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CHAPTER 8

The Evolutionary Psychology of the Emotions and Their Relationship to Internal Regulatory Variables

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Evolutionary psychology is an attempt to unify the psychological, social, and behavioral sciences theoretically and empirically within a single, mutually consistent, seamless scientific framework. The core of this enterprise is the integration of principles and findings drawn from evolutionary biology, cognitive science, anthropology, economics, and neuroscience with psychology in order to produce high-resolution maps of human nature. By "human nature," evolutionary psychologists mean the evolved, reliably developing, species-typical computational architecture of the human mind, together with the physical structures and processes (in the brain, in development, and in genetics) that give rise to this information-processing architecture. For evolutionary psychologists, all forms of knowledge about brains and behavior are relevant, but the pivotal step is using these facts to form accurate models of the information-processing structure of psychological mechanisms.

The discovery of a correct information-processing description of a psychological mechanism is the fundamental clarifying scientific step, because each mechanism came into existence and was organized by natural selection in order to carry out its particular set of information-processing functions. It is not a metaphor but a reality that the brain is a computer—a physical system that came into existence to carry out computations. The computations were needed to solve the adaptive problem of regulating behavior successfully. Hence the brain (and its subsystems) evolved to carry out specific varieties of computation in order to regulate behavior so that it was biologically successful—that is, to assemble the individual somatically and neurally, to prevent prereproductive death, to increase the probability of achieving conditions (social and physical) that would have led to successful reproduction in the ancestral world, to reproduce successfully, and to assist genetic relatives (including children) to achieve and maintain conditions for their own successful reproduction.

In short, the functional subcomponents (programs) that constitute our psychological architecture were designed by natural selection to solve adaptive problems faced by our hunter–gatherer ancestors by regulating behavior in ways that increased genetic propagation—what biologists call "fitness." Against the otherwise disordering forces of entropy that pervade all of physical reality, natural selection is the only process that introduces functional organization into the designs of organisms (Tooby, Cosmides, & Barrett, 2003). So, to the extent that there is functional organization in the human psychological architecture, it was created by, reflects, and is explained by the operation of natural selection among our ancestors. This is why evolutionary psychology is not a specific subfield of psychology, such as the study of vision, reasoning, or social behavior. It is a way of approaching the science of psychology that produces (or is intended to produce) stable functional descriptions of the elements of the mind. (Detailed arguments for these positions can be found in Tooby & Cosmides, 1990a, 1990b, 1992a, 2005, and in Cosmides & Tooby, 1987, 1992, 1997.)

Researchers less familiar with evolutionary psychology often equate adaptive problems exclusively with short-run threats to physical survival. However, survival per se is not central to evolution: All individual organisms die sooner or later. In contrast, genes—which can be thought of as particles of design—are potentially immortal, and design features spread by promoting the reproduction of the genes that participate in building them. Survival is significant only insofar as it promotes the reproduction of design features into subsequent generations. Survival is no more significant than anything else that promotes reproduction, and is often advantageously risked or sacrificed in the process of promoting reproduction in self, children, or other relatives. Nearly every kind of event or condition has the potential to have some impact on the prospect of reproduction for individuals, their children, and their relatives. Consequently, selection on neural designs for functional behavior reaches out to encompass, in a network of cause and effect linkages, virtually all of human life, from the subtleties of facial expression to attributions of responsibility to the intrinsic rewards of play. The realm of adaptive information-processing problems is not limited to one area of human life, such as sex, violence, or resource acquisition. Instead, it is a dimension cross-cutting all areas of human life, as weighted by the strange, nonintuitive metric of their cross-generational statistical effects on direct and kin reproduction.

By "computation," evolutionary psychologists simply mean the organized causation of patterned information input–output relations. Natural selection poses adaptive problems of behavior regulation, and the mechanisms of the brain evolved to engineer solutions in the form of these regulatory input–output relations. Of course, these computational relations must be embodied physically in neural tissue, and must be designed to develop reliably. Adaptations are not just the products of the genes, but are the products of the coordinated interaction of a stable genetic inheritance and the evolutionarily long-enduring features of the environment.

A model of an evolved neurocomputational mechanism or program would answer questions such as these: What information does the program take as input? How is this information encoded, formatted, and represented as data structures? What operations are performed on these data structures to transform them into new representations or regulatory elements? And how do these procedures and data structures interact to generate and regulate behavior? In short, how does each program work in cause-and-effect terms?

