Darwin and Emotion Expression

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In his book The Expression of the Emotions in Man and Animals, Charles Darwin (1872/1965) defended the argument that emotion expressions are evolved and adaptive (at least at some point in the past) and serve an important communicative function. The ideas he developed in his book had an important impact on the field and spawned rich domains of inquiry. This article presents Darwin's three principles in this area and then discusses some of the research topics that developed out of his theoretical vision. In particular, the focus is on five issues—(a) the question of what emotion expressions express, (b) the notion of basic emotions, (c) the universality of emotion expressions, (d) the question of emotion prototypes, and (e) the issue of animal emotions—all of which trace their roots to Darwin's discussion of his first two principles.

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harles Darwin's (1872/1965) book *The Expression of the Emotions in Man and Animals* has been highly influential for research on emotions (almost 3,000 citations according to the Institute for Scientific Information [ISI]). Darwin himself considered the study of emotion expressions something of a "hobby-horse" and had originally intended his observations to be integrated into a chapter in *The Descent of Man, and Selection in Relation to Sex* (Darwin, 1871). However, he eventually decided that the material would not fit into a chapter and warranted its own book. This book very specifically was intended to counter the claim by Sir Charles Bell (1844) that certain muscles were created so as to give humans the ability to express their feelings.

Darwin's basic message was that emotion expressions are evolved and (at least at some point in the past) adaptive. For Darwin, emotion expressions not only originated as part of an emotion process that protected the organism or prepared it for action but also had an important communicative function. Darwin saw in this communicative function a further adaptive value: "We have also seen that expression in itself, or the language of the emotions, as it has sometimes been called, is certainly of importance for the welfare of mankind" (Darwin, 1872/1965, p. 366).

Darwin had no doubt that the expressive behavior that he described was part of an underlying emotional state, that is, that emotion expressions derived their communicative value from the fact that they were outward manifestations of an inner state. As these expressions were considered by him to be hereditary and evolved, Darwin necessarily assumed clear parallels and antecedents to human emotions in the emotions of animals and our humanoid ancestors. On the basis of these notions he elaborated clear ideas as to why emotions are expressed the way they are—his three principles—and he made many predictions regarding their meaning and regulation. The ideas that Darwin formulated generated a rich field of research. Many fundamental questions in contemporary research on emotions and their communication can be traced to issues first raised by Darwin. In what follows we attempt to present the issues that had the most lasting influence on subsequent research.

Darwin himself did not define the term *emotion*. And in fact, the field of emotion research has found a consensual definition of this term elusive (cf. Frijda, 2000). In the present context, emotions are considered to be relatively short-duration intentional states that entrain changes in motor behavior, physiological changes, and cognitions.

We start by briefly presenting Darwin's three principles and then discuss some of the research topics that developed out of his theoretical vision. In particular, we focus on five issues—(a) the question of what it is that emotion expressions express, (b) the notion of basic emotions, (c) the universality of emotion expressions, (d) the question of emotion prototypes, and (e) the issue of animal emotions-all of which trace their roots to Darwin's discussion of his first two principles. Not discussed are Darwin's many casual observations, which to him represented truisms, that later blossomed into rich fields of research. Obvious examples are his remarks on people's tendency to expressively imitate others, the notion that suppressing one's expression of an emotion also suppresses the underlying emotion—the facial feedback hypothesis, and observations about spontaneous (Duchenne) versus intentionally expressed smiles. Given space constraints, our discussions are necessarily brief, ignoring some of the subtleties of arguments presented over the years, but we hope that this overview will demonstrate Darwin's lasting and fruitful impact on a continuously active field.

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Darwin's Principles

The first part of Darwin's (1872/1965) book *The Expression of the Emotions in Man and Animals* is devoted to the elaboration of three principles that explain why emotions are expressed the way they are. These are the principle of serviceable habits, the principle of antithesis, and the principle of the direct action of the excited nervous system on the body.

The Principle of Serviceable Habits

This principle states that useful expressive "habits" acquired during the course of experience are genetically inherited by offspring. This Lamarckian view (Lamarck, 1809) of inheritance was the one to which Darwin subscribed. It was when discussing the serviceable habits principle that Darwin most clearly talked about the functionality of emotions and their expression. For example, the raising of the eyebrows in surprise is a useful habit "so that the field of vision may be increased, and the eyeballs moved easily in any direction" (Darwin, 1872/1965, p. 281).

