



Feature article: *Emotion & Evolution*

Tacit Creationism in Emotion Research

[Randolph M. Nesse](#)

[The Center for Evolution and Medicine](#)
[Arizona State University](#)

Abstract

Recent quantitative studies have advanced emotions research substantially, but they have done little to resolve enduring large-scale controversies. This article suggests that tacit creationism is at the root of the problem. Envisioning emotions as aspects of a designed machine encourages searching for answers of a kind that do not exist. The quest for the Holy Grail of agreement on the number, nature, and functions of emotions is futile because the emotions are aspects of organically complex systems whose structures and functions are radically different from those of machines. A fully evolutionary foundation for emotions research discourages hopes for simple elegant models but it can nonetheless advance research by dispelling misconceptions and suggesting new questions.

Introduction

Substantial recent progress in understanding emotions has done little to resolve fundamental issues (Ekman & Davidson, 1994a; Fox, 2018; Griffiths, 1997). Despite general agreement that some emotions are universal (Ekman, 2016), debates continue about whether emotions are better viewed as discrete states or positions on dimensions. Their adaptive significance remains unclear (Lench, 2018; Oatley & Jenkins, 1992; Roseman & Steele, 2018). The significance of cross-cultural variations remains uncertain (Barrett, 2013; Lindquist et al., 2013). Even the question of what emotions are is still unsettled (Adolphs & Andler, 2018; Griffiths, 1997; Scherer, 2005). These could simply be good questions that need more work. However, the lack of consensus after decades of work by hundreds of capable scientists suggests the

possibility that some of these questions have no answers of the sort we have been seeking.

This article argues that progress in emotions research has been slowed by tacit creationism.

By tacit creationism I mean viewing organisms as if they are products of design, without attributing the design to a deity. Few scientists attribute the characteristics of organisms to a supernatural power, but many nonetheless view organisms as if they were designed machines. Organisms are, however, different from machines in several crucial ways.

Machines serve specific purposes envisioned by a designer, while bodies are shaped by natural selection to maximize gene transmission. A machine has one normal structure defined by blueprints, but there is no single normal DNA code or normal phenotype for a species. Machines are manufactured by a process that aims to make identical copies, but the development of organisms is inherently stochastic, so even genetically identical individuals will vary. Machines have distinct parts that serve specific functions, but most parts of a body serve multiple functions, and many functions, such as combating infection, are distributed among many parts. Failure of one part of a machine is likely to cause malfunction unless the design includes a backup system. Failure of a single gene or other aspect of a body may not result in general malfunction because the parts of organic systems are intermeshed in ways that makes them inherently robust. Finally, the complexity of machines can be described by defining their parts and their connections. The complexity of organisms is qualitatively different, with indistinct parts whose myriad causal connections frustrate attempts to frame simple elegant descriptions. Table 1 summarizes these differences between machines and organisms.

Viewing bodies as machines fosters major misconceptions across biology and medicine. For instance, students learn the Krebs cycle and the clotting cascade as diagrams of simple causal connections between separate boxes, ignoring the organic complexity of multiple molecules interacting with multiple others. They learn the hypothalamic-pituitary-adrenal axis in isolation from its many connections to other endocrine and neuronal systems. Neuroanatomy courses often attribute specific functions to specific

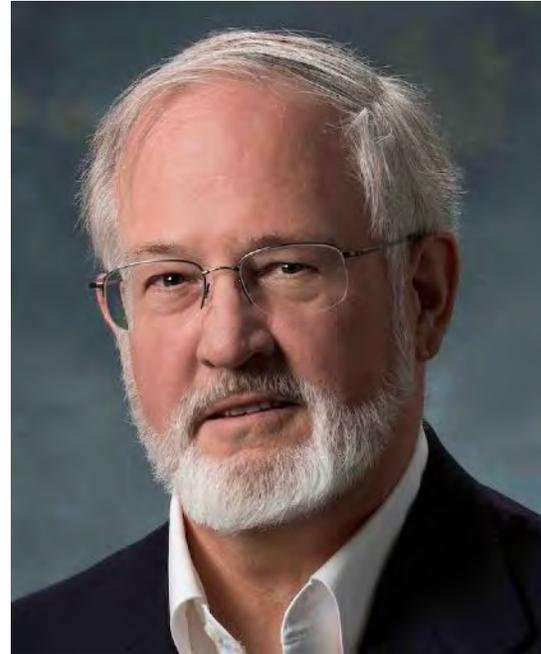
structures. For instance, the hippocampus is often described as the seat of memory, but it also has other functions and the memory network involves many other loci.