AN EVOLUTIONARY-PSYCHOLOGICAL APPROACH TO THE EMOTIONS

Although an evolutionary-psychological approach can be applied to any topic in psychology, it is especially illuminating when applied to the emotions. To the extent that there is functional order to be found in the mechanisms responsible for the emotions, it was forged over evolutionary time by natural selection acting on our ancestors. The analysis of adaptive problems that arose ancestrally has led evolutionary psychologists to apply the concepts and methods of the evolutionary sciences to scores of topics that are relevant to the study of emotion. These include anger, cooperation, sexual attraction, jealousy, aggression, parental love, friendship, romantic love, the aesthetics of landscape preferences, coalitional aggression, incest avoidance, disgust, predator avoidance, kinship, and family relations (for reviews, see Barkow, Cosmides, & Tooby, 1992; Buss, 2005; Crawford & Krebs, 1998; Daly & Wilson, 1988; Pinker, 1997).

Indeed, a rich theory of the emotions naturally emerges out of the core principles of evolutionary psychology (Tooby, 1985; Tooby & Cosmides, 1990a; Cosmides & Tooby, 2000; see also Nesse, 1991). In this chapter, we (1) briefly state what we think emotions are and what adaptive problem they were designed to solve; (2) explain the evolutionary and computational principles that led us to this view; (3) identify how the emotions relate to motivational and other underlying regulatory variables the human brain is designed to generate and access; and (4) using this background, explicate in a more detailed way the design of emotion programs and the states they create.

It may strike some as odd to speak about love, jealousy, or disgust in computational terms. "Computation" has an affectless, flavorless connotation. But if the brain evolved as a system of information-processing relations, then emotions are, in an evolutionary sense, best understood as information-processing relations—that is, programs—with naturally selected functions. Initially, the commitment to exploring the underlying computational architecture of the emotions may seem infelicitous, but viewing them as programs leads to a large number of scientific payoffs. In particular, the claim that emotion is computational does not mean that an evolutionary-psychological approach misconstrues human experience as bloodless, affectless, disembodied ratiocination. It is simply the claim that one can describe the underlying set of informational relationships that explain emotional phenomena, including the nature of emotional experience. Every mechanism in the brain—whether it does something categorizable as "cold cognition" (such as reasoning, inducing a rule of grammar, or judging a probability) or as "hot cognition" (such as computing the intensity of parental fear, the imperative to strike an adversary, or an escalation in infatuation)—depends on an underlying computational organization to give its operation its patterned structure, as well as a set of neural circuits to implement it physically. In these terms, an evolutionary and computational view of emotion can open up for exploration new empirical and theoretical possibilities obscured by other frameworks.

AN EVOLUTIONARY-PSYCHOLOGICAL THEORY OF THE EMOTIONS

Both deductions from theoretical evolutionary psychology and a large supporting body of empirical findings in psychology, biology, and neuroscience support the view that the human mental architecture is crowded with evolved, functionally specialized programs. Each is tailored to solve a different adaptive problem that arose during human evolutionary history (or before), such as face recognition, foraging, mate choice, heart rate regulation, sleep management, or predator vigilance, and each is activated by a different set of cues from the environment.

But the existence of all these diverse programs itself creates an adaptive problem: Programs that are individually designed to solve specific adaptive problems could, if simultaneously activated, deliver outputs that conflict with one another, interfering with or nullifying each other's functional products. For example, sleep and flight from a predator require mutually inconsistent actions, computations, and physiological states. It is difficult to sleep when your heart and mind are racing with fear, and this is no accident: Disastrous consequences would ensue if proprioceptive cues were activating sleep programs at the same time that the sight of a stalking lion was activating ones designed for predator evasion. To avoid such consequences, the mind must be equipped with superordinate programs that override and deactivate some programs when others are activated (e.g., a program that deactivates sleep programs when predator evasion subroutines are activated). Reciprocally, many adaptive problems are best solved by the coordinated activation of a specific subset of programs, with each program being entrained into the computational settings most appropriate for the particular adaptive problem being faced. For example, predator avoidance may require simultaneous shifts in both heart rate and auditory acuity (see below). To do this, a special type of program is required that manages and harmonizes other programs, aligning each of them into the proper configuration at the right time.