However, for most emotion expressions, Darwin insisted that they were functional in the past or were functional in animals but not in humans. On the one hand, he implied that this was because humans were too civilized to avail themselves of this functionality. In the case of the sneer in rage, for example, the canine teeth are bared, and Darwin argued that this was a sign that our progenitors fought with their teeth—whereas civilized humans do not. However, the more important reason why Darwin denied functionality to present-day human emotion expressions was that it was his goal to show that they were not created by divine design—and perfectly functional facial expressions could have been interpreted as God-given tools for

human communication, whereas formerly useful expressions, which have lost functionality, present evidence of evolution.

The Principle of Antithesis

In the principle of antithesis, Darwin asserted that some expressions look the way they do simply because they are the opposite of a serviceable one. In the section of his book describing this principle, the importance of the communication of emotional states and the need for clarity in this communication were most clearly outlined. Thus, the notion of antithesis is closely linked to the notion of communication clarity. Research referring back to this principle has been most extensive in the domain of animal communication, particularly with regard to "ritualized signals" (see Hauser, 1996).

However, it is worthwhile noting that according to Darwin, expressions communicated not only states but also traits. For example, he noted, "No determined man probably ever had an habitually gaping mouth. Hence, also, a small and weak lower jaw, which seems to indicate that the mouth is not habitually and firmly closed, is commonly thought to be characteristic of feebleness of character" (Darwin, 1872/1965, p. 233). He further suggested that some expressions may be used by the organism to simulate desirable traits: "In this case it appears possible that they might have wished to make themselves appear larger and more terrible to their enemies, by voluntarily assuming a threatening attitude and uttering harsh cries; such attitudes and utterances after a time becoming through habit instinctive." (Darwin, 1872/1965, p. 103). This notion, that there is perceptual overlap between emotion expressions and certain trait markers which then influences emotion communication, has been more recently taken up by Zebrowitz (see Zebrowitz & Montepare, 2006) as well as Hess, Adams, and Kleck (2007).

The Principle of the Direct Action of the Excited Nervous System on the Body

According to Darwin's third principle, some expressions occur because the nervous system needs to discharge excess excitement. Basing his ideas on the work of Spencer (1860), Darwin gave the example of laughter as a quasiconvulsive movement that discharges an overflow of nervous energy that was induced by either physical or psychological tension. To explain the reason why something funny will make people laugh, Darwin (1872/1965) used the analogy of tickling: "The imagination is sometimes said to be tickled by a ludicrous idea: and this so-called tickling of the mind is curiously analogous with that of the body" (p. 199). This idea was also shared by Hecker (1873), who, a year after the publication of Darwin's book, proposed that laughter was a kind of protective reflex that aimed at balancing the respiratory and circulatory effects of physical or mental tickling, both of which irritated vasomotor nerves. In fact, it has been shown both via self-report (Fridlund & Loftis, 1990) and with behavioral measures (Harris & Christenfeld, 1997) that people who are more prone to laugh when tickled are also more likely to laugh at



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humorous stimuli—but it is unclear whether this reflects more than just a tendency to laugh more easily under a variety of circumstances (Harris & Christenfeld, 1997).

With the few exceptions noted above, the theories presented in Darwin's three principles have not been directly examined in contemporary research. However, many of the ideas that Darwin expressed in formulating them have found an echo and have fertilized emotion research in the 20th and 21st centuries. In what follows we outline some of Darwin's ideas and suggestions that inspired rich subsequent domains of inquiry.

What Do Emotion Expressions Express?

As mentioned earlier, Darwin considered emotion expressions to be just that—an expression of an underlying emotional state. More specifically, when he talked about serviceable habits (the first principle) he assumed that the underlying emotions ready the organism for dealing with an emotional event. Although some aspects of this process (e.g., increased heart rate) tend not to be visible to perceivers, others (e.g., postural changes and facial expressions) are. He further considered that the communication of emotion was of high importance: "Every true or inherited movement of expression seems to have had some natural and independent origin. But when once acquired, such movements may be voluntarily and consciously employed as a means of communication" (Darwin, 1872/1965, p. 355).

