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What is an animal emotion?

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Emotions suffuse much of the language employed by students of animal behavior—from "social bonding" to "alarm calls"— yet are carefully avoided as an explicit topic in scientific discourse. Given the increasing interest in human emotional intelligence and the explicit attention in neuroscience to the emotions, both human and nonhuman, the taboo that has reigned for so long in animal behavior research seems outdated. The present review seeks to recall the history of our field in which emotions and instincts were mentioned in the same breath and in which neither psychologists nor biologists felt that animal emotions were off limits. One of the tenets supporting a renewed interest in this topic is to avoid unanswerable questions and to view emotions as mental and bodily states that potentiate behavior appropriate to environmental challenges. Understanding the emotionally deep structure of behavior will be the next frontier in the study of animal behavior.

Keywords: evolution; animal cognition; empathy; facial expressions; instinct

Emotions used to be an uncontroversial part of any description of animal behavior, as uncontroversial as the instincts with which they were compared and equated. William James[1]—whose famous title "What is an Emotion?" inspired the one above—rightly regarded the emotions as an unlearned response system, which is precisely why the next century saw the study of emotions go out of fashion.

American behaviorism tried to explain all behavior based on operant conditioning and hence had no room for unlearned predispositions. Skinner[2] dismissed the emotions as "excellent examples of the fictional causes to which we commonly attribute behavior." Until late into the last century, American researchers could scarcely obtain funding for work on the emotions unless they rephrased their questions in terms of learning and memory.[3]

The second major behavioral school—European ethology—similarly abandoned anything considered as sentimental and imprecise as the emotions in a reaction against the subjective "animal psychology" of the time.[4] Even to this day, the *Oxford Companion to Animal Behaviour*[5] urges ethologists to avoid references to the emotions, because "It does nothing to promote our understanding of behavior to attribute it to an emotion if our only evidence of the emotion is the very behaviour the emotion is supposed to explain." Since the 1970s, ethology and its offshoots developed a strictly functionalist approach in which behavioral motivations barely counted, thus adding to the irrelevancy of the emotions. This functionalism went so far that Darwin's own pioneering comparisons between the emotional expressions of humans and other animals[6] came to be regarded as un-Darwinian.[7]

Despite the frequent assertion that animal emotions hardly matter, outright denial of their existence is rare. This leaves us with the curious situation that a widely recognized aspect of animal behavior is deliberately ignored or minimized. Emotions are often presented as too simple for attention. The *Oxford Companion to Animal Behaviour* asserts that "animals are restricted to just a few basic emotions,"[5] and the main difference between human and animal emotions has been proclaimed to be that "animals don't have mixed emotions."[8] Whether animal emotions are pure and simple, however, cannot be ascertained without a scientific program to study them. One only needs to see an aroused chimpanzee, with all its hair on end, pick up a stick to safely poke at a

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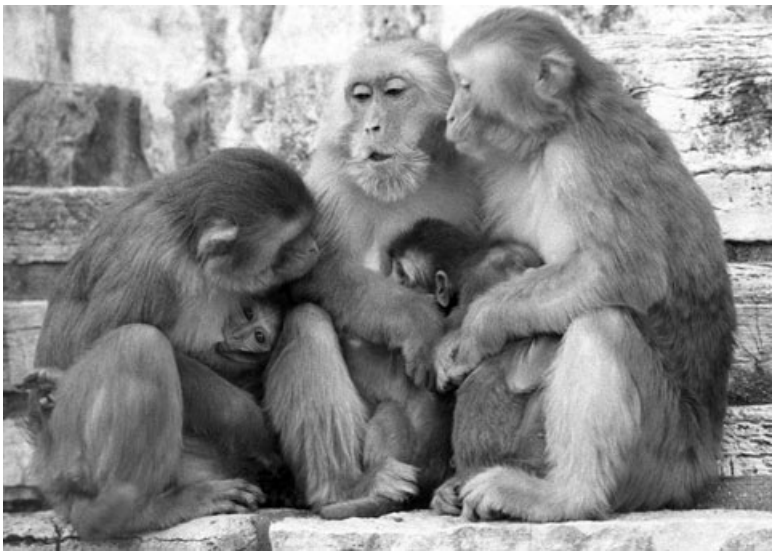

Figure 1. **A rhesus monkey family reunites after a major fight. The matriarch of the family sits in the middle, flanked by her two grown daughters who had chased each other around. All three females huddle closely together while loudly "girning" (a friendly vocalization) and lip-smacking at each other's infants. Typical of macaque reconciliations, eye contact is avoided. Photograph by Frans de Waal.**

snake that it has approached with great hesitation, to understand that mixed inclinations, such as between fear and curiosity, are entirely possible. In fact, when Menzel[9] tested chimpanzees with toy snakes, he found that once one chimpanzee knew about the location of a snake, others who had never seen it would adopt the same cautious, ambivalent posture just from watching the first chimpanzee who had, thus showing the effectiveness and potential survival value of emotional communication.

Survival value is obvious to anyone who watches primate behavior, yet we seem unable to talk about emotions without putting them between skeptical quotation marks. We describe animals not as angry but as "angry" or aggressive, and not as loving, but as "loving" or affiliated and bonded. Greetings between animals may be called loud, elaborate, or intense, but rarely emotional. Apart from descriptive labels, functional labels are preferred provided they are devoid of intentionality. Thus, animals may be called "altruistic," but only in the functional sense in that they benefit others at a cost to themselves. The term is almost never used in its motivational sense to the perplexity of scholars outside behavioral biology, where altruism invariably implies benign feelings and intent.[10] I experienced similar taboos when first describing how chimpanzees kiss and embrace their adversaries during reconciliations after a fight.[11] I was urged to speak instead of "postconflict reunions with mouth-to-mouth contact." That the term *reconciliation* is now widely accepted in primatology is the product of three decades of systematically countering "simpler" explanations, so that the only one left standing is that primates monitor the state of their social relationships and undertake reparatory actions following conflict (Fig. 1).[12]