In general, to behave functionally according to evolutionary standards, the mind's many subprograms need to be orchestrated so that their joint product at any given time is coordinated to deal with the adaptive challenge being faced, rather than operating in a self-defeating, discoordinated, and cacophonous fashion. We argue that such coordination is accomplished by a special class of programs: the emotions that evolved to solve these superordinate demands. In this view, the best way to understand what the emotions are, what they do, and how they operate is to recognize that mechanism orchestration is the function that defines the emotions, and explains in detail their design features. They are the neurocomputational adaptations that have evolved in response to the adaptive problem of matching arrays of mechanism activation to the specific adaptive demands imposed by alternative situations (Tooby & Cosmides, 1990a; Tooby, 1985; Cosmides & Tooby, 2000; Nesse, 1991).

Thus each emotion evolved to deal with a particular, evolutionarily recurrent situation type. The design features of the emotion program, when the emotion is activated, presume the presence of an ancestrally structured situation type (regardless of the actual structure of the modern world). Hence the exploration of the statistical structure of ancestral situations and their relationship to the mind's battery of functionally specialized programs is central to mapping the emotions. This is because the most useful (or least harmful) deployment of programs at any given time will depend critically on the exact nature of the situation being encountered. The abstract, distilled, recurrent characteristics of the situation are reflected in the architecture of the emotion. For example, because sexual rivals could be advantageously driven off by violence or its threat in a substantial fraction of the trillions of ancestral cases of mate competition, sexual jealousy is engineered to prepare the body physiologically for combat, and (when the rival is weak or unwary) motivates the individual to behave violently. In modern situations of potential or actual infidelity, police and prisons create additional consequences, and so violence against a sexual rival is likely to lead to maladaptive outcomes now. However, the design features of jealousy were designed to mesh with the long-enduring structure of the ancestral world, and not the modern world—so the emotion program continues to execute its own ancestral functional logic even under modern conditions.

How did emotions arise and assume their distinctive structures? Fighting, falling in love, escaping predators, confronting sexual infidelity, experiencing a failure-driven loss in status, responding to the death of a family member, and so on each involved conditions, contingencies, situations, or event types that recurred innumerable times in hominid evolutionary history. Repeated encounters with each kind of situation selected for adaptations that guided information processing, behavior, and the body adaptively through the clusters of conditions, demands, and contingencies characterizing that particular class of situation.

The payoffs accruing to alternative mutant designs for program activation, in interaction with recurrent classes of situations, engineered programs each of which jointly mobilizes a subset of the psychological architecture's other programs in a particular configuration. Each configuration was selected to deploy computational and physiological mechanisms in a way that, when *averaged* over individuals and generations, would have led to the most fitness-promoting subsequent lifetime outcome, given that ancestral situation type. Thus an emotion is a bet placed under conditions of uncertainty: It is the evolved mind's bet about what internal deployment is likely to lead to the best average long-term set of payoffs, given the structure and statistical contingencies present in the ancestral world when a particular situation was encountered. Running away in terror, vomiting in disgust, or attacking in rage are bets that are placed because these responses had the highest average payoffs for our ancestors, given the eliciting conditions.

This coordinated adjustment and entrainment of mechanisms constitutes a mode of operation for the entire psychological architecture, and serves as the basis for a precise computational and functional definition of each emotion state (Tooby & Cosmides, 1990a; Tooby, 1985; Cosmides & Tooby, 2000). Each emotion entrains various other adaptive programs—deactivating some, activating others, and adjusting the modifiable parameters of still others—so that the whole system operates in a particularly harmonious and efficacious way when the individual is confronting certain kinds of triggering conditions or situations. The conditions or situations relevant to the emotions are those that (1) recurred ancestrally; (2) could not be negotiated successfully unless there was a superordinate level of program coordination (i.e., circumstances in which the independent operation of programs caused no conflicts would not have selected for an emotion program, and would lead to emotionally neutral states of mind); (3) had a rich and reliable repeated structure; (4) had recognizable cues signaling their presence; and (5) would have resulted in large fitness costs if an error had occurred (Tooby & Cosmides, 1990a; Tooby, 1985; Cosmides & Tooby, 2000). When a condition or situation of an evolutionarily recognizable kind is detected, a signal is sent out from the emotion program that activates the specific constellation of subprograms appropriate to solving the type of adaptive problems that were regularly embedded in that situation, and deactivates programs whose operation might interfere with solving those types of adaptive problems. Programs directed to remain active may be cued to enter subroutines that are specific to that emotion mode, and that were tailored by natural selection to solve the problems inherent in the triggering situation with special efficiency. (Where there was no repeated structure, or there were no cues to signal the presence of a repeated structure, then selection could not build an adaptation to address the situation.)

