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# Human Emotions: An Evolutionary Psychological Perspective

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## Abstract

Evolutionary approaches to the emotions have traditionally focused on a subset of emotions that are shared with other species, characterized by distinct signals, and designed to solve a few key adaptive problems. By contrast, an evolutionary psychological approach (a) broadens the range of adaptive problems emotions have evolved to solve, (b) includes emotions that lack distinctive signals and are unique to humans, and (c) synthesizes an evolutionary approach with an information-processing perspective. On this view, emotions are *superordinate mechanisms* that evolved to coordinate the activity of other programs in the solution of adaptive problems. We illustrate the heuristic value of this approach by furnishing novel hypotheses for disgust and sexual arousal and highlighting unexplored areas of research.

**Keywords**
basic emotion, coordinating mechanisms, disgust, emotion, evolutionary psychology, sexual arousal, superordinate mechanisms

Beginning with Darwin (1872/2009), evolutionary approaches to the emotions have focused on a delimited subset of psychological phenomena. They have largely centered on emotions that solve a subset of adaptive problems, carry distinctive universal signals, are universally recognized by conspecifics, and are present in other primates (e.g., Ekman, 1973, 1992; Ekman & Cordaro, 2011). This approach is empirically fruitful and has been of great scientific import - Ekman and colleagues' theoretical and empirical work has been responsible for immense progress in emotions research over the last several decades. Nonetheless, for three reasons, the principles of modern evolutionary psychology suggest that it is too narrow in scope for a comprehensive theory of the emotions.

First, it places unnecessary emphasis on the subset of emotions that evolved to serve a signaling or communicative function. In fact, many evolved emotions have no distinct facial expression (e.g., sexual jealousy; Buss, 2013), or do not appear to serve a signaling function at all (e.g., sexual regret; Galperin et al., 2013). We discuss why we expect many evolved emotions *not* to have discernible outward signals.

Second, we suggest that emotions have evolved to solve a much wider range of adaptive problems than typically considered, even by evolutionary theorists. Differential reproductive success, not differential survival success, is the "engine" of evolution by selection. Consequently, emotions may have evolved to solve adaptive problems in a broad range of domains tributary to reproductive success. This diverse range includes sexual consummation, intrasexual mate competition, mate retention, mate poaching, hierarchy negotiation, losses of status, gains of status, punishment of coalitional free-riders, retribution for social cost infliction, strategic interference, kin protection, kin investment, food acquisition, and others.

Third, historically valuable evolutionary approaches have yet to incorporate the most important modern novel insight into the evolutionary functions of emotions: that they are hypothesized to have evolved as *superordinate mechanisms* responsible for coordinating suites of other information-processing programs, including those of attention, perception, memory, categorization, learning, and energy allocation, as well as the more typically considered elements of physiology and manifest behavior (Cosmides & Tooby, 2000; Tooby & Cosmides, 2008).

This theoretical approach to the emotions has several important consequences. First, it integrates the study of emotion with domains of psychology such as perception, attention, and learn-

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ing, highlighting the principle that emotions pervade nearly every aspect of psychological functioning. Second, it suggests a dramatic expansion of the number of adaptive problems emotions evolved to solve, and consequently calls for a theory of emotions considerably more complex and nuanced than prior evolutionary theories. Third, it provides a powerful hypothesis-generation heuristic based on *task analyses* (Marr, 1982) of the psychological procedures that must occur in order for an organism to successfully solve an adaptive problem. And fourth, it opens new lines of empirical research, ranging from sexual arousal toward mates exhibiting cues of reproductive value to the vengeance that motivates ostracism of a coalitional violator. An evolutionary psychological approach places emotions at the center of psychological functioning.

## Part I. A Modern Evolutionary Psychological Perspective on the Emotions

Cosmides and Tooby (2000; Tooby & Cosmides, 2008) present an evolutionary psychological view of the emotions that we develop and expand upon here. We concur with many aspects of pioneering evolutionary perspectives on the emotions (Ekman, 1992, 1999; Izard, 1993; Lang, 1995, 2010; Lazarus, 1991; Nesse, 1990; Oatley & Johnson-Laird, 1987; Plutchik, 1980, 1991; Tomkins, 1984), but our approach differs in several important respects.

### Adaptations Are Solutions to Adaptive Problems

Organisms face challenges in all domains of life. An *adaptive problem* is any challenge—such as avoiding predators, securing nutritious food, gaining access to mates, resisting infection, or rearing offspring—that impacts an organism's chances of survival or reproduction (Buss, 2012; Cosmides & Tooby, 1995). Natural selection produces solutions to these challenges called *adaptations*. An adaptation is a structure or mechanism that evolved because it helped its bearers solve a problem that recurrently impacted fitness (roughly, relative reproductive success) during the evolution of a species. These adaptations can be found in psychology, physiology, and morphology, and each is tailored to the solution of a specific adaptive problem (Confer et al., 2010; Tooby & Cosmides, 1992; Williams, 1966).

Adaptive problems can be structurally complex, often consisting of several subtasks requiring different computational solutions (Kurzban, 2012; Marr, 1982; Tooby & Cosmides, 2005). Even the seemingly simple problem of predator avoidance requires the coordination of many distinct processes. Organisms typically must (a) focus attention on the predator, (b) down-regulate attention to distracting stimuli, (c) suppress motivations relevant to other adaptive problems (e.g., approaching mates), (d) determine whether one has been spotted, (e) identify whether there are other predators in the environment, (f) accurately recall the spatial layout of the environment if it is already familiar, (g) select a propitious escape route, (h) move in the determined route, and (i) shunt energy away from nonessential physiological processes (e.g., immune function) and toward those necessary for escape (e.g., catabolism in the muscles; Bracha, 2004; Lima & Dill, 1990; Marks, 1987; Marks & Nesse, 1994). Organisms able to complete the many subtasks of an adaptive problem would have outcompeted conspecifics unable to do so. Organisms capable of producing more efficient solutions would have outcompeted those less adept at solving such problems.

### The Coordination Problem

Successfully solving an adaptive problem's subtasks requires the coordinated operation of many distinct adaptations. For example, programs responsible for fixing attention on a predator may need to be coordinated with programs responsible for suppressing digestion and immune function, down-regulating mating motivations, and motivating escape behavior. The coordination of these distinct mechanisms presents a new adaptive problem, one unlike any other. This is the *coordination problem*.

