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Evolutionary Psychology and the Emotions

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Introduction: Evolutionary Approaches to the Emotions

Charles Darwin launched the evolutionary study of emotion with his 1872 book, *The Expression of the Emotions in Man and Animals*. However, partly for historical reasons, the book had a narrow emphasis, focusing on the *continuity of emotional expression* between humans and nonhuman animals. The prevailing view in Darwin's Victorian England was that God had endowed humans with specific facial muscles that He had specially crafted to allow humans to communicate their emotions to one another (e.g., Keltner et al. 2014). In such a social climate, Darwin's goal was to demonstrate to the scientific community that human facial expressions bore the stamp of their animal ancestry, and that close examination

of emotion expressions demonstrated the phylogenetic continuity between humans and other species (Darwin 1872). In the century and a half since the publication of Darwin's *On the Origin of Species* (Darwin 1859), things have changed dramatically: the fact of evolution has been established beyond any reasonable doubt, and the theory of evolution is one of the most parsimonious, explanatorily successful, and predictively powerful theories in all of science (Alcock 2009; Coyne 2009; Dawkins 2009; Dennett 1996; Dobzhansky 1973). Now that there is no longer any real (scientific) need to demonstrate that humans share ancestry with all other species on earth, scientists have found themselves free to tackle a key question that Darwin largely avoided: the evolved functions of emotions.

In the last few decades, evolutionists have made considerable conceptual and empirical progress in understanding what emotions are and why they evolved. There are several evolutionary approaches in this tradition. The current entry presents a theoretically powerful and empirically promising contemporary approach that is closely associated with evolutionary psychology and was pioneered by John Tooby and Leda Cosmides (Cosmides and Tooby 2000; Tooby and Cosmides 1990, 2008). We can refer to this perspective as the *coordinating mechanism* view of the emotions.

Coordinating Mechanisms: An Evolutionary Psychological Approach

This evolutionary psychological perspective suggests that emotions are *coordinating mechanisms* whose evolved function is to coordinate a variety of programs in the mind and body in the service of solving a specific adaptive problem. For example, fear coordinates programs in the service of preventing or escaping danger (Tooby and Cosmides 1990; Marks and Nesse 1994), disgust regulates mechanisms to prevent infection (Curtis et al. 2004; Oaten et al. 2009; Tybur et al. 2009), and sexual arousal orchestrates physiological and psychological programs for an advantageous mating opportunity (Al-Shawaf et al. 2015b).

In their presentation of the coordinating mechanism approach, Tooby and Cosmides (1990; Cosmides and Tooby 2000) suggest a list of programs regulated by the emotions, including: (1) perceptual mechanisms, (2) attention, (3) memory, (4) categorization, (5) motivational priorities, (6) current goals, (7) information-gathering adaptations, (8) specialized inference mechanisms, (9) communication and expression, (10) learning processes, (11) reflexes, (12) energy level, mood, and effort allocation, (13) physiology, and (14) behavior. The idea of the coordinating mechanisms approach is not that every emotion is expected to regulate every program in every instance of that emotion's activation – rather, the central idea is that emotions can be best understood as regulatory mechanisms whose evolved function is to coordinate a variety of these programs to ensure their harmonious co-activation in the service of solving an adaptive problem.

Fear and Disgust as Illustrative Examples

Fear offers a useful illustration (Tooby and Cosmides 1990; Cosmides and Tooby 2000). When an organism is afraid of a potential threat in the environment, a cascade of changes takes place: perception becomes heightened (especially to potential danger); attentional focus is narrowed so that stimuli of less immediate relevance go

unnoticed; conceptual frameworks that cause organisms to categorize stimuli as dangerous or safe are activated while other conceptual frameworks recede into the background; motivational priorities change such that less urgent concerns such as pathogen avoidance and status enhancement fall by the wayside; and physiology shifts so as to facilitate escape, for example by shunting energy toward the muscles for flight (Tooby and Cosmides 1990; Cosmides and Tooby 2000). The central idea is that fear is a *mode of operation* for the whole body and brain; a coordinating mechanism that regulates a variety of physiological and psychological programs to facilitate the solution of the adaptive problem at hand.