According to this theoretical framework, an emotion is a superordinate program whose function is to direct the activities and interactions of the subprograms governing perception; attention; inference; learning; memory; goal choice; motivational priorities; categorization and conceptual frameworks; physiological reactions (such as heart rate, endocrine function, immune function, gamete release); reflexes; behavioral decision rules; motor systems; communication processes; energy level and effort allocation; affective coloration of events and stimuli; recalibration of probability estimates, situation assessments, values, and regulatory variables (e.g., self-esteem, estimations of relative formidability, relative value of alternative goal states, efficacy discount rate); and so on. An emotion is not reducible to any one category of effects, such as effects on physiology, behavioral inclinations, cognitive appraisals, or feeling states, because it involves evolved instructions for all of them together, as well as other mechanisms distributed throughout the human mental and physical architecture.

FEAR AS A MODE OF OPERATION

Consider the following example. The ancestrally recurrent situation is being alone at night, and a situation detector circuit perceives cues that indicate the possible presence of a human or animal predator. The emotion mode is a fear of being stalked. (In this conceptualization of emotion, there might be several distinct emotion modes that are lumped together under the folk category "fear," but that are at least partially distinguishable, computationally and empirically, by the overlapping but nonidentical constellation of programs each entrains.) When the situation detector signals that one has entered the situation of "possible stalking and ambush," the following kinds of mental programs are entrained or modified:

1. There are shifts in perception and attention. You may suddenly hear with far greater clarity sounds that bear on the hypothesis that you are being stalked, but that ordinarily you would not perceive or attend to, such as creaks or rustling. Are the creaks footsteps? Is the rustling caused by something moving stealthily through the bushes? Signal detection thresholds shift: Less evidence is required before you respond as if there were a threat, and more true positives will be perceived at the cost of a higher rate of false alarms.
2. Goals and motivational weightings change. Safety becomes a far higher priority. Other goals and the computational systems that subserve them are deactivated: You are no longer hungry; you cease to think about how to charm a potential mate; practicing a new skill no longer seems rewarding. Your planning focus narrows to the present; worries about yesterday and tomorrow temporarily vanish. Hunger, thirst, and pain are suppressed.
3. Information-gathering programs are redirected: Where is my child? Where are others who can protect me? Is there somewhere I can go where I can see and hear what is going on better?
4. Conceptual frames shift, with the automatic imposition of categories such as "dangerous" or "safe." Walking a familiar and usually comfortable route may now be mentally tagged as "dangerous." Odd places that you normally would not occupy—a hallway closet, the branches of a tree—suddenly may become salient as instances of the category "safe" or "hiding place."

5. Memory processes are directed to new retrieval tasks: Where was that tree I climbed before? Did my adversary and his friend look at me furtively the last time I saw them?

6. Communication processes change. Depending on the circumstances, decision rules may cause you to emit an alarm cry, or be paralyzed and unable to speak. Your face may automatically assume a species-typical fear expression.

7. Specialized inference systems are activated. Information about a lion's trajectory or eye direction may be fed into systems for inferring whether the lion saw you. If the inference is yes, then a program automatically infers that the lion knows where you are; if no, then the lion does not know where you are (the "seeing-is-knowing" circuit identified by Baron-Cohen, 1995, as impaired in persons with autism). This variable may automatically govern whether you freeze in terror or bolt. Are there cues in the lion's behavior that indicate whether it has eaten recently, and so is unlikely to be predatory in the near future? (Savanna-dwelling ungulates, such as zebras and wildebeests, commonly make this kind of judgment; Marks, 1987.)

8. Specialized learning systems are activated, as the large literature on fear conditioning indicates (e.g., LeDoux, 1995; Mineka & Cook, 1993; Pitman & Orr, 1995). If the threat is real, and the ambush occurs, you may experience an amygdala-mediated recalibration (as in posttraumatic stress disorder) that can last for the remainder of your life (Pitman & Orr, 1995).

9. Physiology changes. Gastric mucosa turn white as blood leaves the digestive tract (another concomitant of motivational priorities changing from feeding to emergency motor activity in pursuit of safety); adrenalin spikes; heart rate may go up or down (depending on whether the situation calls for flight or immobility), blood rushes to the periphery, and so on (Cannon, 1929; Tomaka, Blascovich, Kibler, & Ernst, 1997); instructions to the musculature (face and elsewhere) are sent (Ekman, 1982). Indeed, the nature of the physiological response can depend in detailed ways on the nature of the threat and the best response option (see, e.g., Marks, 1987).