Haphazard and unsystematic program coordination would be maladaptive and extraordinarily unlikely to lead to the solution of an adaptive problem. Uncoordinated program activation can lead to fatal errors such as continuing to forage for food instead of escaping a deadly predator. We propose that adaptations require coordination for at least two reasons: first, adaptations sometimes have conflicting outputs, and second, the efficiency of one adaptation's operation often depends on the operation of others. We consider these in turn.

***The problem of conflicting outputs.*** One reason that adaptations require coordination is that they often have opposing outputs. Consider approach and avoidance motivations. Some mechanisms motivate avoidance of infectious stimuli. For example, disgust promotes avoidance of pathogen-laden substances such as open sores (Tybur, Lieberman, Kurzban, & DeScioli, 2012). Other adaptations motivate approach, such as those promoting pursuit of desirable mates (Sugiyama, 2005). The activation of two conflicting adaptations may lead to maladaptive behavior: indecision, or perhaps intermittent approach and avoidance. For example, a first glance at an attractive potential mate might motivate approach, but up close, infected sores might become unmistakably apparent. Conflicting motivations must therefore be coordinated to result in a successful solution to the adaptive problem at hand. The problem of conflicting outputs can be solved by mechanisms that control the activation and deactivation of programs so as to minimize interference with effective problem solving.

***The concatenation problem.*** The second reason that adaptations need coordination is *the concatenation problem*: many adaptive problems require that subtasks be completed in a specific order. In responding to an apparent act of altruism, for example, the emotion of gratitude should up-regulate the value placed on a benefactor's welfare only *after* determining that the helpful act was intentional. Mechanism coordination is also important when the effectiveness of one mechanism depends on the operation of another. For example, mechanisms that promote fleeing from a predator can produce their output more effectively when other adaptations are concurrently mobilizing energy toward the muscles. Uncoordinated responses to an adaptive problem are inefficient at best, disastrously costly at worst, and frequently unable to solve the adaptive problem at hand.

### *Emotions as Evolved Solutions to Problems of Multimechanism Coordination*

This approach views the emotions as superordinate mechanisms—programs designed to regulate the activity of other programs in the solution of an adaptive problem. Such mechanisms would be designed to process, as input, environmental or somatic cues that the organism is facing a particular adaptive problem. Once activated, the emotion's task is to orchestrate a number of different programs in the service of solving the adaptive problem. To produce an effective solution, an emotion must (a) activate the right programs, (b) deactivate conflicting programs, (c) adjust program thresholds to meet task demands, and (d) manage the sequence and duration of program activation as well as the point of program termination.

The details of these tasks will differ as a function of context. For example, a food acquisition problem may call for different solutions depending on the food's distance from camp and whether one is foraging alone or with others. Emotions must take this contextual variability into account and tailor their activation patterns to meet the demands of the problem at hand. Consequently, a given emotion is not expected to invariably activate the same programs across all contexts (see Tracy, 2014, for a similar argument about variability in emotion output).

This task is computationally complex and critical to fitness. Arguably the best solution to the coordination problem—the most efficient and least likely to lead to errors in functioning—comes from coordinating mechanisms specifically designed for this purpose. Coordinating mechanisms can be thought of as analogous to regulatory genes, whose function is to regulate the expression and operation of other genes (Davidson & Erwin, 2006). Indeed, a variety of fields ranging from genetics to business to politics exhibit evidence of coordinating bodies expressly designed to manage the activity of other entities (e.g., Chenhall, 2003). We suggest that this points to the utility of the superordinate mechanism region of "design space" (Dennett, 1996).

### *How Might Emotions Solve the Coordination Problem?*

In principle, an emotion can coordinate any of the mechanisms in an organism's body. These include cognitive, perceptual, and physiological programs, as well as manifest behavior. Emotions can be thought of as organismic "modes of operation" (Cosmides & Tooby, 2000; LeDoux, 2003; Oatley & Johnson-Laird, 1987). On this view, each emotion represents a distinct mode of operation, characterized by a different profile of cognitive, physiological, and behavioral activity.

Cosmides and Tooby (2000) have suggested that the emotions regulate at least 14 types of programs, worth listing again here: (a) perceptual mechanisms, (b) attention, (c) memory, (d) goals, (e) motivational priorities, (f) information-gathering adaptations, (g) categorization or imposed conceptual frameworks, (h) specialized cognitive inference, (i) communication and expression, (j) learning, (k) reflexes, (l) mood, energy level, and effort allocation, (m) physiology, and (n) behavior.

Although no emotion has been the subject of research exploring all of these programs, work on the emotion of sexual jealousy has made inroads into many (Buss, 2013). For example, hypothesized sex-differentiated design features of jealousy have been discovered in studies of attention, speed of processing, and spontaneous recall (Schützwohl, 2006; Schützwohl & Koch, 2004), information-gathering (Kuhle, 2011), probabilistic inferences (Andrews et al., 2008), physiology (Buss, Larsen, Westen, & Semmelroth, 1992), and manifest behavior (Buss, 1988; Kuhle, Smedley, & Schmitt, 2009).

Not every emotion will coordinate all of these programs, nor will each instance of an emotion activate the same programs. Fear may activate escape behavior in some contexts (e.g., a crocodile that can be outrun on dry land) and not in others (e.g., an adversary who can be overpowered in a fight). Different environmental circumstances present different demands. Consequently, the idea of emotions as program coordinators does not imply that component programs must be strongly correlated. Evidence showing, for example, that the components of surprise are not strongly correlated (Reisenzein, 2000) or that smiling exhibits weak–moderate correlations with certain positive emotions (Reisenzein, Studtmann, & Horstmann, 2013) is perfectly compatible with our perspective on the emotions.

Our framework can be used to systematically generate novel hypotheses using the heuristic tool of *task analysis* (Marr, 1982). A task analysis for an emotion consists of four 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 carrying out these subtasks? and (4) how should these programs be coordinated to facilitate the solution of these subtasks?