Given how common reconciliation turns out to be among primates, as well as other social mammals, such as dolphins, hyenas, and goats,[13] animals must have the capacity to substitute hostility with a friendly attitude, which in humans is ascribed to a complex emotional process known as forgiveness. Do animals, too, know forgiveness? Even if this remains an unestablished fact, it seems prudent to keep an open mind, and replace Morgan's Canon—the traditional principle of cognitive parsimony—with a principle that better fits the evolutionary age. Instead of assuming that animal emotions are necessarily simple and straightforward, it is more likely that if humans and related species respond similarly under similar circumstances, the emotions behind their responses are similar, too. The latter view postulates fewer psychological changes in a relatively brief evolutionary time, hence is more parsimonious

than the assumption that unique mechanisms underpin human behavior.[14]

This essay explores the concept of emotion through the eyes of a student of animal behavior and cognition. It is therefore light on neuroscience, focusing instead on the potential usefulness of emotional concepts for students of animal behavior. Neuroscience is present in the background, however, as the one discipline that can (and some would argue, has) cut the Gordian knot of enduring skepticism about animal emotions.[15] Brain research may not be able to tell us what animals feel—even though it has revealed valences that must be centrally represented—but the argument from homology in the brain is immensely powerful. If humans report high anxiety while showing amygdala activation and rats exhibit flight and freezing responses when their amygdala is electrically stimulated, it is hard to avoid the conclusion that we are dealing with one and the same state, that is, fear.[16,17] The same argument has been applied to emotional attachment, joy, anger, and so on, boosting the case for evolutionary continuity.

Emotions potentiate action

The antiquity of the emotions points at high adaptive value. A rise in core body temperature and increased heart rate not directly attributable to the eliciting stimulus—for example, mild handling by an experimenter—has been measured in mammals, reptiles, and birds, but not amphibians and fish. On the basis of this so-called emotional fever, it has been argued that the first elements of vertebrate anxiety emerged after the amphibians.[18]

James[1] married the emotions to the instincts. Both humans and other animals respond to danger with the emotion of fear, which is associated with the flight instinct. On the other hand, the thwarting of a goal causes frustration, which causes anger, also known as the aggressive instinct. A strange thing happened, though, when instincts went out of favor: the emotions remained, but in a seriously diluted form. Dunlap[19] lamented: "Instincts have quietly passed away after a brief and feverish illness, and the widowed emotions have been left." For evolutionary biology, this dissociation was unfortunate as it removed the most likely reason why emotions exist, which is for their potential to induce adaptive action. What would be the point of reacting to the sight of a predator with a bodily state known as fear? Already one century ago we knew that this state is marked by deeper respiration, higher arterial pressure, a faster heart rate, a shifting of blood away from the digestive system to muscles, heart, and brain, increased vigilance, and the freeing of sugar from liver reserves.[20] These changes by themselves do not do the organism any good: their adaptive value lies in bodily preparation for struggle or escape.

The beauty of the emotional response system, over an instinctual one, is that it is not strictly predetermined. The neurological and physiological changes it produces may be rapid and reflex-like, but the elicited behavior varies with situation and experience. Some primates have different alarm calls for different dangers to which listeners respond accordingly. The alarm call for big cats leads vervet monkeys to quickly climb a tree, the call for aerial predators makes them look up and run into dense bush, and the one for snakes makes them stand upright and look around in the grass.[21] In all cases, the elicited emotion is fear, but it is an "intelligent" fear, one that seeks the most appropriate response to the circumstances.

This variability in response is important in relation to the question about the usefulness of the concept of emotion in behavioral analysis. The tautology charge against the concept, such as the one cited before from the *Oxford Companion to Animal Behaviour*, claims that a behavior indicative of a certain emotion cannot at the same time be explained by it. This charge loses much of its strength, however, if there is more than one behavioral indicator for a given emotion. It weakens even further if not only the outputs but also the inputs are variable. Fear, for example, may be triggered by a sudden noise, the sight or smell of a predator, a conditioned stimulus associated with an aversive event, an alarm call by a conspecific, or a rapidly approaching dominant individual. In humans, many subtypes of fear and anxiety deal with different kinds of threats.[22]

The greater the range of inputs and outputs, the more useful it becomes to postulate a particular physiological and behavioral state that potentiates a response. When we say that individual A "fears" B, we are speaking of a different state with a different set of causes and consequences than when we say that individual A "loves" B. No precise future actions are predicted by these statements, but the behavioral likelihoods are vastly different. Behavioral states, or emotions, thus act as intervening

variables in the same way that Hinde[23] solved tautology charges against the concept of social dominance by proposing it as an intervening variable. The emotion concept ties correlated variables together, and economically summarizes a wide range of inputs and outputs.[24]

This view of emotions, as interfacing environmental challenges and optimal behavioral responses, is reflected in a variety of approaches.[25,26] Barrett *et al.*[27] describe an emotion as an orchestrated response to a significant event across multiple systems at once: perceptual, cognitive, motivational, expressive, bodily, and experiential. Cosmides and Tooby[28] also stress the coordination aspect: "To behave functionally according to evolutionary standards, the mind's many subprograms need to be orchestrated so that their joint product at any given time is functionally coordinated, rather than cacophonous and self-defeating. This coordination is accomplished by a set of superordinate programs—the emotions." Frijda[29] argues that the whole point of having emotions is goal-oriented action: "A passion *wants* something." However, this potential for action, which was central for McDougall and his contemporaries,[30] is curiously absent from many recent definitions. Even if emotions happen inside the individual, they are triggered by the environment and predispose the organism's engagement with it. Their effect on behavioral outcomes is central to any evolutionary account, which assumes that emotions evolved to benefit the organism.[22] In yet another variation on this theme, the philosopher Nussbaum[31] attaches the Aristotelian concept of *eudaimonism* to the emotions in that they help the organism flourish.