10. Behavioral decision rules are activated: Depending on the nature of the potential threat, different courses of action will be potentiated: hiding, flight, self-defense, or even tonic immobility (the last of these is a common response to actual attacks, both in other animals and in humans[1]). Some of these responses may be experienced as automatic or involuntary.

From the point of view of avoiding danger, these computational changes are crucial: They are what allowed the adaptive problem to be solved with high probability, on average over evolutionary time. Of course, in any single case they may fail, because they are only the evolutionarily computed best bet, based on ancestrally summed outcomes; they are not a sure bet, based on an unattainable perfect knowledge of the present.

Whether individuals report consciously experiencing fear is a separate question from whether their mechanisms assumed the characteristic configuration that, according to this theoretical approach, defines the fear emotion state. Individuals often behave as if they are in the grip of an emotion, while denying they are feeling that emotion. We think it is perfectly possible that individuals sometimes remain unaware of (or lose conscious access to) their emotion states, which is one reason we do not use subjective experience as the *sine qua non* of emotion. At present, both the function of conscious awareness, and the principles that regulate conscious access to emotion states and other mental programs, are complex and unresolved questions (but see Tooby, Cosmides, Sell, Lieberman, & Sznycer, in press). Mapping the design features of emotion programs can proceed independently of their resolution, at least for the present.

ADAPTATIONIST FOUNDATIONS

Adaptations, By-Products, and Noise

Because of the different roles played by chance and selection, the evolutionary process builds three different types of outcomes into organisms: (1) adaptations—that is, functional machinery built by selection, and usually species-typical (see Tooby & Cosmides, 1990b, for details and exceptions); (2) by-products of adaptations, which are present in the design of organisms because they are causally coupled to traits that were selected for (usually species-typical); and (3) random noise, injected by mutation and other random processes (often not species-typical) (Tooby & Cosmides, 1990a, 1990b, 1992a; Williams, 1966). The emotion of sexual jealousy is an adaptation (Daly, Wilson, & Weghorst, 1982; Buss, 1994); stress-induced physical deterioration is arguably a by-product of the flight–fight system; and heritable personality variation in emotional functioning (e.g., extreme shyness, morbid jealousy, bipolar disorder) is probably noise (Tooby & Cosmides, 1990b). Evidence of the presence (or absence) of high degrees of coordination between adaptive problems and the design features of putative adaptations allows researchers to distinguish adaptations, by-products, and noise from one another (Williams, 1966; Cosmides & Tooby, 1997).

The emotions are often thought of as crude, but we expect emotions to be very well-designed computational adaptations. Biologists have found that selection has routinely produced exquisitely engineered biological machines of the highest order at all scales, from genetic error correction and quality control in protein assembly to photosynthetic pigments, the immune system, efficient bee foraging algorithms, echolocation, and color constancy systems. Indeed, the best-studied psychological adaptation—the eye and visual system—has been held up for centuries as the apotheosis of engineering excellence, as yet unrivaled by any human engineer. There is no principled reason to expect other neurocomputational (i.e., psychological) adaptations to be less well engineered than the eye. Although Stephen Jay Gould (1997) and his followers have energetically argued in the popular science literature that natural selection is a weak evolutionary force, evolutionary biologists, familiar with the primary literature, have found it difficult to take these arguments seriously (Tooby & Cosmides, 1997). So although adaptations are in some abstract sense undoubtedly far from optimal (and there is genetic noise in all systems), the empirical evidence falsifies the claim that evolved computational adaptations tend to be crude or primitive in design, and instead supports the opposite view: that our mental machinery—including the emotions—islikely to be very well designed to carry out evolved functions. For emotion researchers, this means that their working hypotheses (which are always open to empirical revision) should begin with the expectation of high levels of evolutionary functionality, and their research methods should be sensitive enough to detect such organization. This does not mean that emotions are well designed for the modern world—only that their functional logic is likely to be sophisticated and well engineered to solve ancestral adaptive problems.