Such simplifications are necessary. Describing all of the connections of a molecule or all the functions of a component frustrates the mission of science to simplify, and the need to teach content that can be remembered and tested. Ignoring the organic complexity of evolved systems nonetheless distorts understanding and fosters misconceptions.

Tacit creationism in emotions research is especially problematic. It encourages misconceptions that have fueled decades of controversy about questions that do not have answers of the kind we have looked for. Six such misconceptions each deserve separate consideration (see Table 2).

The Structure of the Emotions

No starting point for scientific studies of emotions could be more natural than trying to describe and classify them. The resulting effort has generated vast data and hundreds of articles that represent real progress compared to the pure philosophizing of previous centuries (Davidson et al., 2009; Ekman, 2016). However, noting that consensus is lacking would be a vast understatement. Locating different emotions in a space defined by dimensions, usually starting with valence and intensity, is an enterprise that continues, with ever more elegant proposals



Professor Randolph Nesse

(Fontaine et al., 2007). This approach has been overshadowed, however, by attempts to specify a few basic emotions and their relationships to derivative emotions (Ekman, 1992). What seemed to be agreement on six primary emotions (happiness, sadness, fear, anger, surprise and disgust) has been challenged by proposals that four suffice (collapsing fear with surprise, and anger with disgust) (Jack et al., 2014), that eight are necessary in four pairs (Plutchik, 1970), or that two, or seven or 13 are needed. To make

Table 1: Seven Differences Between Machines and Organisms

MACHINES	ORGANISMS
Blueprints define the ideal type	Genes vary, so no ideal type exists
Are manufactured in a process that is designed to create identical products	Develop in a process with intrinsic stochasticity, despite canalization
Discrete components each serve specific functions envisioned by the designer	Intermeshed subunits serve multiple overlapping functions
Information processing systems have distinct input, processing and output modules	Information processing systems have indistinct intermeshed components
Serve specific functions envisioned by an engineer	Are shaped by natural selection to maximize gene transmission
Failure of a part causes system malfunction unless a backup system is part of the design	Mutations and damage may not cause malfunction because the networks structure of organically complex systems makes them inherently robust
Even extreme complexity remains describable in terms of specific connections among defined components	Components with nonspecific boundaries and myriad connections make organic systems complex in ways that are difficult to comprehend or describe.

TABLE 2: Tacit Creationism vs. an Evolutionary View of Emotions

Tacit creationist view	Evolutionary view
Emotions can be understood as discrete entities or locations in a dimensional space	Emotions are overlapping suites of responses that evolved from precursor emotions that gave selective advantages in certain situations.
Each emotion has a specific function	Each emotion serves multiple functions and specific functions are served by multiple emotions
Negative emotions are harmful and often pathological	Negative emotions are as useful as positive emotions
The components of an emotion should generally be expressed concordantly	Different aspects of an emotion may be expressed to different degrees depending on the situation
Mechanisms that mediate emotions should be the same for different individuals	Variations in genes and environment create substantial individual variation in emotion patterns and regulation
Emotions benefit individuals	Emotions maximize gene transmission, often at a cost to individual health and welfare

sense of this diversity, some articles emphasize growing agreement that several emotions are universal (Ekman, 2016). A more explicitly evolutionary view considers emotions as specialized states that evolved from related ancestral states so their boundaries and exact number cannot be readily specified (Nesse, 1990; Nesse & Ellsworth, 2009), and the basic 6 emotions capture under 20% of the total variety of emotions (Keltner, 2019). Hope that specific neural correlates will define specific emotions or dimensions turns out to be unfounded (Dubois & Adolphs, 2015; Skerry & Saxe, 2015).

Thinking about emotions as if they were products of design encourages searching for a specific number of emotions with distinct boundaries and specific functions, as if they were parts of a machine. However, because emotions are products of natural selection, we should instead expect many states with indistinct boundaries and multiple functions. The desire for a simple taxonomy of emotions is deep, but such proposals necessarily provide a false sharpening that distorts our view. The system is not only more complex than we would like it to be, it is organically complex in ways that make it difficult to describe.