The utilitarian perspective is a logical starting point to explain the existence of the emotions. Organisms have been selected to enter a particular bodily and mental state under particular circumstances: those who did furthered their interest better than those who did not. In the felicitous phrase of Lazarus and Lazarus,[32] emotional reactions reflect "the wisdom of ages." My definition of an emotion incorporates these causal and functional insights:

> An emotion is a temporary state brought about by biologically relevant external stimuli, whether aversive or attractive. The emotion is marked by specific changes in the organism's body and mind—brain, hormones, muscles, viscera, heart, etcetera. Which emotion is triggered is often predictable by the situation in which the organism finds itself, and can further be inferred from behavioral changes and evolved communication signals. There exists no one-on-one relation between an emotion and ensuing behavior, however. Emotions combine with individual experience and cognitive assessment of the situation to prepare the organism for an optimal response.

Cognition and emotion

Emotion research on humans has not always been as prominent and well accepted as it is today. It received a serious set-back during the cognitive revolution and its favorite comparison between mind and computer. In truly Cartesian fashion, neither the body nor the emotions were considered part of cognition, which was defined in terms of perception and memory.

Times have changed. The body is back in cognition research,[33] and emotional intelligence is a topic of considerable interest.[34] It is impossible to separate the emotions from cognition—attempts at which have been labeled a "sin" in the study of emotion.[35] The brain has no separate cognitive and emotional pathways: what we attend to and the outcomes we are interested in is very much emotionally determined. The modern view is that the pathways overlap because of the need to coordinate processes and functions that are tightly linked. How else could the organism learn which stimuli to avoid or how to interpret the emotional signals of others? Even human rationality is far from emotion free: bodily states that accompany the emotions are part of its chain of operations.[36] This integrative view goes back to David Hume,[37] who went so far as to view reason as the slave of the emotions.

However, the field of animal cognition still shows a strong adherence to a disembodied mind. For example, instead of regarding imitation—originally defined as "doing an act from seeing it done"[38]—as a learning process rooted in social closeness, bodily connections, and a desire to act like others, it was redefined top-down as a process requiring shared intentions. Tomasello and Call[39] placed "true" imitation beyond the grasp of even apes, which "do not understand the other as an intentional agent who is similar to themselves as an intentional agent." Initially, this view was supported by negative findings on ape imitation, but the majority of

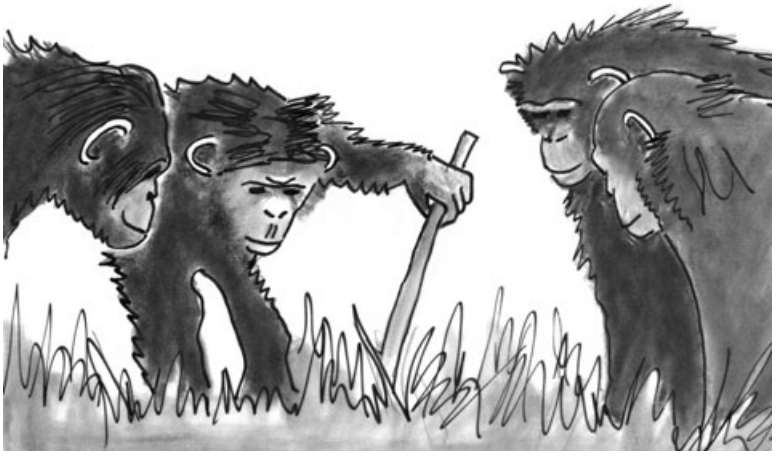

Figure 2. **The first ideas about theory of mind were developed by Emil Menzel,[9] who focused on emotional body language to see what apes know about what others know. One juvenile chimpanzee, poking with a stick at a snake in the grass, is the only one who knows what is hidden there. Well before having seen the danger themselves, the onlooking apes know to be cautious from this individual's body language. Drawing by Frans de Waal.**

studies employed human behavioral models behind a barrier of glass or mesh. In light of alternative theories of imitation, such a cross-species set-up is problematic, however. Alternative theories place less emphasis on intentionality and more on body-mapping and the neural fusion of perception and action, which process is likely enhanced by proximity and identification between observer and model.[40,41] Once the extra effort had been made to train conspecific models and remove physical barriers, the issue of ape imitation was quickly settled to the point that major skeptics have come around.[42] Chimpanzees faithfully and reliably copy tool use, foraging techniques, and arbitrary action sequences of species members.[43] It was furthermore demonstrated that apes learn more from watching another ape open a puzzle box than from hundreds of disembodied demonstrations of the same box's mechanics.[44]

Overly mentalistic approaches were also followed in the most popular research topic of the last few decades: theory of mind (ToM). Even though this topic came originally out of primate research, it is not widely realized that the very first studies about how one individual perceives the knowledge of another revolved around emotional body language (Fig. 2).[9] Unfortunately, the topic was soon redefined with a far more abstract focus, such as knowing what others know.[45] The precise mechanism of such "mindreading" remained unaddressed, however, and to this date there is preciously little evidence, both for humans and other animals, in favor of the rational process implied by the word *theory* in theory of mind.[46,47]

The acquisition of ToM probably starts with emotional connections. Children pass traditional ToM tasks around the age of 4 but appreciate the feelings, needs, and desires of others already at the age of 2 or 3.[48] They often rely on emotional communication to deduce what kind of situation the other faces, showing reactions similar to Menzel's apes, who recognized if one among them had spotted hidden food or danger.[9] It should not surprise, therefore, that after many studies in which apes were challenged to guess what human experimenters knew or did not know, the greatest research progress arrived when scientists adopted a more emotionally relevant approach by testing how one ape perceives the knowledge of another in a direct confrontation between dominant and subordinate individuals.[49]

It is unlikely that perspective taking can be understood without close attention to emotional and bodily connections.[50] In general, animal cognition research would do well to replace mentalistic approaches with a bottom-up perspective.[51] We need to know more about the nuts and bolts of animal intelligence, including emotional factors. For example, just as emotional stimuli activate neural mechanisms that enhance human memory,[52] it has been found that chimpanzees have a better recall of

pictures of conspecifics in an emotional than neutral pose.[53] We also know that chimpanzees, even though capable of following human gaze, are more interested in and motivated by their own species, and more willing to pay attention to their gaze,[54] which may explain their poor performance compared to children when both are tested by humans on social cognition tasks.[55] The lesson here is the same as for imitation and ToM research: test paradigms should take emotional and bodily connections into account, which connections are by definition different within than between species.