Disgust, an emotion whose complexity we are just beginning to understand, provides a second example. When a pathogen threat activates disgust, many changes take place: attention is narrowed (van Hooff et al. 2013), sexual arousal becomes more difficult to achieve (Fleischman et al. 2015), heart rate and skin conductance are affected (Schienle et al. 2001; Vrana 1993), participants are less willing to engage in potentially pathogenic behaviors (Tybur et al. 2011), immune responses are activated (Schaller et al. 2010), avoidant behaviors are engaged (Mortensen et al. 2010), and people report feeling less extraverted and less open to new experiences (Mortensen et al. 2010). The key idea again is the same: pathogen disgust is a coordinating mechanism that regulates and synchronizes the activity of programs in the body and mind to solve the adaptive problem of avoiding infection.

How Does This Approach Differ from Previous Evolutionary Approaches?

This “coordinating mechanisms” view of the emotions shares features with several other evolutionary approaches to emotion. Key elements of overlap include the view that emotions are biological adaptations that evolved to serve a function, that adaptive action would be difficult or impossible without emotions, that many emotions are cross-culturally universal, that our emotions evolved from our hominin ancestors and are

phylogenetically related to the emotions of other species, and that aversive emotions are just as functional and beneficial as pleasant emotions despite their inherent subjective aversiveness.

That said, this approach also differs from other evolutionary approaches in several key respects. The following six are particularly important.

First, the coordinating mechanisms perspective suggests that there is no principled, non-arbitrary reason to draw a distinction between “basic” and “non-basic” emotions (Al-Shawaf et al. 2015b; Tooby and Cosmides 1990; Cosmides and Tooby 2000). There is no evolutionarily compelling reason to privilege some emotions over others, and no principled reason why the privileged few should be limited to disgust, anger, fear, sadness, joy, surprise, and sometimes contempt (cf. Ekman 1992; Ekman and Cordaro 2011).

Second, most evolutionary accounts of emotion have placed undue emphasis on survival to the exclusion of reproduction. But evolutionary scientists recognize that survival is important only insofar as it facilitates reproduction: differential reproductive success is the actual engine of the evolutionary process (Alcock 2009; Hamilton 1964; Williams 1966). Both logic and empirical evidence demonstrate that whenever survival and reproduction conflict, the latter trumps the former (Alcock 2009; Al-Shawaf et al. 2015b; Dawkins 1976; Williams 1966). Consistent with this fundamental evolutionary principle, the coordinating mechanism approach expands the range of adaptive problems emotions evolved to solve to include other adaptive problems tributary to reproductive success, including problems such as acquiring mates, retaining mates, competing with intrasexual rivals, parenting and childrearing, investing in kin, and more. Consequently, the coordinating mechanism perspective expands the range of evolved emotions to include romantic love, parental love, sexual jealousy, guilt, pride, shame, and many others (Al-Shawaf et al. 2015b). An emotion does not need to facilitate survival *per se*; if it evolved to solve any adaptive problem tributary to reproductive success, then it is an evolved emotion.

Third, there is no need to stipulate that an evolved emotion must have a recognizable signal or facial expression (Tooby and Cosmides 1990). Whether or not a given emotion evolved an accompanying signal depends on the ancestral costs and benefits of displaying that emotion to others (Al-Shawaf et al. 2015b). Evolved emotions can have accompanying facial expressions that are fixed and universal, or changeable and context-dependent, or they may not come with an accompanying facial expression at all.

Fourth, whereas other evolutionary approaches often insist that an emotion needs to also exist in other species for it to qualify as an evolved emotion, an evolutionary psychological approach does not. Many adaptations are unique to one species, but this does not make them any less evolved or “basic.” On this view, an evolved emotion can be shared with other species, unique to humans, or shared with other species but with uniquely human features (Al-Shawaf et al. 2015b).

Fifth, an evolutionary psychological perspective is integrative and inclusive – rather than insisting on the primacy of one particular aspect of emotions, such as physiology, behavioral output, facial expressions, or subjective feelings (phenomenology), the coordinating mechanism approach regards all of these elements as important components of emotion. Further, it links them together with other cognitive and perceptual elements (e.g., attention, memory, conceptual categorization) to paint a picture of emotion that is more comprehensive and less narrowly defined than approaches that elevate one particular element, such as physiology or phenomenology, above all else (Tooby and Cosmides 1990; Cosmides and Tooby 2000).