Closely related is the difficulty in answering the fundamental question: what are emotions? Though it is the topic of innumerable articles and many books (Ekman & Davidson, 1994a; Fox, 2018; Griffiths, 1997; Izard, 2010), the question remains unanswered (Adolphs & Andler, 2018). Adding an evolutionary framework provides a way forward by shifting the question instead to ask how emotions came to exist (Nesse, 1990;

Tooby, & Cosmides, 1990). In this perspective, emotions are special states shaped by natural selection that give selective advantages when expressed in situations where they have given fitness advantages over evolutionary time. This view avoids controversies about whether they are natural kinds (Barrett, 2006). Emotions are biological traits, but they are not essentialized, universal, distinct entities with specific boundaries and functions. Instead, as illustrated by Figure 1, they evolved from other emotion precursors and therefore have overlapping boundaries and functions (Nesse, 2004). While there is moderate consistency across members of a species, variations between individuals are expected as a result of differences in genes, experiences and culture.

In summary, the quest for a simple taxonomy of emotions has been like the search for the Holy Grail. The object of the search does not exist, at least not in the simple form we have hoped to find. Accepting the reality that emotions are organically complex states shaped by natural selection requires revisiting the data with different ideas about what we expect to find. Recent efforts to use new available brain, facial expression, video and appraisal data to create a consensus taxonomy of 20 to 25 emotions offer a route that may transcend past difficulties if they acknowledge the organic complexity of the emotions (Keltner, 2019).

The Functions of Emotions

Attention to function traces a great arc of progress in emotions research. Neglect of the functions of emotions early in the 20th century



Figure 1. A Phylogeny of Emotions (Nesse, 2004).

was supplanted by a variety of related approaches to their adaptive significance (Ekman & Davidson, 1994b; Frijda, 1994; Izard, 1992; Izard & Ackerman, 2000; Keltner & Haidt, 1999; Oatley & Jenkins, 1992). Machine parts have specific functions, so it seems sensible to seek specific functions for specific emotions. However, because they are products of natural selection, each emotion has multiple functions, including adjusting physiology, signaling, cognition, and behavior. This integrated perspective grew with the rise of evolutionary approaches to behavior in the late 20th century that shifted the focus to how emotions give a selective advantage (Al-Shawaf et al., 2016; Campos et al., 2006); Evans, 2002; Gilbert, 2015; Keltner & Gross, 1999; Nesse, 1990, 2009; Nesse & Ellsworth, 2009; Plutchik, 1970; Tooby & Cosmides, 1990, 2008; Tracey, 2014). This framework makes it possible to differentiate emotions in terms of their functions of adjusting

multiple aspects of the individual in ways that increase the ability to cope with the threats and opportunities present in a situation.

This focus on situations has major implications for the structure of emotions. Similarities and differences between emotions arise from the similarities and differences of situations that have recurred over evolutionary time. This provides a framework for explaining why different emotions have central tendencies but blurry overlapping boundaries. In this view, different emotions are nothing like different species of animals; they are more like different styles of music with suites of associated characteristics. Blues, jazz, and rock and roll evolved from each other and continue to influence each other. They have clear prototypes, but uncertain histories and blurry boundaries that spur arguments among musicologists akin to debates among emotions researchers.

The functions of negative emotions have been neglected, and for understandable reasons (Harris, 2018; Ketelaar, 1995). Anxiety, sadness, anger and depression may seem useless or harmful, a conclusion that seems to be confirmed by evidence that proneness to negative emotions is associated with worse health and relationships. However, the disadvantages of being on the end of the spectrum with strong tendencies to experience negative emotions says nothing about the adaptive significance of the capacity for experiencing negative emotions in general. Individuals with a deficient experience of negative emotions may experience even greater disadvantages that are covert because they do not give rise to complaints and requests for treatment (Nesse, 2019a).

The illusion that negative emotions are useless is created because they are usually aroused by disadvantageous situations and because they are often expressed excessively or unnecessarily. This is a result of the 'smoke detector principle' (Nesse, 2005). In the face of uncertainty, the costs of expressing an inexpensive response may be far less than the costs of failing to respond if a threat is actually present, so false alarms and excessive responses are expected and normal.