Emotional control

In discussions about the interaction between emotion and cognition, cognition is customarily assigned a superior position, as that which keeps emotions in check. Without cognition, so the argument goes, emotions would run rampant. Animals are often depicted as devoid of such controls, such as in one of the most prominent anthropological theories about the rise of human civilization, which assigns extraordinary weight to the taming of sexual urges.[56] It seems more likely that human civilization is afforded by a long evolutionary history of neural mechanisms that regulate the emotions, such as those also known of other primates.[57]

Sometimes, the relation between cognition and emotion is depicted as a battle between cortical and subcortical brain areas, reflecting a questionable hierarchical view of the brain.[58] Given the two-way street between cerebral cortex and subcortical circuits, emotions are far from reflexive in that they include evaluations of the situation and the weighing of future actions. They are subject to powerful appraisal mechanisms inserted between stimulus and response, as explained by Scherer: "the special role of emotion seems to be that of an intelligent interface that mediates between input and output on the basis of what is most important to the organism at a particular time."[59]

This decoupling of stimulus and response is quite adaptive in the hierarchical society of many primates. A young male chimpanzee may be visibly aroused by a sexually receptive female yet will need to find a way of mating with her out of view of dominant males, who may punish him. With cooperation of the female, he thus waits for the right occasion or engages in evasive tactics. Or, the alpha male may have received a pointed challenge from a younger male but first will do the rounds grooming his supporters before launching a counter attack later in the day. Or a female may experience the kidnapping of her infant by an inexperienced juvenile and is visibly distressed following the kidnapper around. She will need to get her offspring back without chasing the other up a tree or starting a fight, since both actions will be risky for her offspring. Often, mothers do attack the kidnapper, but only after they have retrieved their infant. And then there are the many cases of deception in which a chimpanzee will display a false emotion, such as when an older dominant female has not been able to get a hold of her younger opponent during a chase, after which she feigns conciliatory gestures to lure the other within reach in order to get even. All of these examples stem from *Chimpanzee Politics*.[60]

Emotional inhibitions, even emotional camouflage, are of paramount importance in the complex societies of primates. That these animals are capable of impulse-control is supported by experiments on delayed gratification. Both apes[61] and monkeys[62] will pass up an immediate reward in favor of a better, delayed one. It has further been shown that chimpanzees, like children, play more with toys in the presence of accumulating rewards suggesting deliberate attempts at self-distraction in the face of temptation.[63] Other studies have shown that apes can override an immediate drive in favor of future needs, an essential aspect of successful action planning.[64] It seems, therefore, that the same intertwinement between emotion and cognition known of humans applies to our close relatives, including effective control over the emotions.

A window on the emotions

Facial displays are common in both primates and other visually oriented mammals, such as canids,[65] felids,[66] and ungulates.[67] These displays likely evolved in tandem with the ability to decode them so as to infer the emotional state of others through a perception-action mechanism that produces shared representations (see "Emotional Contagion").[68] A recent study even documented facial signs of pain in rodents.[69] Research on facial expressions will open an evolutionary window on the emotions of animals the same way it has done for those of humans.[70,71] The ability to communicate finely graded emotions is particularly striking in the hominids, with both apes and humans showing a

rich repertoire of facial expressions owing to their highly differentiated facial musculature.[72,73]

Darwin[6] was the first to look at facial expressions the way, at the time, only a biologist would: namely, as structural features to be described and catalogued in the same way as plant or animal morphology. One of his objectives was to show how human facial expressions (a) constitute a shared heritage of our species, (b) have parallels with the expressions of other animals, and hence (c) provide a behavioral argument for evolutionary continuity. Humans may express joy and happiness differently than dogs, but all humans do it one way, and all dogs another way, indicating that the expression of emotions is species-typical. For ethologists, these expressions constitute fixed action patterns.

The concept of homology is applied when the traits of different species can be traced back to a common ancestor. It is not unusual for homologous traits to vary in function, such as in the case of a bird's wing and the human arm, which both derive from the forelimb of the ancestor of birds and mammals. With regards to facial displays, homologous displays may have different meanings in different species through a motivational and functional recasting. Homology is usually contrasted with analogy, or convergent evolution, when similar traits (e.g., the fish-like shape of a dolphin) are independent products of similar environmental pressures. The distinction between homology and analogy is important in relation to fixed action patterns.[74]

This evolutionary approach goes further than what Darwin proposed, but Darwin's strength was that he had picked the one feature of human behavior that seems to fit most or all of the above conceptualizations. In fact, facial expressions fit the mold of inborn behavior better than many of the behaviors now discussed as such in evolutionary psychology, such as mate selection. Not that these patterns necessarily lack a genetic component, but they are highly flexible and their occurrence varies with learning and environment. They are far removed from the stereotypical facial muscle coordinations and vocalizations, such as laughing and crying, that appear early in life and are remarkably uniform across individual humans and cultures.[75] Not only did Darwin pick a prime candidate of innate behavior, he also recognized and carefully documented the similarity of our own facial movements with those of other primates. The implication was, of course, that if our own expressions bring emotions to the surface, then those of other primates probably do so as well.