And sixth – obviously but importantly – this approach differs in its definition of emotions as evolved neurocognitive programs whose function is to regulate psychological and physiological mechanisms in the service of solving an adaptive problem.

What Are the Benefits of This Evolutionary Psychological Approach?

There are at least four major benefits of this approach. First, it provides a non-arbitrary way of classifying emotions. In particular, it avoids the unwarranted basic versus non-basic division and eschews the arbitrary insistence on particular emotion elements such as facial expressions, distinctive physiology, or presence in other species in order for an emotion to count as “basic” or “fundamental.” Second, in broadening the range of adaptive problems that emotions have evolved to solve, this perspective has heuristic value, pointing researchers toward emotions that have so far received scant attention from evolutionary emotions researchers, such as romantic love, parental love, regret, guilt, embarrassment, pride, shame, and gratitude. Third, and perhaps most important, this perspective provides a principled, systematic method for generating *a priori* predictions about emotions: the method of *evolutionary task analysis* (Al-Shawaf et al. 2015b; Marr 1982; see also Lewis et al. *in press*). An evolutionary task analysis for an emotion consists of several key questions: (1) what adaptive problem, if any, did this emotion evolve to solve?, (2) which subtasks must be solved in the solution of this adaptive problem?, (3) which information-processing programs are capable of solving these subtasks?, and (4) how should these programs be coordinated to deliver a well-designed solution to this adaptive problem? (Al-Shawaf et al. 2015b).

Finally, this perspective can be used to generate subtle and nuanced predictions about individual differences in emotion as well as context-specific effects on emotion (Al-Shawaf et al. 2015b). For example, a task analysis might suggest that individuals who are immunocompromised should exhibit higher levels of disgust (Fleischman and Fessler 2011; Al-Shawaf and Lewis 2013); that whether disgust leads to avoidance or approach may depend on who else is present in one’s immediate environment (e.g., approach and kill the pathogen vector if it might endanger one’s offspring; Al-Shawaf et al. 2015b); or that men’s psychological and physiological programs return to baseline after orgasm

more rapidly than do women’s, but that this discrepancy is attenuated for men who are oriented toward committed long-term mating (Al-Shawaf et al. 2015b). The key point is that an evolutionary psychological approach to the emotions offers a principled method for generating nuanced hypotheses about individual differences and context effects. This approach is theoretically powerful, empirically promising, and to our knowledge, unique among theories of emotions in its capacity to generate truly *a priori* hypotheses – let alone such diverse and nuanced ones.

Is This Approach Making Empirical Progress?

This perspective is relatively new, and only a tiny fraction of its potential has been tapped. Nevertheless, there has been some important initial progress. For example, this perspective was recently used to generate an array of novel hypotheses about the effects of disgust on specialized inference mechanisms, information gathering, and memory (Al-Shawaf et al. 2015b). Many of these hypotheses include nuanced predictions about individual differences and the effects of context. All of these hypotheses were generated *a priori* using the coordinating mechanism approach in conjunction with evolutionary task analysis.

Importantly, this predictive power extends to other psychophysiological programs that are not usually regarded as emotions. For example, despite its powerful effects on physiology, psychology, and behavior, sexual arousal does not appear in previous taxonomies of basic emotions and is typically excluded from the category of emotions altogether (e.g., Barrett et al. 2016; Ekman 1992; Keltner et al. 2014). In contrast, an evolutionary psychological approach regards sexual arousal as a critical emotion that evolved to solve one of the most important adaptive problems faced by sexually reproducing organisms – the coordination of a number of disparate mechanisms in the service of conception. Accordingly, the coordinating mechanism approach has recently been used to generate a host of novel

hypotheses about the effects of sexual arousal and orgasm on memory, conceptual frameworks, information gathering, specialized inference, and learning (Al-Shawaf et al. 2015b).

A similar logic may apply to hunger: hunger is typically regarded as a “drive” rather than an emotion, but it is an important psychophysiological state that may coordinate a variety of programs in the body and mind in the service of acquiring food. Recent work suggests that the coordinating mechanism approach can be used to generate a bounty of new hypotheses about the effects of hunger and eating on perception, attention, memory, problem-solving, and conceptual categorization (Al-Shawaf 2016).