Recognition of the utility of negative emotions is growing steadily across the range of emotions research, bringing new research opportunities (Nesse, 2019a). The value of anxiety is widely recognized, although data demonstrating its utility are limited (Stein & Nesse, 2015). Despite extensive behavioral ecological studies that demonstrate the value of adjusting patterns of effort depending on risks and the availability of rewards, the value of low mood remains contentious (Gilbert, 1992; Hagen, 2011; Nettle, 2004; Wakefield et al., 2017). Studies of anger and other social emotions bring in game theory to help explain unpredictability (Haselton & Ketelaar, 2006; Ketelaar, 2004; Skyrms, 1996). Expanding the study of utility to all negative emotions will provide an important missing foundation for dealing with the painful clinical conditions they give rise to.

The Consistency of Emotions and their Expression

Viewing organisms as machines creates an expectation that emotions should be consistent across individuals, consistent across cultures, and that all aspects of an emotion should be expressed concordantly. An evolutionary view challenges all three expectations.

Individuals differ genetically, so their emotion mechanisms will differ. The high heritability and extraordinary variation of emotion expression intensity, from alexithymia to the extremes of borderline personality, provides an illustration (Eley & Plomin, 1997). Differences in life experience also influence an individual's emotion regulation mechanisms. Evolved mechanisms may adjust responses to certain stimuli adaptively, for instance, lack of care early in life increases stress responses (Meaney, 2010). Traumatic experiences may damage normal mechanisms, but it remains uncertain if this damage results from an adaptive adjustment pushed beyond its bounds, or an entirely different mechanism (Cantor, 2009).

Moreover, emotions are different in different cultures (Kitayama & Markus, 1994). Genetic differences are possible but physical and social environment variations are certain to result in emotion variations. Some will turn out to be products of random variation, a few may represent the output of evolved mechanisms that detect aspects of the environment and shift responses accordingly and adaptively, such as the stress response becoming more sensitive when the early environment is harsh (Meaney, 2010).

Different environments also give rise to different situations with different adaptive challenges. For instance, tendencies to intense striving for status may yield increased resources in technological societies but arouse social attacks in hunter gatherer cultures (Boehm, 1999). In response to differences in situations encountered, the various overlapping aspects of an emotion response will tend to be organized differently in different cultures (Barrett, 2014). Furthermore, and separate, are differences in tendencies to describe patterns of emotions with different boundaries and different words (Wierzbicka, 1999).

Appraisal theory avoids many difficulties by focusing on situations and the several kinds of decisions that must be made well to maximize adaptation (Ellsworth & Scherer, 2003;

Roseman, 2013; Smith & Ellsworth, 1985). It helps in the analysis of cultural variation in emotions (Mesquita & Ellsworth, 2001; Scherer, 1997) and allows consideration of how the meaning of a situation may vary depending on an individual's goals. That the effect of life events depends substantially on the individual's life goals has been convincingly demonstrated (Diener & Fujita, 1995), but such research has been hard to extend, perhaps because it is very difficult to identify idiographic goals and link them to nomothetic responses. An evolutionary approach that systematically analyzes a person's resources, desires, strategies and expectations may help to provide a nomothetic framework that can incorporate idiographic data (Nesse, 2019b).

Concordant expression is expected for the components of a special mode of operation of a machine. When the automatic transmission of a car is shifted from "sport" to "eco-mode" a variety of adjustments are made synchronously and consistently every time. The expectation that aspects of emotion should also be coordinated is reflected in the description of other patterns as "desynchronized" (van Duinen et al., 2010). Such desynchronized patterns of expression are well-documented for physiological responses, but they are especially dramatic when conscious experience of an emotion is absent despite other indicators that an emotion is present (Clore & Ketelaar, 1997; Nisbett & Wilson, 1977; Winkielman & Berridge, 2004). While the very idea of an emotion presupposes moderate consistency of response, there are several reasons to expect that the physiological, behavioral and subjective aspects of an emotion will not necessarily be consistently coordinated.

Some variations in coordination of emotion expression arise from genetic variations and other stochastic factors. More interesting is the possibility that some arise from mechanisms shaped to adjust patterns of expression depending on the details of the situation. This has been suggested in specific form for symptoms of depression that turn out to be very different depending on whether the precipitant is a social loss or a failure. Social losses arouse social pain, crying and desire for support, while failed efforts arouse guilt, rumination, pessimism and fatigue (Keller & Nesse, 2005). More work is needed to

assess the hypothesis that such variations are products of an adaptation.