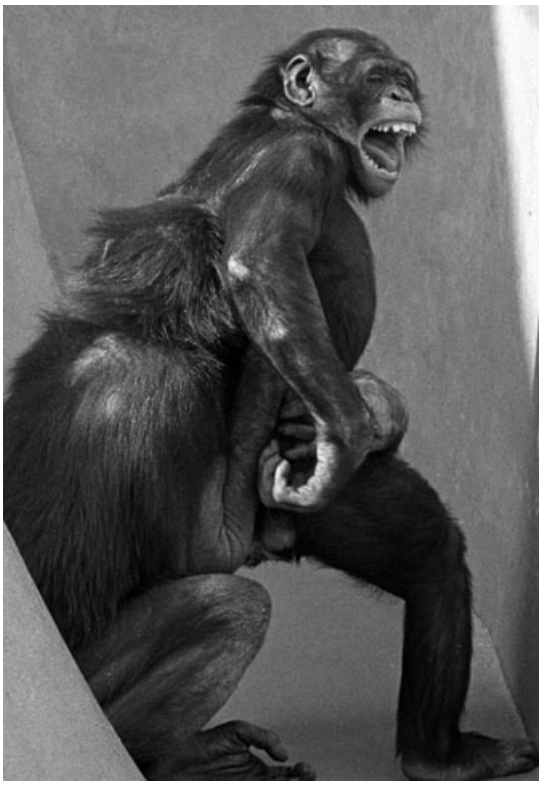

Figure 3. **The so-called play face of primates is homologous with human laughter.[103] Not only does the facial expression resemble laughter, but the accompanying hoarse vocalizations do as well, here uttered by an adolescent male bonobo being tickled in the side by an adult male. Photograph by Frans de Waal.**

With the notable exception of Ladygina-Kohts,[76] who compared the expressive movements of her own son and a juvenile male chimpanzee, we had to wait until the 1960s for an extension of Darwin's observations. Van Hooff[77,78] speculated about the causal underpinnings of facial expressions, such as the laugh and smile, tracing their phylogeny among a great variety of monkeys and apes. A recent acoustical analysis of the guttural panting by young apes being tickled confirmed the homology with human laughter to the point that a phylogenetic tree reconstructed from acoustic data matched a tree based on comparative genetics (Fig. 3).[79]

Van Hooff opted for a purely descriptive terminology followed by ways to establish the meaning of each display. A display associated with withdrawal

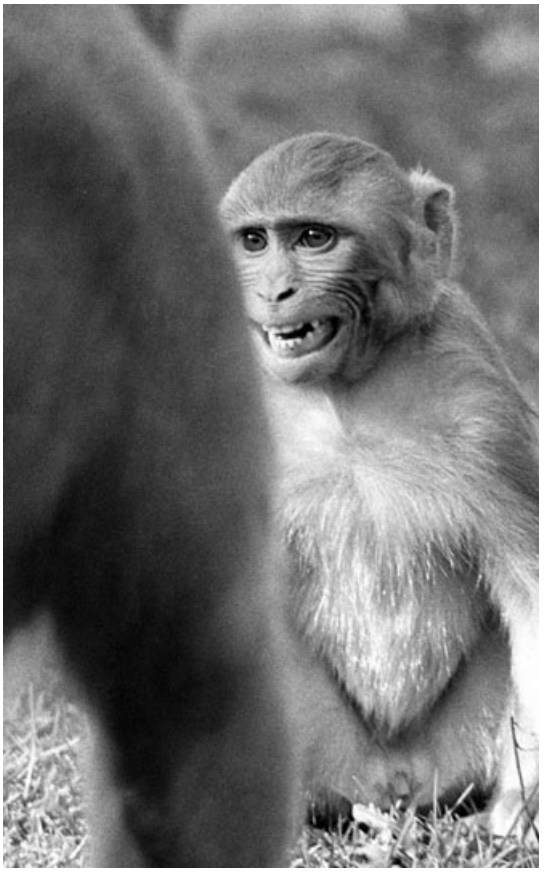

Figure 4. The teeth-baring expression of macaques is commonly known as the *fear grimace,* even though it is often given in the absence of a flight response. Here, a juvenile rhesus monkey bares his teeth to an approaching dominant but stays put. The expression serves as status signal and mixes fear with a desire for good relationships. Photograph by Frans de Waal.

would be considered fearful, for example, and one associated with attack would be considered aggressive. Those emotional interpretations would not affect the naming of the display, however. The problems the latter might cause can be illustrated with the common term *fear grimace* for the wide grin of macaques. This label obscures both the display's visual characteristics (a "grimace" being a mere facial contortion) as well as its precise meaning, which is closer to submission than fear, that is, the bared-teeth display signals fear mixed with a desire for peaceful integration (Fig. 4).[80,81]

In addition to such overt expressions, primates often communicate by means of minor changes in the face. One of the most striking illustrations of this capacity is the cooperative avoidance paradigm in which one macaque needed to deduce from the face of another on a television screen if an electrical shock was forthcoming so as to turn it off in time (Fig. 5).[82] The monkeys were surprisingly effective at avoiding shock by extracting emotional information from their partner's face despite its apparent blankness, leading Miller to comment "It was our conviction that a monkey was a much more skilled interpreter of facial expression in another monkey than was man."[83]

Emotional contagion

Miller's experiment on facial cuing illustrates the value of emotional communication: one monkey reads another's subtle body language and reacts appropriately. But more may have been going on: not merely the reading of an emotion for one's own benefit, but actually adopting the same emotion as the other. Known as *emotional contagion,* this process forms the basis of empathy. Empathy relies on emotions: the capacity makes no sense without them.