## Part II. What Does an Evolutionary Psychological Perspective Contribute to Our Understanding of the Emotions?

### *Nonarbitrary Criteria for Classifying Emotions*

The perspective we present here has implications for how emotions are classified. Current perspectives classify emotions as "basic" or fundamental on the basis of criteria that are misguided from a modern evolutionary perspective (Buss, 2014; Confer et al., 2010; Tooby & Cosmides, 2008). An evolutionary psychological perspective suggests conceptual shifts in three areas: diversity of adaptive problems, distinctive universal signals, and emotions in nonhuman species.

***Emotions solve a wide variety of adaptive problems.*** Evolutionary approaches have traditionally focused on a limited subset of emotions, many of which solve problems of survival. Fear, anger, and disgust, for example, evolved to solve survival problems and are widely regarded as "basic" (Ekman, 1992, 1999; Ekman & Cordaro, 2011; Lazarus, 1991; Plutchik, 1980). By contrast, evolutionary approaches in the field have largely neglected emotions such as romantic love (e.g., Buss, 2003; Hazan & Shaver, 1987), sexual arousal (Symons, 1979, 1995), sexual jealousy (Buss, 2000; Wilson & Daly, 1992), and parental love (Daly & Wilson, 1998). There now exists evidence for the universality of these emotions, pointing to evolved functions related to challenges of mating, reproduction, and childrearing. There is no conceptually principled reason why they should be considered less fundamental than survival-oriented emotions such as disgust, anger, or fear. In our view, a) the defining criterion for an evolved emotion is whether it coordinates programs in the solution of an adaptive problem and (b) emotions can evolve to solve adaptive problems in *any* domain, including mate selection, mate retention, parenting, food acquisition, navigating status hierarchies, and many others.

The emphasis on survival in the evolutionary emotions literature may reflect an earlier view that emphasized natural selection to the exclusion of sexual selection, and survival to the exclusion of reproduction. By contrast, a modern evolutionary perspective emphasizes that the bottom line of evolution by selection is differential *reproductive* success. Evolutionary biologists recognize that survival is critical, but only to the extent that it is tributary to reproductive success. When the two conflict, reproduction inevitably trumps survival (Dawkins, 1976; Hamilton, 1964; Williams, 1966). Adaptations that promote an organism's reproduction at a cost to its survival are ubiquitous in the animal kingdom (Alcock, 2009; Buss, 2012; Dawkins, 1976). Examples include the brilliant plumage of peacocks (Darwin, 1871), suicidal mating among male honeybees (Woyciechowski, Kabat, & Kroll, 1994), and adaptations for elevated testosterone that promote success in mate competition at an on-average cost to male survival (Trivers, 1985; Williams & Nesse, 1991). Adaptations that promote an organism's *survival* to the detriment of its overall reproductive success, on the other hand, are entirely absent (Alcock, 2009; Dawkins, 1976, 1999).

This suggests a class of emotions that are critical but have not received much evolutionary attention: those that evolved to solve a broad range of adaptive problems tributary to reproductive success. This class of emotions includes states such as envy (e.g., DelPriore, Hill, & Buss, 2012), pride (e.g., Tracy & Robins, 2007), embarrassment (e.g., Keltner & Buswell, 1996), shame (e.g., Tracy & Matsumoto, 2008), guilt (e.g., Tangney & Dearing, 2003), sexual jealousy (e.g., Buss et al., 1992), sexual arousal (Symons, 1979, 1995), sexual regret (Galperin et al., 2013), sexual disgust (Tybur et al., 2012), romantic or passionate love (e.g., Hazan & Shaver, 1987), and parental love (e.g., Daly & Wilson, 1998). For example, sexual arousal motivates the pursuit of intercourse, sexual jealousy protects a mateship from interlopers, and parental love motivates behaviors that contribute to the health and success of offspring (Daly & Wilson, 1998; Hatfield & Sprecher, 1986; Symons, 1979). On our view, these emotions are all part of our fundamental, evolved emotional architecture.

***Distinctive universal signals.*** Historically seminal evolutionary perspectives typically maintain that basic emotions have distinctive universal signals (e.g., Ekman, 1992, 1999; Ekman & Cordaro, 2011). This theoretical position, which has been highly empirically fruitful (Ekman, 1992, 1999; Ekman & Friesen, 1971, 1986), may be conceptually rooted in Darwin's initial work on the emotions. In his classic book on emotions, Darwin's central goal was to document continuity in emotion *expression* between humans and nonhuman animals—an important focus at the time, but one that came at the expense of the critical question of adaptive function (Darwin, 1872/2009).

By contrast, a contemporary focus on evolved function highlights why the "distinctive signal" criterion is too restrictive. Whether an emotion carries with it a distinctive communication display depends on whether its evolved function includes signaling to others. For example, one hypothesized function of anger is to cause other individuals to back down in social conflict, which requires a manifest signal. In contrast, one hypothesized function of sexual jealousy is to motivate vigilance of a partner's behavior with potential interlopers, which typically does not require a distinctive signal.

Ultimately, the evolution of a signal is contingent on the ancestral costs and benefits of conveying that emotional state to others. During the evolution of a particular emotion, if the costs of advertising were high and benefits were low, we would not expect a signal to evolve.

Emotions researchers may benefit from evolutionary biologists' distinction between *signals* and *cues*. A signal is observable output whose function is conveying information to, or influencing, another organism (Krebs & Dawkins, 1984). By contrast, a cue is observable output that did *not* evolve to communicate information to others. For instance, a fear expression may have evolved to signal danger to allies. By contrast, fear-induced sweaty palms or brow may be visible by-products of physiological arousal that did not evolve to transmit information (e.g., Bradbury & Veherncamp, 1998; Maynard Smith & Harper, 2003, Shariff & Tracy, 2011). An important task for evolutionary emotions research is therefore to accurately distinguish signals and cues. Both may be universal and both important, but the distinction is critical in understanding the evolved function of each emotion.

A modern evolutionary perspective therefore suggests that the "distinctive universal signal" criterion is needlessly restrictive. Instead, some evolved emotions include distinctive signals, whereas others, such as regret, lack signals altogether. Evidence that certain emotions may not have signals or may not be universally recognizable (e.g., Nelson & Russell, 2013) is perfectly compatible with their status as evolved emotions.