The Early View: Emotion Expressions as Cultural Signals

Yet, right from the beginning, Darwin's view of emotion expressions as the visible part of an underlying emotional state has been disputed and rejected by those who considered facial expressions as social or cultural signals only. Specifically, a number of studies in the early years of the 20th century came to the conclusion that emotions could only be recognized at chance levels; however, other studies found good recognition rates (see Bruner & Tagiuri, 1954, for a review). This disparity in findings led Bruner and Tagiuri in their 1954 Handbook of Social Psychology chapter to state that "the evidence for the recognizability of emotional expressions is unclear" (p. 634). They concluded that, if anything, emotional facial expressions are culturally learned. This view remained basically unchanged until 1972, when Ekman, Friesen, and Ellsworth wrote a book to explicitly vindicate Darwin's idea that emotional expressions are universal and directly associated with an underlying emotional state. This book and related research by Ekman and colleagues (e.g., Ekman, 1972; Ekman et al., 1987; Ekman, Sorenson, & Friesen, 1969) as well as Izard (e.g., Izard, 1971) were successful in making these notions predominant in the field (see below).

Fridlund's View: Emotion Expressions Signal Behavioral Intentions

However, as noted above, Darwin had himself emphasized the use of emotion expressions for communicative purposes. This role of expressions is central to Fridlund's (1994) behavioral ecology theory. Specifically, Fridlund described the appellation *emotion expressions* as a misnomer. According to behavioral ecology theory, emotion expressions do not express emotions but rather intentions. Fridlund emphasized that for emotion expressions to be truly useful as a communicative signal they should be linked to the organism's social motives rather than to quasi-reflexive emotions, and he concluded that emotion expressions should be considered unrelated to an underlying emotional state (Fridlund, 1994). In particular, he pointed out the problem posed by positing an emotion system, which first produces emotional facial expressions and then is overridden by social display rules (e.g., Ekman's, 1972, neurocultural theory described below). Consequently, the behavioral ecology view of emotional facial expressions asserts that they should be viewed as communicative signals only.

This assertion is problematic from several perspectives. Parkinson (2005), for example, questioned why a specific display should be linked to a specific motive or why communicating motives should be adaptive since when such motives are feigned they can also be used to cheat. His extensive review concluded that facial expressions may well serve as both symptoms of an underlying state and communicative signals. This notion was first empirically tested by Hess, Banse, and Kappas (1995), who showed in a partial replication of Fridlund's 1991 study that smiles vary both as a function of social context (and thus social motives) and of the emotional content of the stimulus. These findings were extended by Jakobs and colleagues (e.g., Jakobs, Manstead, & Fischer, 1999, 2001) to different contexts and emotions.

An Appraisal View

Yet, the view that emotional facial expressions function as both a communicative signal and as a symptom of an emotional state has to face the conceptual challenge originally posed by Fridlund (1994)—how can social norms and rules and biological emotion processes be combined? This problem was at the center of Fridlund's (1994) critique of the two-factor theory of emotion, in which an emotion program that starts in response to an emotion elicitor is somehow interrupted by a social norm, which replaces the emotion expression output of the program with a socially demanded expression.

However, the question of how such an interruptive process can work may be the wrong question to ask. Specifically, appraisal theories of emotion (e.g., Frijda, 1986; Scherer, 1984) would predict that social norms and rules—to the degree that they are endorsed by the individual—are an integral part of the appraisal process (cf. Kappas, 2003). Such a view implies that emotional facial expressions are not first produced by an emotion-eliciting process and then filtered or modified by a social-rule-driven process but rather that social norms and motives are an inherent part of the emotion elicitation process. Put another way, the emotion-eliciting situation is appraised in the light of the situation-relevant social norms. For example, when learning simultaneously that one has received an A+ and one's best friend has received a C- in a course, the resulting joy is tempered by the appraisal of this second piece of information, and no cumbersome filter has to be applied to keep from jumping up and down in front of the disappointed friend.1

Thus, using an appraisal framework, it is possible to reconcile both signal and symptom functions of emotions. Specifically, because appraisal theories consider emotions as inherently determined by the organism's motivational state and hence its intentions (Frijda, 1986; Scherer, 1984), emotion expression by its very nature should express intentions—as these are part of emotions in a fundamental way (Hess & Kappas, in press).