Recent work on anger and shame is also highly promising (Sell et al. 2009a, b; Sell 2011; Sznycer et al. 2012, 2015, 2016). The recalibrational theory of anger suggests that anger is triggered when an organism detects evidence that another individual is placing insufficient value on its welfare. The primary evolved function of anger, on this view, is to “convince” the target of the anger to upregulate the value he places on the angry individual’s welfare (Sell et al. 2009). This work is guided by the coordinating mechanism perspective: the central idea motivating this research is that anger coordinates physiology, attention, communication, facial expressions, body posture, behavior, and other psychological programs in order to cause another individual to recalibrate the weight he places on the angry individual’s welfare. This research is relatively new but has already demonstrated that: (a) the anger face is not an arbitrary set of muscular contractions, but rather a specific constellation of changes that increases the perceived fighting ability of the angry individual (Sell et al. 2014), (b) the conditions that trigger anger are exactly what you would expect according to the welfare-recalibration theory (e.g., stronger anger is triggered when the cost to the victim was large, the benefit to the perpetrator was small, and the perpetrator knew exactly who he was harming; Sell 2005; Sell et al. [under review](#)), (c) the content of apologies and attempts to decrease anger are also exactly what you would expect according to this theory (e.g., the benefit to me was large, I thought the cost to you was small,

and/or I didn’t know you were the person incurring the cost from my behavior; Sell 2005; Sell et al. [under review](#)), and (d) individual differences in anger thresholds are predictable *a priori* on the basis of one’s bargaining power, such that those who are better able to confer benefits and inflict costs tend to anger more easily and more readily (e.g., attractive women and attractive and muscular men; Sell et al. 2009).

Recent work on shame also points to the utility of the coordinating mechanism approach. This approach suggests that shame is a species-wide, cross-culturally universal mechanism that evolved as a defense against being devalued by others (Sznycer et al. 2012, 2016). Guided by the coordinating mechanism perspective, this research proposes that shame coordinates changes in physiology, perception, cognition, motivation, and behavior in order to reduce the likelihood and costs of social devaluation. This involves (a) refraining from behaviors that may lead to devaluation, (b) concealing information that may lead to devaluation, and (c) minimizing the negative impact of devaluation when it does occur (Sznycer et al. 2016). To this end, and consistent with the coordinating mechanism approach, researchers have discovered that shame motivates the avoidance of behaviors and the concealment of information that lead to devaluation (Rockenbach and Milinski 2011), and that when such information is discovered, shame leads an individual to withdraw (Tangney et al. 1996), accept subordination (Gilbert 2000), become more cooperative (Masclat et al. 2003), and appease social others (Keltner et al. 1997). Additionally, shame regulates endocrinology and immunology, raising cortisol levels (Dickerson and Kemeny 2004) and upregulating pro-inflammatory cytokines to provide a defense against infection (Dickerson et al. 2009).

The coordinating mechanism perspective on the emotions has also led to important advances in our understanding of pride, but space constraints prohibit us from discussing this research in depth (see Sznycer et al. 2017; Tracy and Robins 2007; Tracy et al. 2010, for more information). Despite the relative youth of this theoretical perspective and the novelty of the research

programs discussed above, researchers are using this approach to make rapid gains in our understanding of emotions as varied as disgust (Al-Shawaf et al. 2015b), sexual arousal (Al-Shawaf et al. 2015b), hunger (Al-Shawaf 2016), anger (Sell et al. 2009a, b, 2014), shame (Sznycer et al. 2012, 2015, 2016), and pride (Sznycer et al. 2017; Tracy et al. 2010). The next few years are sure to bring novel insights and new discoveries – and to witness the extension of this coordinating mechanism perspective to other emotions that are ripe for investigation within its framework, including romantic love, parental love, guilt, regret, gratitude, and many more.

Culture, Context, and Individual Differences

Three theoretical sidenotes bear mentioning here. First, an evolutionary psychological approach to the emotions does not imply that emotions are innate, rigid, and inflexible. As with the rest of evolutionary psychology, our evolved neurocomputational emotion programs are built by the joint interplay of genes and environment, and are highly responsive to environmental input (Buss 1995; Confer et al. 2010; Tooby and Cosmides 1992). By definition, these emotions are inextricably tied to what is going on in the environment around us, and this evolutionary perspective on the emotions would obviously not make sense if one were to try to remove the environment from the equation. An evolutionary psychological approach to the emotions regards the environment as critical in driving the evolution of the mechanism in the first place, crucial in the ontogenetic development of the mechanism, and indispensable as a trigger of the mechanism in the immediate present (see Buss 1995; Confer et al. 2010; Lewis et al. *in press*). This evolutionary psychological perspective is thus environment-centered at all three stages of the causal process: evolution across generations, development within a generation, and immediate causation. Misinformed allegations that evolutionary approaches regard the emotions as rigid, inflexible, genetically determined, or environmentally insensitive are simply

incorrect. For example, see Al-Shawaf et al. 2015b for a number of evolutionary hypotheses about context effects and individual differences in emotions.