Moreover, some emotions may exhibit context-dependent signaling or context-dependent suppression of expression (see Fridlund, 1997, for a similar discussion). For example, in some contexts a fear expression may signal a dangerous predator, but in different circumstances, fear displays may be suppressed to convey bravery. This important context-dependence reinforces the key point that signaling is linked only to a limited subset of emotions, and even with those, to limited contexts in which signaling is central to evolved function. A modern evolutionary perspective acknowledges the importance of signals, but does not support the notion that a distinctive universal signal—or *any* signal for that matter—is a necessary component of evolved emotions.

***Cross-species evidence.*** It is often stipulated that basic emotions must be present in nonhuman species (Ekman, 1992; Ekman & Cordaro, 2011). Modern evolutionary theory suggests a different conclusion. Each species has an emotional repertoire appropriate for dealing with the adaptive problems it recurrently faced during its evolution. When adaptive problems differ, species evolve different solutions. Uniquely human adaptations are no less basic than those shared with other species. Language and the ability to accurately throw high-speed projectiles, for example, are uniquely human adaptations that are properly regarded as fundamental aspects of human nature (Pinker, 2007; Pinker & Bloom, 1992; Roach, Venkadesan, Rainbow, & Lieberman, 2013). Pride, guilt, envy, embarrassment, and love are all examples of emotions that may have evolved uniquely in humans, or at a minimum have uniquely human design features. These evolved human emotions are just as fundamental as emotions shared with other species.

Even emotions that *are* shared with other species are likely to have unique design features in humans. For example, fear and disgust are widespread across taxa, but differ from species to species in the cues they take as input, the decision rules they implement, and the outputs they produce. For instance, the mere thought of having sex with one's sibling is repulsive to most humans (Haidt, 2001; Lieberman, Tooby, & Cosmides, 2007), but presumably not to species with inbreeding mating systems (e.g., Hamilton, 1967; Herre, 1985). Humans are revolted at the prospect of feeding on a rotting deer carcass; scavengers such as vultures are not. The key point is that an evolved human emotion can be fundamental regardless of whether it is: (a) shared with other species, but with many unique features, (b) shared with other species, with few unique features, or (c) entirely unique to our species.

In sum, we argue that three features of existing perspectives require reformulating. Emotions can evolve to solve a broad array of adaptive problems; do not need to include distinctive signals; and can be unique to humans (see Table 1).

Beyond these classificatory emendations, an evolutionary psychological approach makes two additional contributions: highlighting the centrality of information processing and offering heuristic value in hypothesis generation.

### *The Centrality of Information Processing*

An evolutionary psychological approach recognizes the importance of emotion outputs such as behavior—they are indispensable in the solution of real-life adaptive problems. But it places outputs in context by situating them in the input-algorithm-output chain. This approach leads to novel empirical predictions about the nature of these outputs. In traditional evolutionary approaches, for example, distinctive signals must be universal and universally recognizable. The current approach suggests a different conclusion: some outputs will indeed be universal, but this isn't necessary. In most cases, *design at the information-processing level* will be universal, but manifest output need not be. Some emotions may be designed for context-dependent output: that is, designed to produce expressions that differ predictably by context, or to produce signals only in a subset of contexts.

Stated differently, an evolutionary psychological perspective suggests that universality and evidence of adaptive design are to be found at the level of computational structure, not manifest output (Buss, 1995; Symons, 1979; Tooby & Cosmides, 1992). In the example of facial expressions, the critical question is not whether the output (emotion expression) is universal or variable, but rather whether the variability in output is underlain by uniformity in the information-processing procedures that produce the output (e.g., see Tooby & Cosmides, 2005).

This characterization—universal at the information-processing level, but variable at the manifest level—suggests an analogy with language. All humans have species-typical language mechanisms, but the particular language learned during ontogeny differs from culture to culture (Pinker & Bloom, 1992), resulting in the rich variability of the world's approximately 6,800 living languages (Gordon, 2005).

### *Heuristic Value and Predictive Power*

This perspective can be combined with *task analysis* of adaptive problems (Marr, 1982) to yield a powerful framework for hypothesis generation. This entails determining the adaptive problem that an emotion evolved to solve and identifying the psychological programs that are capable, in principle, of accomplishing the problem's subtasks. Task analysis can also be used to identify psychological procedures that would result in a *better* or more efficient solution to the adaptive problem in question. This process leads to a series of hypotheses about the coordinating effects of an emotion on a variety of programs.

Some emotions coordinate a larger subset of programs than others (Cosmides & Tooby, 2000; Tooby & Cosmides, 2008), and different contexts may reliably elicit different subsets of programs. In principle, these context effects can be predicted *a priori*, a theoretical strength that is largely absent in existing evolutionary approaches. As an illustration, we use this framework to generate a series of hypotheses for two distinct emotions.

## Part III. Novel Hypotheses and New Directions

### *Disgust: An Established Emotion*

Disgust is a well-established emotion that primarily coordinates psychological and physiological mechanisms in the service of

**Table 1.** Differing evolutionary perspectives on the emotions.

| *Traditional evolutionary perspectives: Basic emotions* | *Evolutionary psychological perspective: Superordinate mechanisms* |
|---|---|
| (e.g., Ekman, 1973, 1992; Ekman & Cordaro, 2011) | (Al-Shawaf et al, 2015 (this article); Cosmides & Tooby, 2000; Tooby & Cosmides, 2008) |
| There are 7 basic emotion families (disgust, fear, anger, surprise, sadness, happiness, contempt). | Evolved emotions are larger in number, including emotions such as love, guilt, jealousy, and gratitude. Each is defined according to its evolved function. |
| Focus on subset of adaptive problems. Heavier emphasis on survival, weaker emphasis on reproductive success. | Focus on broad range of adaptive problems, including any that historically contributed to reproductive success in any domain, directly or indirectly. |
| Present in other species, especially nonhuman primate species. | May be (a) unique to humans, (b) shared with other species, or (c) shared with other species but with uniquely human features. |
| Characterized by distinctive physiological activation (e.g., distinctive patterns of autonomic nervous system activity). | Evolved emotions are distinct if they are (a) designed to solve different adaptive problems and (b) characterized by a different overall profile of psychological, physiological, and behavioral activation. |
| Include a universal, universally recognizable signal. | May (a) include a universal signal, (b) not include a signal at all, or (c) be designed for context-dependent signaling. |

avoiding parasitic infection (Curtis, Aunger, & Rabie, 2004; Curtis, de Barra, & Aunger, 2011; Rozin, Haidt, & McCauley, 1993; Schaller & Duncan, 2007; Tybur et al., 2012). The particular pattern of mechanism activation differs by context and by type of disgust (*pathogen disgust, sexual disgust,* or *moral disgust*; see Tybur, Lieberman, & Griskevicius, 2009; Tybur et al., 2012). We focus here on pathogen disgust, generating hypotheses for how this emotion coordinates programs in the service of avoiding infection.