Preston and de Waal[68] propose that empathy rests on a perception-action mechanism that provides an observer (the subject) with access to the internal state and situation of another (the object) through the subject's own neural representations. When the subject attends to the object's state, the subject's neural representations of similar states that it has experienced are automatically and unconsciously activated. The more similar and socially close two individuals are, the easier this activation. This form of empathy may be widespread in mammals, such as the intensified pain response of mice that have watched other mice in pain.[84]

Emotional contagion may lead individuals frightened by the alarm of others to hide or flee. It may cause a mother distressed by her offspring's vocalizations to reassure both herself and her offspring by warming or nursing them. It may inhibit an individual from inflicting pain upon another because of vicarious negative arousal triggered by the other's distress vocalizations. These empathic emotional reactions may benefit both the actor and individuals close to them. More complex forms of empathy occur when the subject takes the object's perspective, a capacity thought present in some large-brained mammals.[85] Such perspective-taking permits targeted helping (i.e., helping geared toward to other's specific situation and needs) or the consolation of

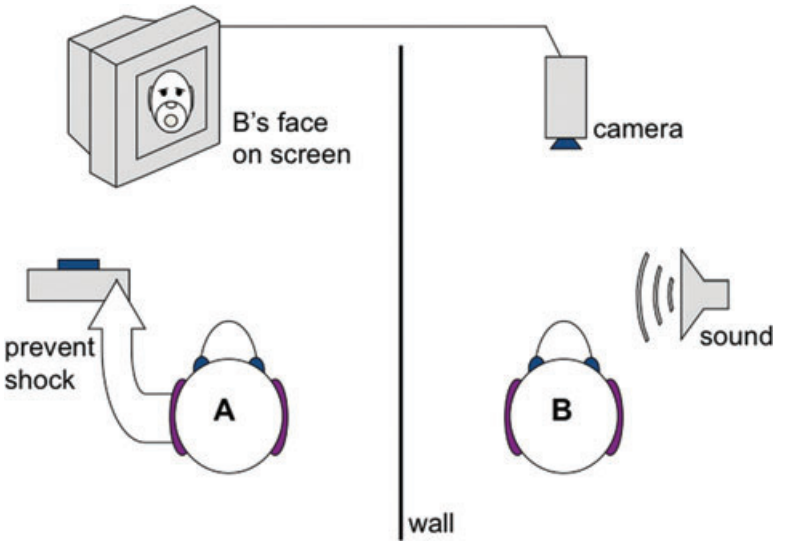

Figure 5. **The cooperative avoidance paradigm of Miller,[82] in which monkey B hears a sound announcing an electric shock while monkey A sits in another room, watching a video monitor that shows B's face live. Monkey A uses this behavioral information to press a bar that prevents shock to both A and B.**

victims of aggression by means of kissing, embracing, grooming, and so on. The latter behavior has been extensively studied in apes, in which it follows predictions from the empathy hypothesis such as that consolation reduces the other's distress,[86] is more common in females than males (cf. human sex differences),[87,88] and directed more to socially close than distant individuals.[89]

Long before the current interest in animal empathy, McDougall recognized its importance for gregarious animals as "the cement that binds all animal societies together, renders the actions of all members of a group harmonious, and allows them to reap some of the prime advantages of social life."[30] Because of their effect on others, emotions bring individuals together by converging internal states such as fear, hunger, playfulness, and sleepiness. The study of this phenomenon is crucial for our understanding of social life. This is as true for the spreading of alarm as it is for the role of the emotions in altruism and care. Empathy is considered the main proximate mechanism underlying human altruism,[90] and the same has been argued for other mammals.[68,91]

We cannot know what they feel

As recently as 2009, an essay in *Nature* chided Darwin for the "far-fetched" idea that humans and other animals might share passions and emotions.[92] Why is the study of emotions so well accepted in humans, but—except in comparative neuroscience[15,93]—still under a cloud of suspicion when it comes to animal behavior?

I would argue that it is eminently possible to study the emotions and theorize about how they work and what they do for the organism, without knowing much or anything about associated experiences. Yet feelings are an aspect to which we attach extraordinary importance, since they are our most direct source of knowledge about the emotions. This explains why the greatest obstacle to the study of animal emotions is the common objection that "we cannot know what they feel." While this is undeniably true, we should realize that it also holds for fellow human beings. Most of the time, we trust that members of our species feel similar to ourselves under similar circumstances, a trust enhanced by our similarity to them, but it remains a mere assumption. It is hard to verify this assumption unless one trusts human verbalizations of feelings, which relies on yet another assumption, that is, that humans accurately perceive their own emotions. In light of these assumptions, postulating feelings in animals is not as big a leap as it may seem.

For James,[1] subjective feelings formed the essence of emotions, but there is a reason why English and other languages have different words for *feelings* and *emotions.* The two are conflated in common usage, but only because we limit ourselves to felt

emotions whenever we discuss them. This is also true for the self-report measures typically used by psychologists, which of necessity only access emotions that we are aware of. As a result, for most people, emotions are about feelings. It is best, however, to distinguish three levels of experience regarding emotions: (1) unconscious emotions, (2) centrally represented or felt emotions, and (3) reflected-upon feelings. We are most familiar with the third category, even though it represents only the tip of the emotional iceberg.