Cui Bono?

Machines are designed to serve functions that benefit their designers and users. Cars are designed for transportation, telescopes for viewing at a distance, and saws for cutting. Some machines, such as computers, have multiple functions, but those functions are nonetheless in the service of the user. The generally-justified expectation is that machines are designed to maximize their utility and trouble-free functioning.

The parallel expectation, that natural selection shapes organisms to maximize health, welfare and longevity, is widespread but incorrect. Most genetic variations that increase health and longevity will also increase Darwinian fitness; that is why bodies usually function remarkably well for an extended period. These benefits are, however, wonderful side-effects of selection for maximizing gene transmission (Nesse & Williams, 1994). Genetic tendencies that increase reproduction are selected for even if they compromise health.

The three-fold higher mortality rates for young men compared to young women in modern societies is a dramatic example (Kruger & Nesse, 2004). Selection for male competitive drive and ability at the expense of risk avoidance and capacities for tissue healing is typical in species where males compete for mates. In species where females choose mates, males are often burdened with extraordinarily costly traits, such as peacock tails (Cronin, 1991). Occasionally, costly useless traits show up in machines for similar reasons—Cadillac models from 1959 to 1969 sported huge fins with no purpose other than appearance and status display. The inordinate status striving that characterizes many human lives is similar.

Analysis of human emotions that benefit gene transmission at a cost to the individual offer major opportunities for research to better understand when emotions are best suppressed because they benefit our genes at a cost to us (Chisholm, 1999; Nesse, 2019a; Sterelny & Griffiths, 1999). The cognitive distortions aroused by romantic passion often result in rueful retrospective wisdom. Intense status striving often seems to benefit potential reproduction at a

great cost to individual happiness. And the joy people experience on news of their children's success, and the pain on hearing news of their troubles, benefits their shared genes.

Conclusion

Thinking about bodies and minds as designed machines is natural, but it reflects a tacit creationism that fosters major misconceptions that obstruct progress in emotions research. These misconceptions are not universal among emotions researchers, and they are fading as evolutionary perspectives are coming to be accepted as essential. However, embracing a fully evolutionary view of emotions will not be fast or easy. We especially love science when it provides simple generalizations that explain otherwise complex phenomena, for instance, the laws of gravity. Simple principles can make prediction and control possible. Discovering an underlying simple reality can also arouse pleasure and awe. Confronting the organically complex reality of biological systems can arouse very different responses. One that has been prevalent in emotions research is to persist in trying to describe the system as if it were a simple product of design. The result is frustration and controversy as different schemas compete without a clear way to adjudicate their claims. The other response is to acknowledge that organically complex systems do not have the kinds of simple structures and functions we crave. This arouses disappointment (Nesse, 2014). However, it also can relieve the frustration of looking for what does not exist, and it can open up opportunities to ask new questions with new kinds of answers.

Acknowledgements

Thanks to Richard Nisbett and Phoebe Ellsworth for very helpful comments

References

Adolphs, R., & Andler, D. (2018). Author Reply: We Don't Yet Know What Emotions Are (But Need to Develop the Methods to Find Out). *Emotion Review*, 10(3), 233–236. doi: 10.1177/1754073918772092

Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2016). Human Emotions: An Evolutionary Psychological Perspective.

Emotion Review, 8(2), 173–186. doi: 10.1177/1754073914565518

Barrett, L. F. (2006). Are emotions natural kinds? *Perspectives on Psychological Science*, 1(1), 28–58.

Barrett, L. F. (2013). Psychological construction: The Darwinian approach to the science of emotion. *Emotion Review*, 5(4), 379–389.

Barrett, L. F. (2014). The Conceptual Act Theory: A Précis. *Emotion Review*, 6(4), 292–297. doi: 10.1177/1754073914534479

Boehm, C. (1999). *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Harvard University Press.