***Disgust memory.*** The effects of disgust on memory are largely unknown, but this perspective furnishes testable hypotheses. We propose that disgust mobilizes memory resources to encode potentially infectious items, a device that may be useful in avoiding future exposure. Individuals who appear infectious may be encoded as such in memory, along with a tag marking them as unsuitable social partners.

Research on "adaptive memory" shows that survival-related adaptive problems trigger especially strong encoding, even outperforming encoding techniques such as visual image generation (Nairne & Pandeirada, 2008; Nairne, Pandeirada, & Thompson, 2008). We hypothesize that strong disgust activation may have similarly powerful effects on memory, allocating memory resources to information relevant to avoiding future contamination.

***Disgust information-gathering mechanisms.*** Acquiring information can be vital in avoiding contamination. For example, smelling a foul stench of unknown origin may prompt a search for the source, enabling a person to identify whether the disgusting object is alive or dead, mobile or immobile, close or distant - different combinations of which should result in different behavioral responses.

Disgust may regulate information gathering in other contexts as well. For example, seeing a gaping wound on your child's leg may activate a search to find out how far the infection spreads, whether pus is visible, and whether the wound is worsening over time. This information would have been useful in reducing the risk of infection for self, offspring, and kin. More broadly, an evolutionary psychological perspective calls attention to the ways in which emotions adaptively regulate information-gathering mechanisms, a topic that has thus far received little attention.

***Communication and emotional expression.*** This approach yields hypotheses about the expression of disgust, as well as the ways that disgust might regulate communication in other domains. Facial displays of disgust are hypothesized to serve at least two distinct functions—self-protective and communicative (Chapman, Kim, Susskind, & Anderson, 2009; Shariff & Tracy, 2011). We propose that the communicative value of disgust expressions vary as a function of context: first, these displays should be less common when individuals are alone. Second, parents and kin may produce more pronounced displays if children are present *and* observational learning is important for appropriate disgust development. Third, overt displays may be adaptively suppressed in some contexts. For example, men may suppress disgust in mating contexts because the intensity of one's disgust reaction reveals information about the quality of one's immune system (Fessler, Pillsworth, & Flamson, 2004). These are precise, testable predictions about the context-dependence of emotion display.

Disgust communication may also infuse gossip and competitor derogation. In principle, gossip about disgusting individuals conveys information that can be used to track people's infection risk and regulate social interactions accordingly. In the domain of competitor derogation, Buss and Dedden (1990) found that men and women derogate their intrasexual rivals in the areas of hygiene (e.g., he mentioned that his rival never showered) and disease (e.g., she mentioned that her rival had sexually transmitted diseases).

***Specialized disgust inference mechanisms.*** Disgust activates specialized inference mechanisms that appear biased toward false positives (Haselton & Buss, 2000; Haselton & Nettle, 2006). For example, humans are disgusted by noninfectious conditions such as obesity and burn wounds (Park, Faulkner, & Schaller, 2003), reluctant to eat fake excrement that they know is really chocolate fudge (Rozin, Millman, & Nemeroff, 1986), and require less evidence to infer that someone is sick than healthy (Kurzban & Leary, 2001). We suggest that disgust may activate other "paranoid" inferential biases as well (Haselton & Nettle, 2006). To take just one example, knowing that a person's spouse is ill may lead us to treat that person as infectious - even in the absence of sufficient evidence.

***Disgust behavior.*** Disgust's behavioral output must be coordinated with changes in cognition and perception. Quickly approaching pathogens, for example, require different motor responses than immobile contaminants. Behavioral output also depends on social factors. If the object of disgust is another human, we expect people to downplay their avoidance because of the social costs of shunning in-group members. Because these costs are usually absent for contaminated foods or dead animals, this suppression should be stronger in response to humans than to other contaminant vectors. For similar reasons, we expect greater effort to downplay disgust in response to individuals of high than low social status. An evolutionary psychological approach suggests that disgust regulates behavior in context-specific ways—a richer conceptualization than the broadband notion of "avoidance," and one that yields a number of testable context-specific hypotheses.

Disgust usually produces avoidance, but in some instances it can motivate approaching and repelling or killing the source. We suggest that such behavior will be more frequent when there are vulnerable young kin in proximity, or when one is seeking to impress mates or other social partners. Lastly, disgust appears to motivate washing, cleaning, and other hygienic behavior designed to reduce the likelihood of infection (Curtis, 2007; Curtis, Cairncross, & Yonli, 2000; Fleischman et al., 2011).

***Overriding disgust.*** In extreme cases, disgust may be suppressed in order to solve a more pressing adaptive problem, such as consummating a valuable mating opportunity or fending off starvation. As starvation draws near, we expect a muted disgust response to pathogenic foods that would otherwise trigger revulsion (Hoefling et al., 2009). This disgust suppression should be specific to food. For example, mounting hunger should not affect repulsion toward bodily effluvia or open sores.

Hunger-induced disgust suppression may partly explain human willingness to eat repugnant food during dire circumstances. Consider the historical examples of "survival cannibalism" during the 1972 Andes flight crash (Read, 1975), the Donner Party disaster (Stewart, 1960), or the Nazi siege of Leningrad (now St. Petersburg; Salisbury, 2009), in which people resorted to eating human meat to fend off starvation. Eventually, when hunger dissipates, this disgust suppression should lift, reactivating previous disgust thresholds.

## Sexual Arousal: An Unexplored Emotion

An evolutionary psychological approach promotes the inclusion of states that are traditionally excluded from emotions research. States such as hunger, pain, curiosity, and sexual arousal may qualify as emotions as long as they evolved to coordinate other programs in the solution of an adaptive problem (Cosmides & Tooby, 2000; Tooby & Cosmides, 2008).

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. In contrast, an evolutionary psychological approach regards sexual arousal as a fundamental emotion that evolved to solve one of the most important adaptive problems faced by sexually reproducing species—the coordination of a number of disparate mechanisms in the service of conception.