The idea that emotions are always felt is considered yet another "sin" of emotion research.[35] In the same way that we have become familiar with implicit memory and implicit perception, we may need to get used to implicit emotions.[94] Fear, for example, may be subcortically activated before any conscious cognition.[95] Damasio[96] has suggested that deep brain structures generate primary, unconscious stages of fear, anger, affection, and so on, and Berridge and Winkielman[97] speak of subcortical "core processes" that only secondarily produce cortical correlates that allow an awareness of feelings. These authors review evidence for measurable emotional preferences that humans are unable to report on. Additionally, there are the "gustofacial" responses—facial expressions of taste enjoyment shared by our species with other primates[98,99]—of human infants born with a brainstem but no cortex and little forebrain. Even though some have taken this as evidence that emotions may be wholly unconscious, others have argued that the approach/avoidance reactions of anencephalic infants and decorticated mammals hint at central representation of emotions probably involving some level of consciousness.[15,100] If so, the first level listed above (unconscious emotions) becomes questionable, and all emotions are experienced along at least two dimensions: valence and arousal. As Mendl put it, "neutral states are not emotional states."[26]

Among the founders of animal ethology, Tinbergen was a life-long skeptic about subjective feelings and consciousness, whereas Lorenz thought that the discharge of an instinctive action (called "consummatory behavior") must be accompanied by pleasurable sensations.[4] Earlier students of animal behavior had no trouble ascribing subjective feelings to animals, often seeing these feelings as facilitating instinctive actions required for survival, the same way that eating, drinking, nursing, and sex are subserved by self-rewarding neurological substrates. Thus, Whitman assumed that pigeons found it "agreeable" to sit on their eggs, a sensation that ensured their incubation.[101]

Among modern neuroscientists, the closest to these views comes perhaps Panksepp, for whom emotions, including those of animals, are inseparable from experiences. Panksepp[102] argues against the behaviorist position that experiences will forever remain off limit, saying: "If affective states are the underlying psycho-neural substrates for many behavioral choices, perhaps even the fundamental nature of reward and/or reinforcement, a behavior-only analysis is surely discarding critical scientific dimensions from active consideration." Panksepp promotes an affectively centered view of animals since we know that (1) they seek the same rewards and drugs that we do, (2) the subcortical brain systems are strikingly homologous between humans and other mammals, and (3) artificial stimulation of deep brain structures affects approach-avoidance behavior similarly in all species, including humans.

Like Maclean,[103] Panksepp[15] considers feelings associated with emotions an evolutionary birthright embedded subcortically within the mammalian brain. He considers them an essential part of the emotions and disagrees with LeDoux, for whom feelings are cortical and represent mere "frills that have added icing to the emotional cake."[104] In the first view, the connection between emotions and consciousness is obligatory, whereas the second view sees conscious feelings as secondary and perhaps inessential. The discrepancy between these views may be caused by what exactly is meant by "consciousness," which for LeDoux seems to refer to feelings that the organism is aware of and reflects upon, whereas for Panksepp it includes experiences as simple as pleasure versus aversion.

Given that human neocortex size relative to the rest of the brain is less exceptional than previously thought,[105] there is no *a priori* reason to assume substantial differences in the emotional experiences of humans and other primates. If a baboon female returns a week after the disappearance of her offspring to the spot where it happened, to climb high up into a tree and scan the environment while uttering plaintive contact calls, repeating her agitation, and calling for weeks every time her troop passes through this specific area,[106] it is hard for the human observer not to assume a sense of loss or grieving. Similarly, I have heard female chimpanzees who had lost an

offspring wail and whimper, and sometimes burst out screaming in the middle of the day or night. We also know from fecal analysis that wild primates that have recently lost close kin show increased corticosterone, thus indicating stress.[107] Such behavioral observations and physiological measures suggest felt emotions.

Parr[108] applied a computerized matching-to-sample task to emotional processing in chimpanzees. Five-second video clips were shown depicting emotionally charged scenes, such as a detested veterinary procedure or favorite food items. The apes were then required to match the video to one of two species-typical facial expressions, that is, a play face normally seen in tickling matches and a teeth-baring expression normally seen after defeat. Instead of looking for visual similarities between the videos and the facial images, which is what the apes were trained to do, they were asked to use emotional valence as the basis for matching. Their response was measured upon first presentation of the stimuli. Measures of peripheral skin temperature confirmed that the video clips had physiological effects on the chimpanzees similar to those reported for humans,[109] and subsequent research even indicated human-like lateralized changes in brain temperature.[110] These neural and physiological responses may explain how the apes spontaneously connected "happy" and "sad" videos with the corresponding facial expressions. Instead of using cognitive matching, which may be hard to account for, their choices may have been facilitated by what they felt watching the various stimuli.

In the same way that humans scratch their heads during conflicted situations, psychopharmacological research has shown that heightened emotional arousal is associated with self-scratching in nonhuman primates, probably through sympathetic nervous activation.[111,112] Chimpanzees scratch themselves, for example, during poor performance on cognitive tasks,[113] and mother monkeys do the same while monitoring a straying infant in a risky situation, such as when it approaches a dominant individual.[114] Similarly, victims of aggressive conflict show a dramatic increase in self-scratching, but drop back to base level following a friendly reunion with their opponent, indicating the calming effect of reconciliation.[115] Self-directed behavior therefore serves as an external index of internal anxiety, all the more so since this behavior occurs in the same situation as heart rate increases.[116] Aureli and Schaffner[24] conclude that self-directed behavior tracks the way primates emotionally evaluate and regulate their social relationships.

There are many more examples, but the above suffice to show how primates respond in very human-like ways to situations that are emotion eliciting in humans (Fig. 6). Since they do so both behaviorally and physiologically, it is hard to see why their responses should not also resemble those of humans emotionally and experientially. But obviously we have to leave it at this, that is, we may assume similar feelings, but the actual experiences of animals remain inaccessible. Neuroscience may one day shed light on this aspect of animal emotions and the level of consciousness involved, but so long as such research is underdeveloped our goal should be to define animal emotions such that progress can be made with verifiable methods that separate emotions from feelings. Without in any way denying or downplaying the experiences of animals, the future of emotion research should not be held hostage to the as yet unanswerable question, "What do they feel?"

An indispensable concept

The categorization of emotions is a complex issue that this essay does not seek to resolve. The human literature often proposes distinctions between basic and secondary emotions, and likes to draw lines between various emotions even if they are notoriously hard to demarcate.[27] Arising from a messy process like natural selection, crisp and clear distinctions are unlikely as reflected in the "dimensional" view of Nesse's phylogenetic emotion tree (Fig. 7).[117] The blurred boundaries should not be held against the emotion concept in general, because whether we like it or not, emotional language is widely applied in animal behavior.