In sum, neither Ekman's (1972) neurocultural theory nor Fridlund's (1994) behavioral ecology theory satisfactorily describes what emotion expressions express. In fact, the evidence cited above suggests that emotion expressions are neither expressions of "pure" emotions nor "pure" communicative signals but rather both. However, more research is needed to clarify the process that determines what will be shown in which context. Appraisal theories may provide the relevant theoretical framework for such research.

Basic Emotions

It would be difficult to write about Darwin and emotion expression without touching on the notion of basic emotion expressions. Darwin himself discussed in his book a large number of expressions of emotional states, including not only states commonly accepted as emotional, such as joy and anger, but also such states as patience and sulkiness. In these discussions, Darwin did not single out specific emo-

tions as basic. Nor did he specifically focus on facial expressions. The current canon of six or seven basic emotions with a specific prototype expression can be traced to Paul Ekman (1972), who posited hardwired programs that link the so-called basic emotions (happiness, sadness, fear, disgust, anger, surprise, and possibly contempt, Ekman & Friesen, 1986) to specific (facial) expressions. Ekman's (1972) neocultural theory posits that these hardwired links are interrupted by socially learned display rules, which accounts for the fact that these hardwired facial expressions are not frequently observed in social interaction (see below). Evidence for basic emotions has been drawn from cross-cultural recognition research, comparative research, studies of infant facial expressions, and neurological studies.

In all of these domains, supportive evidence for the notion that facial expressive patterning is systematically linked to certain emotional states has been found. Thus, the so-called basic emotions are indeed cross-culturally recognized at a level above chance (e.g., Ekman, 1972; Ekman et al., 1987; Elfenbein & Ambady, 2002; Izard, 1971)—but see below for a critique of these findings. Evidence from comparative research suggests overlap between the expressions of human and nonhuman primates (e.g., Chevalier-Skolnikoff, 1973; Redican, 1982). Findings that chimpanzees react differentially to different human expressions (Itakura, 1994) and that human children's ability to interpret monkey vocalizations of aggression, fear, dominance, positive emotions, and submission develops simultaneously with their ability to interpret human emotional behavior (Linnankoski, Laasko, & Leinonen, 1994) also suggest similarities between the expressions of human and nonhuman primates. However, the interpretation of these findings is complicated by the fact that it is often difficult to assure that expressions actually serve as homologues across species or to ascertain emotional states in animals.

Affective neuroscience has made great strides in identifying emotion-relevant brain regions involved in both emotion recognition and production, but no brain circuits that are uniquely emotional have been identified—nor should they be expected to exist in this form (see Davidson, 2003). Finally, research on infant facial expressions also suggests a genetic basis for some facial expressive displays. In one now classic study Eibl-Eibesfeldt (1973) reported that deaf and blind children showed expressions of anger, happiness, and other emotions in suitable situations even though they could not have learned them through observation. Young infants also respond differently to different emotion expressions, which suggests an ability to discriminate emotion expressions (see Izard et al., 1995). However, the correspondence between prototype expressions of basic emotions and infants' expressions is often rather low (see Camras, Malatesta, & Izard, 1991).

¹ However, if a rule is not endorsed—such as, for example, the rule to show happiness when receiving a disappointing gift—then a more cumbersome filter process may indeed be an adequate conceptualization.

In sum, no consistent and unequivocal picture of the genetic basis for a limited set of basic emotions emerges. However, the available evidence tends to support the notion of some partial genetic basis of facial patterning as a function of emotion. Yet research is needed to better understand the link between facial expression and mental states.

Prototypical Expressions

Closely linked to the notion of basic emotions is the notion of prototypical expressions. The facial expressions used by Ekman and colleagues for their intercultural research and the expressions described by Darwin for a wider range of emotions are typically constrained to just one expression to represent any specific emotional state. However, as became evident in the research conducted in the first part of the 20th century (cf. Bruner & Tagiuri, 1954), in a given emotional context a number of different emotion expressions can be shown, and more than one expression is typically associated with a given emotion in recognition studies (e.g., Wiggers, 1982). This raises a question regarding the status of the prototype expression compared to those other expressions.