Before generating hypotheses, we address a theoretically important sex difference. Among humans, the minimum obligatory parental investment is greater for women than for men. In species characterized by a sex difference in minimum parental investment, the higher investing sex suffers more severe costs as a consequence of injudicious mating decisions. Consequently, easy-to-cross thresholds of sexual arousal are more costly for women than for men (Symons, 1979). The theoretical optimum for sexual arousal thresholds is higher for women than it is for men. Selection therefore favors higher thresholds in women, making men more sexually excitable in response to more minimal stimulation. Once activated, however, the broad function of sexual arousal is the same for both sexes: the orchestration of a diverse array of programs in pursuit of sexual intercourse.

***Motivational priorities.*** Sexual arousal can effect a profound shift in motivational priorities, elevating sexual activity and demoting goals such as obtaining food and avoiding pathogens. For example, sexual arousal can inhibit disgust (Borg & de Jong, 2012; Fleischman, 2014; Stevenson, Case, & Oaten, 2011) and promote interest in sex with partners one normally finds socially inappropriate or even undesirable (Ariely & Loewenstein, 2006). The strength of motivational reprioritization should depend partly on the intensity of the emotion, with more intense sexual arousal leading to more dramatic reprioritization.

Sexual arousal should calibrate the extent of motivational shifts in response to cues that ancestrally were reliably predictive of the costs and benefits of pursuing a particular sexual goal. Sexual arousal should have a strong impact on motivational priorities when a potential partner is of high mate value, the likelihood of a successful mating is high, the temporal proximity to sexual consummation is close, and the costs of pursuing such an opportunity are low. Because the costs of a missed sexual opportunity are typically greater for men than for women (Symons, 1979; Trivers, 1972), motivational shifting should be stronger, on average, for men than for women, with notable exceptions such as a rare opportunity for sex with a partner of unusually high status (Greiling & Buss, 2000) or unusually good genes (Gangestad & Thornhill, 2008).

***Sexual information-gathering adaptations.*** Sexual arousal should activate a search for information relevant to the costs and benefits of pursuing a potential mate. Such programs may seek information on a potential mate's relationship status and sexual receptivity, as well as the presence or absence of mating rivals. We expect information-gathering programs to seek data about the potential partner's preferred mating strategy, personality, and values and interests.

The information sought and the way in which it is used will differ across individuals and contexts, and this may be predictable in advance. For example, men who are interested in mate poaching (Schmitt & Buss, 2001) may seek information about a mated woman's sexual fidelity. More monogamous individuals may refrain from searching for this information in the first place. More broadly, this framework calls attention to information-gathering mechanisms as key components of evolved mating strategies.

***Imposed conceptual frameworks and sexual categorization.*** Emotions may regulate conceptual frameworks, compelling division of the world into categories relevant for solving the adaptive problem at hand. We propose that sexual arousal alters conceptual frameworks, temporarily categorizing members of the opposite sex as mateable or unmateable, and members of the same sex as rivals, nonrivals, protectors, or enablers ("wingmen" and "wingwomen").

***Sexual memory.*** Sexual arousal may regulate memory, encoding the physical features of desirable mates and the circumstances that led to mating success. When accompanied by long-term mating intentions, sexual arousal should strengthen encoding of many types of information about the desired other, including personal details revealed in the process of courtship. This information can be useful in courtship and valuable in conveying commitment intent.

Memory effects should show sex-differentiated design features. Circumstantial evidence for this hypothesis comes from recent studies of sexual regret. Men recalled and regretted more acts of sexual omission; women recalled and regretted acts of sexual comission with inappropriate partners (e.g., men who were unattractive or uninterested in commitment; Galperin et al., 2013). Negatively valenced memories presumably provide guidance about what to do in the present and future, and these sex differences in regret should influence men and women's sexual decision-making.

***Sexual learning.*** We propose that sexual arousal guides learning to facilitate intercourse. In most species, frequent copulation and sensitivity to sexual opportunities pays greater fitness dividends to males than to females. Consequently, males should learn to associate environmental cues linked with copulatory opportunity more easily and more rapidly than females. Evidence confirms this prediction—Japanese quail exhibit conditioned sexual arousal to cues previously associated with copulatory opportunity, an effect that is stronger among males than females (Crawford, Holloway, & Domjan, 1993). Male quail even respond sexually to arbitrary stimuli—such as artificial bright orange feathers—that were previously associated with copulatory opportunity in experiments (Domjan, O'Vary, & Greene, 1988). Humans and rats show similar sexual conditioning effects, and these are typically weaker or absent in females (Crawford et al., 1993; Pfaus, Kippin, & Centeno, 2001).

The human male combination of low sexual arousal thresholds and adaptively biased sexual learning mechanisms may partly explain the greater prevalence of sexual fetishism among males than females (Laws & Marshall, 1990; O'Donohue & Plaud, 1994). Evidence shows that paired associations of erotic stimuli with colored squares or women's boots can lead men to become sexually aroused in response to the squares or boots alone (McConaghy, 1974; Rachman & Hodgson, 1968). We are not, of course, claiming that these fetishes are adaptations; they are likely functionless byproducts of the male combination of easy-to-cross thresholds of sexual arousal and adaptively biased sexual learning. In sum, an evolutionary psychological perspective on sexual arousal points to the importance of sex-differentiated learning mechanisms and reveals a pattern of greater male sensitivity to copulatory opportunity and cues associated with sex.

***Specialized sexual inference mechanisms.*** We hypothesize that sexual arousal activates the *sexual overperception bias*, the adaptive male tendency to overestimate the sexual interest of women displaying ambiguous cues such as a smile (Abbey, 1982; Abbey & Melby, 1986; Haselton & Buss, 2000; Haselton & Nettle, 2006). By activating the overperception bias, sexual arousal presumably motivates approach, minimizes missed opportunities, and may even transform an initially uninterested woman into an interested one (Haselton & Buss, 2009). Circumstantial support for this hypothesis comes from the experimental finding that physically attractive women, known to preferentially activate men's sexual arousal, are especially likely to evoke men's sexual overperception bias (Perilloux, Easton, & Buss, 2012).