Second, it is worth noting that an evolutionary psychological approach does not predict complete invariance in emotions across cultures. Recall that the computational architecture of a psychological mechanism consists of three stages of information-processing: environmental cues are taken as inputs, which are then stored and operated upon by computational procedures, which are subsequently turned into outputs (e.g., behavior). As a general principle, evolutionary psychological approaches do not predict universality at the level of *output*, but rather at the level of *computational design* (Al-Shawaf et al. 2015b; Lewis et al. *in press*; Tooby and Cosmides 1992). Importantly, culturally variable input combined with universal neurocognitive mechanisms often yields culturally variable output (Gangestad and Buss 1993; Lewis et al. *in press*). This culturally variable output is not necessarily a sign that the mechanism in question is not a product of evolution. Rather, it is often a sign that the inputs that trigger the mechanism differ across cultures. Stated differently, if you start with different cultural or ecological inputs you will likely get different outputs. Consequently, this view of the emotions does *not* predict that every aspect of emotions will be culturally invariant. Instead, it expects variability in emotion output to be underlain by cross-cultural uniformity in neurocomputational design. This is precisely the pattern that seems to emerge from cross-cultural studies on emotion (e.g., Neumann et al. 2009; Sznycer et al. 2012, 2017). Perhaps the most interesting aspect of this discussion is that rather than being arbitrary and unpredictable, these cultural differences are often systematically predictable *a priori*. An evolutionary psychological perspective makes it possible to generate theoretically principled predictions about what cultural differences one should expect to observe *in advance* rather than observing cultural differences and then concocting post hoc explanations for them (see e.g., Sznycer et al. 2012 for an emotion example or Gangestad and Buss 1993 for a non-emotion example).

Third, an evolutionary psychological perspective does not imply the absence of individual differences in emotion. On the contrary, individual differences in emotion are a natural part of the coordinating mechanisms perspective. Providing a nice parallel to the case of cultural differences, an evolutionary psychological approach provides one with a means for making theoretically grounded *a priori* predictions about individual differences. For example, it has been suggested that individuals with less robust immune systems may have lower disgust thresholds (e.g., Fessler et al. 2004; Al-Shawaf and Lewis 2013; Al-Shawaf et al. 2015b) and that the emotions that arise after orgasm are likely different for men oriented toward short-term mating compared to those who are oriented toward long-term mating (Al-Shawaf et al. 2015b). Researchers using this perspective have also predicted and found that attractive women anger more easily than their less-attractive counterparts (Sell et al. 2009b), that attractive and physically formidable men anger more readily than their less-attractive and physically weaker counterparts (Sell et al. 2009), that individuals with less bargaining power are more prone to shame (Sznycer et al. 2012), that individuals with lower relational mobility are more shame-prone around their friends (but not around strangers, Sznycer et al. 2012), and that individuals with a stronger proclivity for short-term mating have stably lower sexual disgust (Al-Shawaf et al. 2015a). The key point here is that, as with cultural differences, individual differences are not only *consistent* with an evolutionary psychological approach to the emotions; they can be predicted *a priori* according to theoretical principles.