Campos, J. J., Thein, S., & Owen, D. (2006). A Darwinian Legacy to Understanding Human Infancy: Emotional Expressions as Behavior Regulators. *Annals of the New York Academy of Sciences*, 1000(1), 110–134. doi: [10.1196/annals.1280.040](https://doi.org/10.1196/annals.1280.040)

Cantor, C. (2009). Post-Traumatic Stress Disorder: Evolutionary Perspectives. *Australian & New Zealand Journal of Psychiatry*, 43(11), 1038–1048. doi: [10.3109/00048670903270407](https://doi.org/10.3109/00048670903270407)

Chisholm, J. S. (1999). *Death, hope and sex: Steps to an evolutionary ecology of mind and morality*. Cambridge University Press.

Clore, G., & Ketelaar, T. (1997). Minding our emotions: On the role of automatic, unconscious affect. In *The automaticity of everyday life: Advances in social cognition* (Vol. 10, pp. 105–120). Lawrence Erlbaum Associates, Inc.

Cronin, H. (1991). *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today*. Cambridge University Press.

Davidson, R. J., Scherer, K. R., & Goldsmith, H. H. (Eds.). (2009). *Handbook of affective sciences*. Oxford University Press.

Diener, E., & Fujita, F. (1995). Resources, personal strivings, and subjective well-being: A nomothetic and idiographic approach. *Journal of Personality and Social Psychology*, 68(5), 926–935. doi: [10.1037/0022-3514.68.5.926](https://doi.org/10.1037/0022-3514.68.5.926)

Dubois, J., & Adolphs, R. (2015). Neuropsychology: How Many Emotions Are There? *Current Biology*, 25(15), R669–R672. doi: [10.1016/j.cub.2015.06.037](https://doi.org/10.1016/j.cub.2015.06.037)

- Ekman, P. (1992). Are there basic emotions? *Psychological Review*, 99(3), 550–553.
- Ekman, Paul. (2016). What Scientists Who Study Emotion Agree About. *Perspectives on Psychological Science*, 11(1), 31–34. doi: 10.1177/1745691615596992
- Ekman, Paul, & Davidson, R. J. (Eds.). (1994a). *The nature of emotion: Fundamental questions*. Oxford University Press.
- Ekman, Paul, & Davidson, R. J. (Eds.). (1994b). What is the function of emotions? In *The nature of emotion: Fundamental questions* (pp. 97–136). Oxford University Press.
- Eley, T. C., & Plomin, R. (1997). Genetic analyses of emotionality. *Current Opinion in Neurobiology*, 7(2), 279–284. doi: 10.1016/S0959-4388(97)80017-7
- Ellsworth, P. C., & Scherer, K. R. (2003). Appraisal processes in emotion. In *Handbook of affective sciences* (pp. 572–595). Oxford University Press.
- Evans, D. M. (2002). *Emotion: The Science of Sentiment*. Oxford University Press.
- Fontaine, J. R., Scherer, K. R., Roesch, E. B., & Ellsworth, P. C. (2007). The world of emotions is not two-dimensional. *Psychological Science*, 18(12), 1050–1057.
- Fox, A. S. (Ed.). (2018). *The nature of emotion: Fundamental questions* (Second edition). Oxford University Press.
- Frijda, N. H. (1994). Varieties of affect: Emotions and episodes, moods and sentiments. In Paul Ekman & R. J. Davidson (Eds.), *The Nature of Emotion* (pp. 59–67). Oxford University Press.
- Gilbert, P. (1992). *Depression: The Evolution of Powerlessness*. Guilford.
- Gilbert, P. (2015). An Evolutionary Approach to Emotion in Mental Health With a Focus on Affiliative Emotions. *Emotion Review*, 7(3), 230–237. doi: 10.1177/1754073915576552
- Griffiths, P. (1997). *What emotions really are: The problem of psychological categories*. University of Chicago Press.
- Hagen, E. H. (2011). Evolutionary theories of depression: A critical review. *The Canadian Journal of Psychiatry*, 56(12), 716–726.
- Harris, C. R. (2018). Understudied Negative Emotions: What They Can Tell Us About the Nature of Emotions. *Emotion Review*, 10(4), 269–271. doi: 10.1177/1754073918801177
- Haselton, M. G., & Ketelaar, T. (2006). Irrational emotions or emotional wisdom? The evolutionary psychology of affect and social behavior. *Affect in Social Thinking and Behavior*, 8, 21.
- Izard, C. E. (1992). Basic emotions, relations among emotions, and emotion-cognition relations. *Psychological Review*, 99(3), 561–565.
- Izard, C. E. (2010). The Many Meanings/Aspects of Emotion: Definitions, Functions, Activation, and Regulation. *Emotion Review*, 2(4), 363–370. doi:10.1177/1754073910374661
- Izard, C. E., & Ackerman, B. P. (2000). Motivational, organizational, and regulatory functions of discrete emotions. *Handbook of Emotions*, 2, 253–264.
- Jack, R. E., Garrod, O. G. B., & Schyns, P. G. (2014). Dynamic Facial Expressions of Emotion Transmit an Evolving Hierarchy of Signals over Time. *Current Biology*, 24(2), 187–192. doi: 10.1016/j.cub.2013.11.064
- Keller, M. C., & Nesse, R. M. (2005). Is low mood an adaptation? Evidence for subtypes with symptoms that match precipitants. *Journal of Affective Disorders*, 86(1), 27–35.
- Keltner, D. (2019). Toward a consensual taxonomy of emotions. *Cognition and Emotion*, 33(1), 14–19. doi: 10.1080/02699931.2019.1574397
- Keltner, D., & Gross, J. J. (1999). Functional accounts of emotions. *Cognition & Emotion*, 13(5), 467–480.
- Keltner, D., & Haidt, J. (1999). Social Functions of Emotions at Four Levels of Analysis. *Cognition & Emotion*, 13(5), 505–521.
- Ketelaar, T. (1995). Emotions as mental representations of gains and losses: Translating prospect theory into positive and negative affect. *Meeting of the American Psychological Society, New York, NY*.
- Ketelaar, T. (2004). Ancestral emotions, current decisions: Using evolutionary game theory to explore the role of emotions in decision making. In C. B. Crawford & C. Salmon (Eds.), *Evolutionary Psychology, Public Policy and Personal Decisions*. Lawrence Erlbaum.
- Kitayama, S., & Markus, H. R. (Eds.). (1994). *Emotion and culture: Empirical studies of*

