and not all of these accounts can be easily reconciled with ours (e.g., see Barrett, 2011, this issue). Nonetheless, we believe that the totality of evidence is best and most parsimoniously explained by the two-stage account reviewed above. That said, the third chapter of this account is only partially complete (see Fig. 2); though evidence for a coherent explanation of the evolution of emotion expressions *in general* is accumulating, the adaptive physiological and communicative functions of several specific expressions remain poorly understood, and many hypotheses await empirical testing.

EMOTION EXPRESSION	HYPOTHESIZED PHYSIOLOGICAL FUNCTION	HYPOTHESIZED COMMUNICATIVE FUNCTION	RELEVANT RESEARCH
Happiness 	Research Needed	Communicates a Lack of Threat	Preuschoft & Van Hoof, 1997 Ramachandran, 1998
Sadness 	Research Needed	Tears Handicap Vision to Signal Appeasement and Elicit Sympathy	Hasson, 2009
Anger 	Research Needed	Alerts of Impending Threat, Communicates Dominance	Marsh, Ambady, & Kleck, 2005 Wilkowski & Meier, 2010
Fear 	Widened Eyes Increase Visual Field and Speed Up Eye Movements	Alerts of Possible Threat, and Appeases Potential Aggressors	Marsh et al., 2005 Ohman & Mineka, 2001 Susskind et al., 2008
Surprise 	Widened Eyes Increase Visual Field to See Unexpected Stimulus	Research Needed	Ekman, 1989
Disgust 	Constricted Orifices Reduce Inhalation of Possible Contaminants	Warns About Aversive Foods, as Well as Distasteful Ideas and Behaviors	Rozin et al. 1994, Chapman, Kim, Susskind, & Anderson, 2009
Pride 	Boosts Testosterone and Increases Lung Capacity to Prepare for Agonistic Encounters	Communicates Heightened Social Status	Carney, Cuddy, & Yap, 2010 Shariff & Tracy, 2009 Tracy & Matsumoto, 2008
Shame 	Reduces/Hides Bodily Targets From Potential Attack	Communicates Lessened Social Status, Desire to Appease	Keltner & Harker, 1998 Shariff & Tracy, 2009 Tracy & Matsumoto, 2008
Embarrassment 	Reduces/Hides Bodily Targets From Potential Attack	Communicates Lessened Social Status, Desire to Appease	Keltner & Buswell, 1997

Fig. 2. The state of the evidence for the adaptive functions of nonverbal expressions of emotion. Existing research on the adaptive functions of nonverbal expressions of various emotions is unevenly distributed among the various expressions. For some, such as fear and pride, a significant amount of work has been conducted, using a variety of methodological approaches. For others, such as surprise, research remains in the speculative stages. Future studies on the latter expressions would benefit from treating the former as a model, guiding approaches and methods. Images taken from the UC Davis Set of Emotion Expressions (UCDSEE; Tracy, Robins, & Schriber, 2009).

Given that intense selection pressures for rapidly coping with threat have left mammals with a vast and salient psychological and neurophysiological fear apparatus, it is unsurprising that fear has been among the first and most comprehensively studied expressions. The resulting extensive and methodologically diverse body of work on fear can and should be used as a model for future research uncovering the evolved functions of other expressions. Such studies might address basic, as-yet unanswered questions like: What is the communicative utility of the contempt expression? Why are smiles associated with happiness?

The challenge in this enterprise—as with any evolutionary psychological research program—is moving from speculation to evidence. Firm proof of special design is notoriously elusive. However, studies that confirm a priori predictions, discount alternative explanations, and produce convergent evidence can provide compelling support for an underlying evolved nature. Accomplishing this will require the continued and disciplined use of our full empirical toolbox, including comparative ethology, cross-cultural fieldwork, developmental psychology, and cognitive neuroscience. Few of these tools were available in Darwin's time (and none in their current advanced forms), but they may allow us to finally complete the program of research he began nearly 150 years ago.

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Notes

1. The present article should be considered a subset of a larger investigation into the evolution of all components of emotions. Thus, emotions hypothesized to have adaptive functions but no prototypic expression (e.g., jealousy) are not discussed here.
2. Ritualization may account for Darwin's principle of "antithesis"—that morphological differences between displays associated with "opposite-functioning" emotions, such as pride and shame, are exaggerated to appear antithetical to each other.
3. But see also Marsh, Ambady, and Kleck (2005), which further supports the signaling function of fear expressions by demonstrating that fear can also elicit *approach* behaviors. Thus, in addition to warning bystanders of threat, fear may function to appease and disarm the threat's source.

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