Specifically, whereas there is evidence that the patterns of emotion expressions described by Darwin and by Ekman and Friesen (1978) as prototypical for certain emotions tend to be highly recognizable (e.g., Ekman, 1972; Ekman et al., 1987; Elfenbein & Ambady, 2002; Izard, 1971), there is much less evidence that these specific expressions are actually shown by people who report feeling the relevant emotions. That is, whereas a number of studies have found that specific facial displays can be linked to self-reports of specific affective states (e.g., Cacioppo, Petty, Losch, & Kim, 1986; Smith & Scott, 1997) or to clearly defined emotional situations (Matsumoto & Willingham, 2006), others have not (see Fernández-Dols & Ruiz-Belda, 1997). These contradictory findings could of course be attributed to differences in the procedures employed to elicit specific emotions or to differences in the complexity of the experimental situations in which they were elicited. Yet even across well-controlled studies, perfect overlap with prototypes is rarely observed. One explanation may be that facial expressions do not in fact result from emotions but rather from the underlying appraisals of the social context in which the emotion is experienced (Scherer, 1992; Smith & Scott, 1997).

An Appraisal View of Prototype Expressions

Specifically, it has been postulated that there is a direct causal relationship between specific appraisals and specific expressive elements such that each appraisal outcome is associated with a specific facial movement (Scherer, 1992; Smith & Scott, 1997). For example, goal obstruction is associated with the drawing together of the eyebrows as suggested by Darwin. As appraisals progress, the cumulative appearance of facial movements constitutes the resulting emotion expression. Support has been found especially for goal obstruction and pleasantness appraisals (Aue,

Flykt, & Scherer, 2007; Lanctôt & Hess, 2007; see also Smith & Scott, 1997), but more systematic research is needed to verify this proposal.

From this perspective, emotion prototypes are shown only when a situation is appraised in an emotion-prototypical fashion. However, as mentioned above, social interactions are heavily rule based. As such, emotion regulation is an integral part of any interaction and is part of the appraisal process. Hence it should not surprise us that "classic" prototypical expressions are the exception and not the rule in average everyday interactions. Considering emotion expressions as a readout of appraisals would therefore help to solve some of the most persistent problems in the research on emotion expressions.

Are Emotions Universal?

A central implication of Darwin's view of emotion expressions was that there should be continuity of expression across species and universality of expressions within humans. Darwin conducted a survey by sending letters to individuals who lived in various parts of the world asking them to report on the emotion expressions they observed when interacting with the native inhabitants of these places. He concluded from this survey that expressions were indeed universal. But as mentioned above, his contention was not systematically supported by later research in the early 20th century. Ekman et al. (1972) outlined a number of methodological problems with studies failing to find universality and provided evidence in support of Darwin's view. However, even though this and related research (Ekman, 1972; Ekman et al., 1987; Izard, 1971) had a great impact on the field, the view was not without serious critiques. A number of discussions in leading journals took issue with the methodology employed in the studies that found support for universality (e.g., Ekman, 1994; Izard, 1997; Russell, 1991, 1994, 1995), and social constructivist approaches to emotion emphasized differences in emotion vocabularies and disputed universality on these grounds (see, e.g., Wierzbicka, 1994). A number of researchers advocated intermediate positions (see, e.g., Fiske, Kitayama, Markus, & Nisbett, 1998; Mesquita, Frijda, & Scherer, 1997) acknowledging both universals and cultural variations in the expression and recognition of emotion, but the issue cannot as yet be considered settled.

Cultural Dialects

More recently, Elfenbein and Ambady (2002) conducted a meta-analysis of cross-cultural emotion recognition studies and found—across different research procedures and nonverbal channels—that individuals were relatively better at recognizing emotional expressions from members of their own cultural group. Geographical proximity and cross-cultural contact seemed to reduce the extent of this ingroup advantage. Accordingly, Elfenbein and Ambady (2002, 2003) speculated that the in-group advantage might stem from subtle variations in the style of encoding across cultures, such that judgments are faster and more accurate for perceivers familiar with these subtle variations. They

argued that a universal language of emotion could have dialects that differ subtly from each other. A recent study by Elfenbein, Beaupré, Lévesque, and Hess (2007) comparing expressions from Quebec and Gabon found evidence for the posited dialects such that different muscles were activated for the same expressions by members of the two cultures. These differences emerged most clearly for serenity, shame, contempt, anger, sadness, surprise, and happiness, but not for fear, disgust, or embarrassment. A decoding study also reported by these investigators showed that individuals were better at decoding expressions from their own group but also showed considerably better than chance accuracy for expressions from the other group.