Future Directions

What are the next key steps for this evolutionary approach to the emotions? First, researchers should continue to generate and test novel hypotheses based on this approach. The coordinating mechanism view is heuristically valuable and predictively powerful, but given its youth, there is still a great deal of work to be done at the

hypothesis-generation stage and even more to be done at the design-and-testing stage. Researchers have reaped only a small portion of the empirical fruits of this approach so far, and this suggests an exciting and promising future. Second, researchers should continue to generate subtle and nuanced hypotheses about context effects, cultural differences, and individual differences in emotion. As we move toward a more complete explanation of species-typical mechanisms, sex-typical mechanisms, cultural differences, and individual differences, we move toward a more comprehensive understanding of the mind – both in the science of emotion and in psychology more broadly. Finally, it would be valuable for evolutionary psychologists to devote greater attention to positive emotions. As it currently stands, we understand the structure and evolved function of the “negative emotions” a great deal better than we do the “positive emotions.” This is slowly starting to change with emotions such as gratitude (Forster et al. 2016; McCullough et al. 2008) and pride (e.g., Tracy and Robins 2007; Tracy et al. 2010), but our understanding of these emotions – along with others such as joy, contentment, and love – still does not compare to our understanding of emotions such as anger, fear, and disgust. Great benefit is likely to come from thinking about the evolved function of positive emotions in a rigorous, systematic, and theoretically principled way. We look forward to this development and suggest that the coordinating mechanism perspective presented here offers an especially fruitful path forward.

Conclusion

Summary

An evolutionary psychological perspective suggests that the emotions are coordinating mechanisms whose evolved function is to orchestrate psychological and physiological programs to facilitate the solution of a particular adaptive problem. The current entry presented this approach, described how it differs from other evolutionary approaches to the emotions, and discussed the benefits of this approach. Key

benefits include a more theoretically principled method of classifying emotions, a broader consideration of the adaptive problems that emotions evolved to solve and a broader consideration of the range of emotions that evolved to solve them, and – crucially – the use of evolutionary task analysis to generate *a priori* hypotheses about each emotion, including hypotheses about context effects, individual differences, and cultural variability. We then detailed the empirical progress this approach has made in understanding certain emotions, including anger, pride, shame, disgust, and sexual arousal. Finally, this entry offers some useful future directions, including further testing, theoretical and empirical progress in understanding cultural and individual differences, and greater attention to positive emotions. We hope that this entry helps introduce the coordinating mechanism perspective to non-evolutionists as well as to those familiar with other evolutionary approaches to the emotions, and motivates researchers to use this theoretically grounded approach to generate and test novel *a priori* hypotheses about a wide range of emotions.

Cross-References

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- ▶ [Basic Emotions](#)
- ▶ [Culture](#)
- ▶ [Darwin, Charles](#)
- ▶ [Desire](#)
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References

- Alcock, J. (2009). *Animal behavior: An evolutionary approach*. Sunderland: Sinauer Associates.
- Al-Shawaf, L. (2016). The evolutionary psychology of hunger. *Appetite*, *105*, 591–595.
- Al-Shawaf, L., & Lewis, D. M. G. (2013). Exposed intestines and contaminated cooks: Sex, stress, & satiation predict disgust sensitivity. *Personality and Individual Differences*, *54*, 698–702.
- Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2015a). Human emotions: An evolutionary psychological perspective. *Emotion Review*, 1–14.
- Al-Shawaf, L., Lewis, D. M. G., & Buss, D. M. (2015b). Disgust and mating strategy. *Evolution and Human Behavior*, *36*, 199–205.
- Barrett, L. F., Lewis, M., & Haviland-Jones, J. M. (Eds.). (2016). *Handbook of emotions*. New York: Guilford Publications.
- Buss, D. M. (1995). Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry*, *6*(1), 1–30.
- Confer, J. C., Easton, J. A., Fleischman, D. S., Goetz, C. D., Lewis, D. M., Perilloux, C., & Buss, D. M. (2010). Evolutionary psychology: Controversies, questions, prospects, and limitations. *American Psychologist*, *65*(2), 110.
- Cosmides, L., & Tooby, J. (2000). Evolutionary psychology and the emotions. In M. Lewis & J. M. Haviland-Jones (Eds.), *Handbook of emotions* (2nd ed., pp. 91–115). New York: Guilford.
- Coyne, J. A. (2009). *Why evolution is true*. New York: Penguin.
- Curtis, V., Aunger, R., & Rabie, T. (2004). Evidence that disgust evolved to protect from risk of disease. *Proceedings of the Royal Society B*, *271*, 131–133.
- Darwin, C. (1859). *On the origin of species by means of natural selection*. London: John Murray.
- Darwin, C. (1872). *The expression of the emotions in animals and man*. Chicago: Chicago University Press. (Reprinted 1965).
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Dawkins, R. (2009). *The greatest show on earth: The evidence for evolution*. New York: Simon and Schuster.
- Dennett, D. C. (1996). *Darwin's dangerous idea: Evolution and the meanings of life*. New York: Simon and Schuster.
- Dickerson, S. S., & Kemeny, M. E. (2004). Acute stressors and cortisol responses: A theoretical integration and synthesis of laboratory research. *Psychological Bulletin*, *130*, 355–391.
- Dickerson, S. S., Gable, S. L., Irwin, M. R., Aziz, N., & Kemeny, M. E. (2009). Social evaluative threat and proinflammatory cytokine regulation. *Psychological Science*, *20*, 1237–1244.
- Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher*, *75*(2), 87–91.