- mutual influence*. American Psychological Association. doi: 10.1037/10152-000
- Kruger, D. J., & Nesse, R. M. (2004). Sexual selection and the male: Female mortality ratio. *Evolutionary Psychology*, 2, 66–85.
- Lench, H. C. (Ed.). (2018). *The function of emotions: When and why emotions help us*. Springer Science+Business Media.
- Lindquist, K. A., Siegel, E. H., Quigley, K. S., & Barrett, L. F. (2013). The hundred-year emotion war: Are emotions natural kinds or psychological constructions? Comment on Lench, Flores, and Bench (2011). *Psychological Bulletin*, 139(1), 255–263. doi: 10.1037/a0029038
- Meaney, M. J. (2010). Epigenetics and the biological definition of gene × environment interactions. *Child Development*, 81(1), 41–79.
- Mesquita, B., & Ellsworth, P. C. (2001). The Role of Culture in Appraisal. In K. R. Scherer, A. Schorr, & T. Johnstone (Eds.), *Appraisal Processes in Emotion: Theory, Methods, Research* (pp. 233–248). Oxford University Press.
- Nesse, R. M. (1990). Evolutionary explanations of emotions. *Human Nature*, 1(3), 261–289.
- Nesse, R. M. (2004). Natural selection and the elusiveness of happiness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1449), 1333–1347. doi: 10.1098/rstb.2004.1511
- Nesse, R. M. (2005). Natural selection and the regulation of defenses: A signal detection analysis of the smoke detector principle. *Evolution & Human Behavior*, 26(1), 88–105.
- Nesse, R. M. (2009). Evolutionary origins and functions of the emotions. In D. Sander & K. R. Scherer (Eds.), *The Oxford companion to emotion and the affective sciences* (pp. 158–164). Oxford University Press.
- Nesse, R. M. (2014). Comment: A General “Theory of Emotion” Is Neither Necessary nor Possible. *Emotion Review*, 6(4), 320–322. doi: 10.1177/1754073914534497
- Nesse, R. M. (2019a). *Good Reasons for Bad Feelings: Insights from the Frontier of Evolutionary Psychiatry*. Dutton Books.
- Nesse, R. M. (2019b). How to Understand an Individual Human Being. In *Good Reasons for Bad Feelings: Insights from the Frontier of Evolutionary Psychiatry* (pp. 141–159). Dutton Books.
- Nesse, R. M., & Ellsworth, P. C. (2009). Evolution, emotions, and emotional disorders. *American Psychologist*, 64(2), 129–139. doi: 10.1037/a0013503
- Nesse, R. M., & Williams, G. C. (1994). *Why We Get Sick: The New Science of Darwinian Medicine*. Vintage Books.
- Nettle, D. (2004). Evolutionary origins of depression: A review and reformulation. *Journal of Affective Disorders*, 81(2), 91–102. doi: 10.1016/j.jad.2003.08.009
- Nisbett, R. E., & Wilson, T. D. (1977). The halo effect: Evidence for unconscious alteration of judgments. *Journal of Personality and Social Psychology*, 35(4), 250.
- Oatley, K., & Jenkins, J. M. (1992). Human Emotions: Function and Dysfunction. *Annual Review of Psychology*, 43(1), 55–85. doi: 10.1146/annurev.ps.43.020192.000415
- Plutchik, R. (1970). Emotions, Evolution, And Adaptive Processes. In *Feelings and Emotions* (pp. 3–24). Elsevier. doi: 10.1016/B978-0-12-063550-4.50007-3
- Roseman, I. J. (2013). Appraisal in the Emotion System: Coherence in Strategies for Coping. *Emotion Review*, 5(2), 141–149. doi: 10.1177/1754073912469591
- Roseman, I. J., & Steele, A. K. (2018). Concluding Commentary: Schadenfreude, Gluckschmerz, Jealousy, and Hate—What (and When, and Why) Are the Emotions? *Emotion Review*, 10(4), 327–340. doi: 10.1177/1754073918798089
- Scherer, K. R. (1997). The Role of Culture in Emotion-Antecedent Appraisal. *Journal of Personality and Social Psychology*, 73, 902–922.
- Scherer, Klaus R. (2005). What are emotions? And how can they be measured? *Social Science Information*, 44(4), 695–729. doi: [10.1177/0539018405058216](https://doi.org/10.1177/0539018405058216)
- Skerry, A. E., & Saxe, R. (2015). Neural Representations of Emotion Are Organized around Abstract Event Features. *Current Biology*, 25(15), 1945–1954. doi: [10.1016/j.cub.2015.06.009](https://doi.org/10.1016/j.cub.2015.06.009)
- Skyrms, B. (1996). *Evolution of the social contract*. Cambridge University Press.