In sum, the evidence to date suggests that emotion expressions are by and large universally recognized—at least with regard to emotions that have been categorized as basic. However, the evidence is also clear that many emotions are not universally expressed in exactly the same manner—even though there is enough overlap that they can be recognized well across cultures and subgroups. This poses the question of why emotions are expressed differently—but not dramatically differently—and why they can still be well recognized by members of other groups. Research is required to study not so much whether or not there are differences in expression and recognition but rather why there are differences and how they can be explained.

An Appraisal View of Cultural Dialects

One plausible explanation is that emotion expressions do not represent a unitary phenomenon but rather, as mentioned in the context of prototypes, are the cumulative result of underlying appraisals (Scherer, 1992; Smith & Scott, 1997). Scherer (1987) conceived of emotions as families. Thus, irritation, rage, and anger would all be members of an anger family. Members of these families share central appraisals (such as goal obstruction for anger) but may differ with regard to other appraisals. He proposed that within a given culture a "modal" (in the sense of statistically most common) appraisal pattern will develop for each emotion as a function of the cultural constraints posed. As emotional facial expressions are a function of appraisal outcomes and because central appraisals are shared among members of the family, key recognizable elements of the expression are shared as well. Yet the subtle differences in appraisals would result in subtly different expressions. From this perspective, emotions would be expressed somewhat differently in different cultures because modal emotions are subtly different, but they would retain enough similarity to allow crosscultural decoding.

Emotions as a Continuum Across Species

The question "Do animals have feelings?" received an affirmative answer from Darwin in the mid-1800s when he stated in his book that human beings are not the only members of the animal kingdom who experience and display a variety of emotions and feelings. Darwin is usually

given credit for being the first scientist to systematically study emotions in animals. In support of his theory of evolution, Darwin noted the similarities between some animal expressions of emotions and human expressions. For Darwin, if physiological and morphological traits were phylogenetically continuous in man and animals, the same must apply to mental and psychological states. Therefore Darwin assumed continuity between the emotional lives of animals and humans.

Yet this notion has been contentious. Some consider the notion of animal emotions as simple anthropomorphizing. Hebb (1946), for example, referring more specifically to nonprimate species remarked, "There has been a marked and necessary scientific reaction against the mentalistic extravagances of earlier writing on animal behavior. There is little justification and less explanatory value in ascribing man's elaborate conscious processes to animals, and discussing emotions in such terms would be futile" (p. 88). In its most general form, this view has been extended into this century. One problem is clearly that emotions in humans are strongly associated with language and that we cannot ask animals about their emotional states. Yet the observation of behavior is fraught with the difficulty of establishing homologues. A classic example is the open-mouth bared teeth display in chimpanzees, which looks like a human smile but is a gesture of submission (but see Preuschoft & van Hooff, 1997, for an account of the overlap of both functions in humans and primates).

Panksepp (1998, 2005) is probably the most vocal proponent of animal emotions. Because all organisms have to face basic challenges to survive, such as finding food, finding mates, and defending themselves against aggression, and because emotions are adaptive means for doing so (e.g., Frijda, 1986; Panksepp, 1998; Scherer, 1984), it makes little sense to separate human and animal emotions (Panksepp, 1998, 2005). A number of neurological circuits common to both animals and humans subserve certain "basic emotions," which Panksepp referred to as "blueribbon" emotions. Other emotions are seen as more specific to humans as they require more cognitive capacities. From this perspective, not all animals are considered to have emotions (e.g., ants would not, as they lack the relevant neural circuits), but those who have them are at an advantage because emotions allow for a flexible response to classes of similar challenges.