- Ekman, P. (1992). An argument for basic emotions. *Cognition and Emotion*, 6(3–4), 169–200.
- Ekman, P., & Cordaro, D. (2011). What is meant by calling emotions basic. *Emotion Review*, 3, 364–370.
- Fessler, D. M., Pillsworth, E. G., & Flanson, T. J. (2004). Angry men and disgusted women: An evolutionary approach to the influence of emotions on risk taking. *Organizational Behavior and Human Decision Processes*, 95(1), 107–123.
- Fleischman, D. S., & Fessler, D. M. (2011). Progesterone's effects on the psychology of disease avoidance: Support for the compensatory behavioral prophylaxis hypothesis. *Hormones and Behavior*, 59(2), 271–275.
- Fleischman, D. S., Hamilton, L. D., Fessler, D. M., & Meston, C. M. (2015). Disgust versus lust: Exploring the interactions of disgust and fear with sexual arousal in women. *PLoS One*, 10(6), e0118151.
- Forster, D. E., Pedersen, E. J., Smith, A., McCullough, M. E., & Lieberman, D. (2016). Benefit valuation predicts gratitude. *Evolution and Human Behavior*. doi:10.1016/j.evolhumbehav.2016.06.003.
- Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology*, 14(2), 89–96.
- Gilbert, P. (2000). The relationship of shame, social anxiety and depression: The role of the evaluation of social rank. *Clinical Psychology & Psychotherapy*, 7, 174–189.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17–52.
- van Hooff, J. C., Devue, C., Vieweg, P. E., & Theeuwes, J. (2013). Disgust-and not fear-evoking images hold our attention. *Acta Psychologica*, 143(1), 1–6.
- Keltner, D., Young, R. C., & Buswell, B. N. (1997). Appeasement in human emotion, social practice, and personality. *Aggressive Behavior*, 23, 359–374.
- Keltner, D., Oatley, K., & Jenkins, J. M. (2014). *Understanding emotions* (3rd ed.). Hoboken: Blackwell.
- Lewis, D. M. G., Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (in press). Evolutionary psychology: A how-to guide. *American Psychologist*.
- Marks, I. M., & Nesse, R. M. (1994). Fear and fitness: An evolutionary analysis of anxiety disorders. *Ethology and Sociobiology*, 15(5), 247–261.
- Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: Freeman.
- Masclet, D., Noussair, C., Tucker, S., & Villeval, M. C. (2003). Monetary and nonmonetary punishment in the voluntary contributions mechanism. *American Economic Review*, 93, 366–380.
- McCullough, M. E., Kimeldorf, M. B., & Cohen, A. D. (2008). An adaptation for altruism: The social causes, social effects, and social evolution of gratitude. *Current Directions in Psychological Science*, 17(4), 281–285.
- Mortensen, C. R., Becker, D. V., Ackerman, J. M., Neuberg, S. L., & Kenrick, D. T. (2010). Infection breeds reticence: The effects of disease salience on self-perceptions of personality and behavioral avoidance tendencies. *Psychological Science*, 21(3), 440–447.
- Neumann, R., Steinhäuser, N., & Roeder, U. R. (2009). How self-construal shapes emotion: Cultural differences in the feeling of pride. *Social Cognition*, 27(2), 327.
- Oaten, M., Stevenson, R. J., & Case, T. I. (2009). Disgust as a disease-avoidance mechanism. *Psychological Bulletin*, 135(2), 303.
- Rockenbach, B., & Milinski, M. (2011). To qualify as a social partner, humans hide severe punishment, although their observed cooperativeness is decisive. *Proceedings of the National Academy of Sciences*, 108, 18307–18312.
- Schaller, M., Miller, G. E., Gervais, W. M., Yager, S., & Chen, E. (2010). Mere visual perception of other people's disease symptoms facilitates a more aggressive immune response. *Psychological Science*, 21, 649–652.
- Schielen, A., Stark, R., & Vaitl, D. (2001). Evaluative conditioning: A possible explanation for the acquisition of disgust responses? *Learning and Motivation*, 32(1), 65–83.
- Sell, A. (2005). Regulating welfare tradeoff ratios: Three tests of an evolutionary–computational model of human anger. *Dissertation Abstracts International. Section B: The Sciences and Engineering*, 66(8-B), 1–244.
- Sell, A. (2011). The recalibrational theory and violent anger. *Aggression and Violent Behavior*, 16(5), 381–389.
- Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., & Gurven, M. (2009a). Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1656), 575–584.
- Sell, A., Tooby, J., & Cosmides, L. (2009b). Formidability and the logic of human anger. *Proceedings of the National Academy of Sciences*, 106(35), 15073–15078.
- Sell, A., Cosmides, L., & Tooby, J. (2014). The human anger face evolved to enhance cues of strength. *Evolution and Human Behavior*, 35(5), 425–429.
- Sell, A., Cosmides, L., Tooby, J., Lim, J., Krauss, A., Feldman, A., Rascanu, R., Al-Shawaf, L., Sznycer, D., & Sugiyama, L. (under review). The grammar of anger: Mapping the computational architecture of a recalibrational emotion.
- Sznycer, D., Takemura, K., Delton, A. W., Sato, K., Robertson, T., Cosmides, L., & Tooby, J. (2012). Cross-cultural differences and similarities in proneness to shame: An adaptationist and ecological approach. *Evolutionary Psychology*, 10(2), 352–370.
- Sznycer, D., Schniter, E., Tooby, J., & Cosmides, L. (2015). Regulatory adaptations for delivering information: The case of confession. *Evolution and Human Behavior*, 36(1), 44–51.
- Sznycer, D., Tooby, J., Cosmides, L., Porat, R., Shalvi, S., & Halperin, E. (2016). Shame closely tracks the threat