Many central concepts in animal behavior have emotional connotations. For example, primatologists typically define *social bonding* by the amount of time individuals spend together, but this concept obviously goes much deeper. Fish in the same school and bees in the same hive also spend time together, but no one would claim them to be bonded. Bond strength is a hypothetical construct the true measure of which is the emotional reaction to separation, such as signs of distress.[118] Since measuring this reaction is unpractical under most circumstances,

Figure 6. A juvenile chimpanzee tries to reclaim food that a dominant individual has taken away through multimodal signaling that combines an open-hand begging gesture with vociferous screaming. Free manual gesturing is uncommon in the animal kingdom, only seen in apes and humans. Photograph by Frans de Waal.

we use proxy measures of bonding, such as time spent together, but should not forget the term's implied emotional attachment. Similar emotional connotations are recognizable when we describe animals as rivals, challengers, and friends, or speak of alarm, courtship, reconciliation, and distress. We routinely employ emotionally loaded concepts that we try to define objectively, stressing observable behavior, yet the concepts themselves are rooted in the way we, humans, organize the social world around us, which is invariably along emotional lines.

Instead of running away from this practice, students of animal behavior are advised to come to grips with it. If we cannot keep ourselves from assuming emotions, why not explicitly address them? Even with regards to the most complex human emotions, animal parallels cannot be ruled out. Human shame, for example, typically stems from the violation of social norms and is characterized by a desire for invisibility. It is expressed in a shrinking body posture and downcast gaze, which brings it morphologically close to the submission displays of primates and other animals. Due to its self-conscious nature, human shame appears cognitively more complex than submission, but the associated emotions may not be so different.[119,120] Similarly, guilt reflects regret at an action that may have hurt another, but that at the same time also hurt the relationship between actor and recipient. Guilt may thus help regulate reciprocity relationships.[22] Similarly, we know that nonhuman primates exhibit external signs of anxiety after aggressive acts that undermine their social relationships, and do so more often the more valuable their partner.[24] Bonobo aggressors, for example, often approach their victim immediately after having attacked them to inspect and lick the injuries they themselves inflicted, which appears close to regret of previous behavior.[121] If we cannot rule out evolutionary continuity with regards to shame and guilt, there is all the more reason to expect continuity concerning emotions such as fear, anger, curiosity, and affection.

We may never be able to fully appreciate the experiential side of animal emotions—although calls to try have been heard[122]—but should start assessing how they impact daily decision making with regards to needs, intentions, and wants, which are closely intertwined with the emotions and organize behavior in a way that has proven hard to capture by purely descriptive methods. Donald Hebb, the neuropsychologist who drafted his groundbreaking *The Organization of Behavior*[123] during his time at

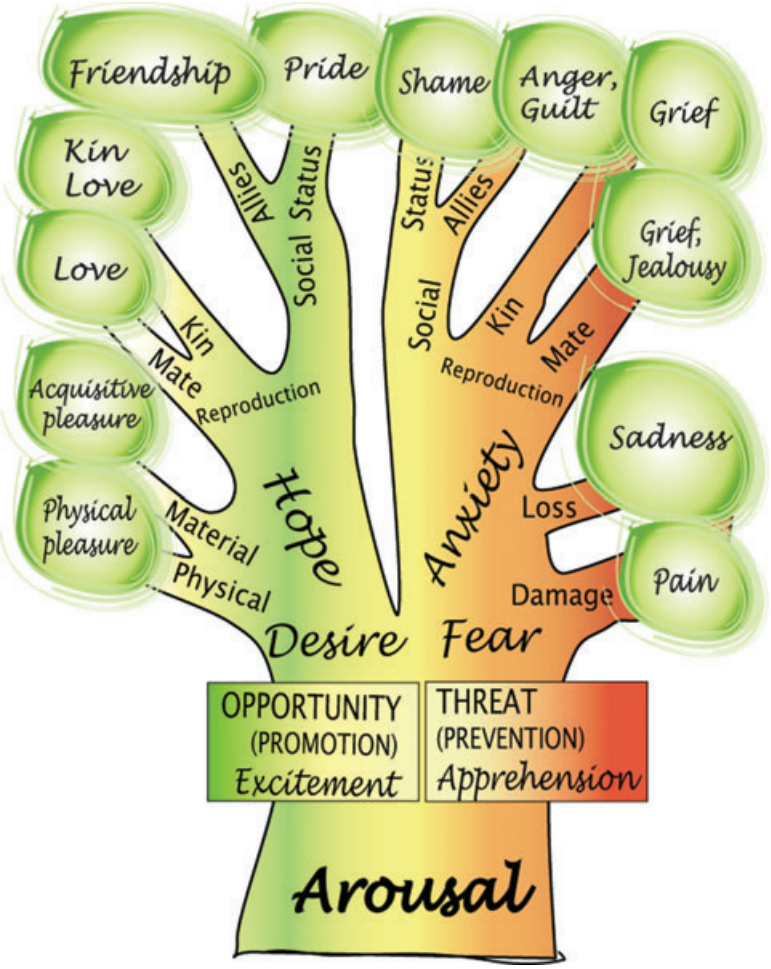

Figure 7. **A tree of emotions, which shows the resources (upright font) and situations (capitals) that emotions (italics) are about, while tracing possible phylogenetic connections between them. Drawing by and courtesy of Randolph Nesse.[117]**

the Yerkes Primate Center, perceptively concluded from a failed attempt to account for chimpanzee behavior: "The objective categorization missed something . . . that the ill-defined categories of emotion and the like did not—some order, or relationship between isolated acts that is essential to comprehension of the behavior."[124]

The challenge faced by students of animal behavior is to move from these "ill-defined categories" to replicable, objective methods to document the emotional deep structure of behavior.

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Conflicts of interest

The author declares no conflicts of interest.

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