In fact, there is a literature full of examples of animal emotions (see, e.g., Bekoff, 2002; Masson & McCarthy, 1995; Morris, 1986). Indeed, the faces of animals, their eyes, their bodies, their posture, the sounds they produce, all carry information that one can use to draw inferences about what the animals may be feeling. Thus, when observing pets, humans tend to describe their behavior in emotional terms and are able to accurately react to the motivational states of cats and dogs (Fiedler, Light, & Costall, 1996; Turner, 1991). Also, Wemelsfelder and Lawrence (2001) reported that even people with only little experience in observing animals were able to make inferences and to agree with one another about what the animals were likely feeling. All of these findings concord with

Darwin's notion that animal behavior can be easily classified in terms of emotional behavior.

The answer to the question of whether animal emotions are like human emotions differs according to different emotion theories. Certain views of emotion, such as the social constructivist view, consider emotions to be socialized by participation in a social discourse (see, e.g., Armon-Jones, 1985; Wierzbicka, 1994). This view most certainly does not allow for animal emotions that directly parallel human emotions. By contrast, affective neuroscience approaches (Panksepp, 1998), which posit that all organisms have to deal with certain challenges to survive and that emotions are means of accomplishing these tasks, are not constrained by the lack of language in animals, at least in regard to states such as Panksepp's "blue-ribbon" emotions.

Appraisal theories of emotions also allow for considerable overlap between animal and human emotions. Thus, Leventhal and Scherer (1987) and others more recently (e.g., Scherer, 2005; Smith & Kirby, 2001) have proposed process models that postulate at least two levels of treatment of environmental events along the lines of the preattentive and automatic versus reflective and explicit distinctions. Thus, the same appraisal—for example, goal obstruction—can be executed on a conceptual level (as an obstruction of a goal or plan) or on a schematic level (as the frustration of a need) without adding "special emotion modules" for humans. This conceptualization makes it possible to postulate a single consistent emotion theory that allows for the smooth transition from animal to human emotion that Darwin assumed.

This should raise the question of where emotions originate. In fact, this question is usually neither raised nor answered. A hint may be found in research by Balasko and Cabanac (1998) showing that iguanas, which prefer salad over iguana chow, will choose to go to a separate colder room to obtain salad even though iguana chow is freely available in the warm home room. If we consider the capacity for hedonic valence to drive behavior to be indicative of emotional processes, then this would be a first indication of emotion-driven behavior.

Conclusion

Darwin wrote his book on emotion expression not with a specific interest in emotions and their communication, but rather in support of his theory of evolution. However, his work turned out to be the first scientific investigation into this matter. He attempted cross-cultural validation for his observations and was the first to use judgment studies for the assessment of the meaning of expressions. In this too he laid the groundwork for future research on emotion communication.

His book was written from a perspective in which animal and human emotions were readily perceived as homologous and is, despite his attempts at scientific verification, largely based on anecdotes and semiformal observations. This could have resulted in a publication that would by now be a simple curiosity for scholars of emotion. Yet Darwin's powers of observation and his analytic

mind were able to produce a work that has remained thought provoking and inspiring—even though not all his observations and ideas have withstood the test of time. Many of his observations have been found to be pertinent to the work of contemporary investigators, and whole fields of research can trace their origins to Darwin's book. One should note that some credit also belongs to Ekman and his colleagues, as well as to Izard, who did much to remind the scientific community of the pertinence of Darwin's work.

The field of emotion communication would be much poorer were it not for Darwin's work. However, a review of research that traces its roots back to Darwin also shows that much work remains to be done. A central goal of Darwin's was to explain why emotion expressions take the form they do. Why do we frown in anger and smile in happiness and not vice versa? His explanations were hampered by a lack of genetic and physiological knowledge at the time, but even now more than 100 years later the question remains to be fully addressed. For a long time the field has engaged in hot disputes about some of the core ideas that can be traced to Darwin, such as whether emotion expressions are universal and the status of prototypical expressions. In recent years these questions have been moved closer to a middle ground, but many of the issues that sparked the debates remain open. How is it that prototype expressions are universally quite well recognized but seemingly rarely shown? What is shown instead? How do social rules influence emotion expressions? In our overview we have suggested that appraisal theories of emotions may hold the answers to some of these questions—but the relevant theoretical formulations remain to be provided. Thus the field that Darwin helped to open will remain a challenge for some time yet to come.

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