The *commitment skepticism bias* refers to women's tendency to underestimate the commitment intent of potential mates (Haselton & Buss, 2000; Haselton & Nettle, 2006). Commitment skepticism evolved because of a large cost asymmetry in the types of error a woman could make when inferring a man's commitment intent: underestimating commitment may result in wasted time, but overestimating commitment can lead to deception and exploitation. The latter error can impose the severe fitness costs associated with being impregnated and left to rear offspring without the provisioning of a committed mate. Counterintuitively, because the men who are most sexually attractive to women are also the men who are most unfaithful and least likely to commit (Buss, 2003; Gangestad & Thornhill, 2008), sexual arousal may initially amplify the commitment skepticism bias—a testable prediction that awaits future research.

***The orgasmic dissolution hypothesis.*** Orgasm is an important part of the sexual and emotional lives of both sexes. Among men, orgasm is necessary for conception and indicates the end of the primary adaptive problem that sexual arousal is designed to solve. The same is not true of orgasm in women.

Consequently, this event should have sex-differentiated effects on sexual arousal. Among men, but not women, orgasm should lead to a dramatic and precipitous decline in arousal. And because sexual arousal coordinates the mechanisms discussed above, orgasm should suddenly terminate these coordinating effects—but again only among men.

We call this the *orgasmic dissolution hypothesis* because in males, orgasm suddenly "dissolves" the coordination effects of sexual arousal. This hypothesis predicts that orgasm should have the following sudden effects for men but not women:

> *Prediction 1*: Reverse the narrowing of attentional focus, broadening it back out again.
>
> *Prediction 2*: Cause memories of other duties and responsibilities to become accessible again.
>
> *Prediction 3*: Reorder priorities so that previously suppressed motivations to eat, further one's career, or avoid pathogens come online again.
>
> *Prediction 4*: Deactivate specialized inference mechanisms activated by sexual arousal (e.g., the sexual overperception bias).
>
> *Prediction 5*: Deactivate sexual categorization (e.g., enablers vs. obstacles).
>
> *Prediction 6*: Down-regulate information-gathering mechanisms geared toward intercourse.
>
> *Prediction 7*: Previously suppressed physiological processes can come online again (e.g., digestion, cell repair).
>
> *Prediction 8*: Previously suppressed emotions can be reactivated (e.g., disgust, worry).

These effects must come after orgasm, not before—an example of the *concatenation problem*. We expect these effects to be strikingly sex-differentiated: Among men, they should be profound and near immediate. Among women, they should be weaker and more gradual, and in some cases entirely absent.

These predictions can be tested experimentally. Participants can complete psychological assessments while stimulating themselves sexually (e.g., Strassberg, Mahoney, Schaugaard, & Hale, 1990). This can be done at progressive stages of arousal leading up to orgasm and immediately thereafter. The orgasmic dissolution hypothesis proposes that men, much more than women, will show a sudden and profound shift from preorgasm to postorgasm on psychological mechanisms ranging from motivational priorities to conceptual categorization to attention.

***Context-dependent effects of orgasm.*** Orgasmic dissolution should be context-dependent. Men pursuing long-term mating are interested in forging or maintaining a committed relationship that persists over time. For them, sexual intercourse solves more than just the problem of conception; it also contributes to the solution of adaptive problems related to satisfying one's mate and forming a stable bond together. The "dissolving" effects of orgasm should therefore be less dramatic for men seeking commitment. These men may experience a more gradual return to baseline after orgasm. Committed men may also see sexual arousal give way to a positive emotion such as affection, whereas men oriented toward short-term mating appear more likely to experience a negative affective shift after orgasm (see Haselton & Buss, 2001).[1]

## *The Science of Testing Evolution-Based Emotion Hypotheses*

The collection of hypotheses generated by this framework raises the question of how to best test hypotheses and interpret results. The answer depends on the level at which the question is posed. We have presented ideas at three different levels in the hierarchical structure of evolutionary psychology (Buss, 1995): (a) the "middle-level" theory of emotions as superordinate mechanisms, (b) broad hypotheses about the function of each individual emotion, and (c) numerous specific hypotheses about the effects of each emotion on a variety of programs in the mind and body.

The last of these three levels is the most straightforward. Specific hypotheses about the effects of a given emotion on memory or attention are used to generate predictions, which are tested in empirical studies. The results are used to interpret the truth or falsity of the hypothesis in the standard scientific manner. If a single hypothesis generates multiple predictions, some may be verified and others falsified. The hypothesis, like all hypotheses in psychology, must be evaluated according to the cumulative weight of the evidence.

Broad hypotheses and middle-level theories are evaluated in much the same way, but two additional points are worth mentioning. First, a hypothesis at a particular level of the hierarchy is evaluated on the basis of the empirical harvest it yields at more specific levels. For example, the broad hypothesis that disgust coordinates programs in the service of avoiding infection must be evaluated on the basis of the specific hypotheses it yields about physiology, memory, attention, and other processes. Evidence against the memory hypotheses may falsify those memory hypotheses, but does not immediately falsify the broad disgust hypothesis. Instead, this broad hypothesis is falsified when the cumulative evidence weighs against the multiple specific hypotheses it yields. The same principle applies to the middle-level theory of the emotions as superordinate mechanisms. The theory of emotions as superordinate mechanisms is best evaluated in light of all the broad hypotheses that fall under its umbrella: disgust, anger, love, sexual arousal, happiness, gratitude, and so on.

Second, there is no single, definitive evolutionary hypothesis for the effects of disgust on memory, or for the effects of happiness on information gathering, or for anything else. There are usually multiple, competing evolutionary hypotheses for the same phenomenon (e.g., Buss, 1995; Symons, 1979; Tinbergen, 1963). A broad hypothesis, such as the idea that disgust coordinates programs in the service of avoiding infection, can be used to generate multiple *competing* specific hypotheses about how disgust regulates memory. The specific hypotheses we propose in this article are by no means the only viable evolutionary hypotheses.

The existence of competing evolutionary hypotheses cautions strongly against assuming a particular hypothesis to be "the" evolutionary hypothesis, and then equating the verification or falsification of that particular hypothesis with the verification or falsification of the entire theory on which it is based.

### The Role of the Emotions in Conflict and Manipulation

Conflict and manipulation are ripe but relatively untapped areas in emotions research. The fact that different individuals have different fitness interests suggests that social conflict will be ubiquitous. We expect the emotions to play a crucial role in these battlegrounds.