- of devaluation by others, even across cultures. *Proceedings of the National Academy of Sciences*, 2625–2630.
- Sznycer, D., Al-Shawaf, L., Bereby-Meyer, Y., Curry, O. S., De Smet, D., Ermer, E., Kim, S., Kim, S., Li, N. P., Lopez Seal, M. F., McClung, J., O, J., Ohtsubo, Y., Quillien, T., Schaub, M., Sell, A., van Leeuwen, F., Cosmides, L., & Tooby, J. (2017). Cross-cultural regularities in the cognitive architecture of pride. *Proceedings of the National Academy of Sciences*, 114(8), 1874–1879.
- Tangney, J. P., Miller, R. S., Flicker, L., & Barlow, D. H. (1996). Are shame, guilt, and embarrassment distinct emotions? *Journal of Personality and Social Psychology*, 70, 1256–1269.
- Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, 11, 375–424.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). Oxford: Oxford University Press.
- Tooby, J., & Cosmides, L. (2008). The evolutionary psychology of the emotions and their relationship to internal regulatory variables. In M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (Eds.), *Handbook of emotions* (3rd ed., pp. 114–137). New York: Guilford.
- Tracy, J. L., & Robins, R. W. (2007). Emerging insights into the nature and function of pride. *Current Directions in Psychological Science*, 16(3), 147–150.
- Tracy, J. L., Shariff, A. F., & Cheng, J. T. (2010). A naturalist's view of pride. *Emotion Review*, 2, 163–177.
- Tybur, J. M., Lieberman, D., & Griskevicius, V. (2009). Microbes, mating, and morality: Individual differences in three functional domains of disgust. *Journal of Personality and Social Psychology*, 97(1), 103–122.
- Tybur, J. M., Bryan, A. D., Magnan, R. E., & Hooper, A. E. C. (2011). Smells like safe sex olfactory pathogen primes increase intentions to use condoms. *Psychological Science*, 22(4), 478–480.
- Vrana, S. R. (1993). The psychophysiology of disgust: Differentiating negative emotional contexts with facial EMG. *Psychophysiology*, 30(3), 279–286.
- Williams, G. C. (1966). *Adaptation and natural selection*. Princeton: Princeton University Press.