- Smith, C. A., & Ellsworth, P. C. (1985). Patterns of cognitive appraisal in emotion. *Journal of Personality and Social Psychology*, 48(4), 813.
- Stein, D. J., & Nesse, R. M. (2015). Normal and Abnormal Anxiety in the Age of DSM-5 and ICD-11. *Emotion Review*, 7(3), 223–229. doi: [10.1177/1754073915575407](https://doi.org/10.1177/1754073915575407)
- Sterelny, K., & Griffiths, P. E. (1999). *Sex and death: An introduction to philosophy of biology*. University of Chicago Press.
- Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, 11(4–5), 375–424.
- Tooby, J., & Cosmides, L. (2008). The evolutionary psychology of the emotions and their relationship to internal regulatory variables. In *Handbook of emotions*, 3rd ed. (pp. 114–137). Guilford Press.
- Tracey, J. (2014). An Evolutionary Approach to Understanding Distinct Emotions. *Emotion Review*, in press.
- van Duinen, M., Schruers, K., & Griez, E. (2010). Desynchrony of fear in phobic exposure. *Journal of Psychopharmacology*, 24(5), 695–699. doi: 10.1177/0269881108098821
- Wakefield, J. C., Lorenzo-Luaces, L., & Lee, J. J. (2017). Taking People as They Are: Evolutionary Psychopathology, Uncomplicated Depression, and Distinction between Normal and Disordered Sadness. In *The Evolution of Psychopathology* (pp. 37–72). Springer, Cham. doi: 10.1007/978-3-319-60576-0_2
- Wierzbicka, A. (1999). *Emotions across languages and cultures: Diversity and universals* (2405036). Cambridge University Press.
- Winkielman, P., & Berridge, K. C. (2004). Unconscious Emotion. *Current Directions in Psychological Science*, 13(3), 120–123.