Animal signals are best conceptualized as adaptations designed to influence and manipulate other organisms, rather than as purely veridical messages (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984). Emotions can be used to influence or manipulate others in at least two ways: (a) exploitatively inducing an emotion and (b) communicating false emotion. A wide array of emotions may be amenable to such tactics, but here we consider guilt, anger, and empathy as examples.

The more valuable another individual is to oneself, the more weight one places on that person's welfare. This relative weighting of another individual's welfare to one's own is called a *welfare trade-off ratio*. This internal regulatory variable is hypothesized to play a central role in navigating social relationships. It is also hypothesized to be critical to "recalibrational" emotions such as guilt, anger, gratitude, and shame (Cosmides & Tooby, 2000; Sell, Tooby, & Cosmides, 2009). For example, evidence suggests that one evolved function of anger is to induce another individual to recalibrate his welfare trade-off ratio: feeling slighted motivates an angry response designed to impel the slighter to recalibrate his welfare trade-off ratio and treat the victim more favorably in the future (Sell et al., 2009).

Guilt, too, appears to be a recalibrational emotion. Guilt functions to recalibrate one's *own* welfare trade-off ratio toward another individual, leading to greater valuation of the other individual and better treatment in the future (Tooby & Cosmides, 1990, 2008).

***Exploitative induction of emotions.*** The existence of guilt suggests the possibility of deliberately inducing guilt in order to manipulate someone into recalibrating his or her welfare trade-off ratio. The empirical discovery of guilt induction as a mate retention tactic (e.g., "I pretended to be mad so that my partner would feel guilty"; Buss, 1988) may be an instance of this form of manipulation. More generally, the existence of emotions that function to recalibrate welfare trade-off ratios renders organisms vulnerable to exploitation.

The evolution of an exploitative strategy, however, selects for coevolved defenses against exploitation, and this often results in an antagonistic coevolutionary arms race (Dawkins & Krebs, 1979; Ridley, 1993). Humans likely have mechanisms designed to detect and defend against exploitative induction of emotions.

Exploitative induction of one emotion is sometimes achievable through the exaggerated display of another. For example, pity and empathy can be exploitatively induced through exaggerated displays of sadness. The very existence of empathy mechanisms renders these mechanisms vulnerable to exploitation, leading selection to favor the disingenuous amplification of sadness displays (within credible limits). In this way, even if an emotion such as sadness initially evolved for non-exploitative purposes, selective pressures can drive it to acquire new exploitative functions.

***Disingenuous displays of emotion.*** Deceptive displays of emotion can be effective manipulation devices. For instance, an accused party may mollify his accusers by feigning remorse. A false display of guilt conveys that one acknowledges one's culpability, feels remorse, and is in the process of recalibrating one's welfare trade-off ratio. When the display is believable, this can be a useful, minimal-effort manipulative tactic for escaping punishment.

Exaggerated displays of anger can also be used for manipulation. In antagonistic encounters across the animal kingdom, exaggerated displays of aggression often work as successful threats and are used to negotiate social hierarchies (Alcock, 2009; Dawkins, 1976; Zahavi & Zahavi, 1997). In close relationships, exaggerated displays of anger—for example, feigning indignation in response to a transgression—may be a useful tactic to induce a relationship partner to place greater weight on one's welfare.

In sum, an evolutionary psychological approach points to the important role of the emotions in conflict. Emotions can be used for manipulation in at least two ways: exploitative induction and disingenuous displays. These two may become coupled; for example, when exaggerated sadness is used to elicit empathy or exaggerated guilt to induce forgiveness. Emotions likely play a critical role in the battlegrounds of conflict and social manipulation.

## Conclusions

Modern evolutionary psychology provides important conceptual insights into human emotions. We described the *coordination problem*, arguing that adaptive problems include a number of different subtasks, each of which requires the activation of a different program for its solution. These programs must be smoothly and efficiently coordinated, as the effectiveness of one program often depends on the prior or concurrent activation of another (*the concatenation problem*), and programs sometimes have conflicting outputs (*the problem of conflicting outputs*). The coordination problem can be computationally complex. Consequently, we propose that selection has fashioned adaptations whose function is to coordinate other mechanisms in the service of solving an adaptive problem (Cosmides & Tooby, 2000; Tooby & Cosmides, 2008). These are the emotions.

We highlight several conceptual contributions of our approach: (a) more cogent criteria for classifying the emotions, (b) an emphasis on information processing in addition to outputs, and (c) systematic hypothesis generation based on task analyses of adaptive problems. Emotions can evolve to solve adaptive problems in any domain tributary to fitness, many evolved emotions lack recognizable signals, and evolved human emotions need not be present in other species to qualify as basic.

These conceptual revisions enhance classificatory accuracy, lead to the identification of a broader array of evolved emotions, and point to a greater role for emotions in psychological functioning than historically envisioned. Our framework also highlights many sex-differentiated design features of human emotions, each corresponding to sex-differentiated adaptive problems men and women recurrently faced over human evolutionary history—features that have been largely absent from prior evolutionary theories of the emotions.

Our illustrations of these principles yielded a series of novel hypotheses about the effects of disgust and sexual arousal. Many of these hypotheses are context-specific, such as those pertaining to audience effects on the expression of disgust or mating strategy effects on orgasmic dissolution. Researchers can use this framework to generate novel hypotheses about *any* evolved emotion. Emotions such as guilt, gratitude, envy, jealousy, pride, *schadenfreude*, embarrassment, and curiosity may have evolved to solve a broad array of adaptive problems tributary to reproductive success. Such wide-ranging problems include hierarchy negotiation, sexual consummation, reputation management, moralistic punishment, childrearing, kin-directed altruism, and many others.

This approach appears scientifically fruitful: it broadens the conceptualization of the emotions, advances important theoretical principles, generates novel hypotheses, and poses new questions. From the vantage point of evolutionary psychology, emotions are critical to many domains of life and central to the science of psychology.

## Declaration of Conflicting Interests

None declared.

## Note

1. The main author (L.A.S.) presents the following faux limerick as a humorous summary of the sexual arousal hypothesis and orgasmic dissolution hypothesis:

*Kablam*

Arousal leadeth cognitive programs,
Spurring passionate and fertile wham-bams
It coordinates as it whirrs,
With different ends for his and hers –
So only one's done at the big kablam!

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