The Environment of Evolutionary Adaptedness

Behavior in the present is generated by evolved information-processing mechanisms that were constructed in the past. They were constructed in the past because they solved adaptive problems that were recurrently present in the ancestral environments in which the human line evolved. For this reason, evolutionary psychology is both environment-oriented and past-oriented in its functionalist orientation. Adaptations become increasingly effective as selection makes their design features more and more complementary to the long-enduring structure of the world. The articulated features of the adaptation are designed to mesh with the features of the environment that were stable during the adaptation's evolution, so that their interaction produced functional outcomes. The regulation of breathing assumes the presence of certain long-enduring properties of the atmosphere and the respiratory system. Vision assumes the presence of certain evolutionarily stable properties of surfaces, objects, and terrestrial spectral distributions. The digestive enzyme lactase presupposes an infant diet of milk with lactose. Fear presupposes dangers in the environment, and even presupposes higher probabilities of specific kinds of dangers, given certain cues: darkness, spiders, snakes, heights, predators, open spaces, and so on (Marks, 1987). That is, each emotion program presupposes that certain cues signal the presence of a structure of events and conditions that held true during the evolution of that emotion. Disgust circuits presume a world in which rotten smells signal toxins or microbial contamination, for example.

Accordingly, to understand an adaptation as a problem solver, one needs to model the enduring properties of the task environment that constituted the problem and provided materials that could be exploited for its solution: the "environment of evolutionary adaptedness," or (EEA). Although the human line is thought to have first differentiated itself from the chimpanzee lineage on the African savannahs and woodlands, the EEA is not a place or time. It is the statistical composite of selection pressures that caused the genes underlying the design of an adaptation to increase in frequency until they became species-typical or stably persistent (Tooby & Cosmides, 1990a). Thus statistical regularities define the EEA for any given adaptation. The conditions that characterize the EEA are usefully decomposed into a constellation of specific environmental regularities that had a systematic (though not necessarily unvarying) impact on reproduction, and that endured long enough to work evolutionary change on the design of an adaptation. Some of these regularities are extremely simple: Distance from a predator is protection from the predator. Sex with an opposite-sex adult is more likely to produce offspring than sex with a child or a nonhuman. These regularities can equally well include complex conditionals (e.g., if one is a male hunter–gatherer *and* one is having a sexual liaison with someone else's mate *and* that liaison is discovered, then one is the target of lethal retributory violence 14% of the time). Descriptions of these regularities are essential parts of the construction of a task analysis of the adaptive problem a hypothesized adaptation evolved to solve (Tooby & Cosmides, 1990a). Conceptualizing the EEA in probabilistic terms is fundamental to the functional definition of emotion that we have presented above and will elucidate below.

Each adaptive problem recurred billions or trillions of times in the EEA, and so manifested a statistical and causal structure whose elements were available for specialized exploitation by design features of the evolving adaptation. For example, predators use darkness and cover to ambush (Marks, 1987). Physical appearance varies with fertility and health (Symons, 1979). Among hunter–gatherers, infants that a mother primarily cares for are almost invariably genetic siblings (Lieberman, Tooby, & Cosmides, 2007). Specialized programs—for predator fear, sexual attraction, and kin detection, respectively—could evolve whose configuration of design features embodied and/or exploited these statistical regularities, allowing these adaptive problems to be solved economically, reliably, and effectively. Such specializations, by embodying "innate knowledge" about the problem space, operate better than any general learning strategy could. Children did not have to wait to experience being ambushed and killed in the dark to prudently modulate their activities. Adults did not need to observe the negative effects of incest, because the human kin detection system mobilizes disgust toward having sex with individuals the mind has tagged as siblings (Lieberman et al., 2007).

The Functional Structure of an Emotion Program Evolved to Match the Evolutionarily Summed Structure of Its Target Situation

Each emotion program was constructed by a selective regimen consisting of repeated encounters with a particular kind of evolutionarily recurrent situation. By an "evolutionarily recurrent situation," we mean a cluster of repeated probabilistic relationships among events, conditions, actions, and choice consequences that endured over a sufficient stretch of evolutionary time to have favored some variant designs over others. Many of these relationships were probabilistically associated with cues detectable by humans, allowing psychophysical triggers to activate the task-appropriate program.

For example, the condition of having a mate plus the condition of the mate's copulating with someone else constitutes a situation of sexual infidelity—a situation that has recurred over evolutionary time, even though it has not happened to every individual. Associated with this situation were cues reliable enough to allow the evolution of a "situation detector" (e.g., observing a sexual act, flirtation, or even the repeated simultaneous absence of the suspected lovers were cues that could trigger the categorization of a situation as one of infidelity). Even more importantly, there were many necessarily or probabilistically associated elements that tended to be present in the situation of infidelity as encountered among our hunter–gatherer ancestors. These additional elements included (1) a sexual rival with a capacity for social action and violence, as well as allies of the rival; (2) a discrete probability that one's mate had conceived with the sexual rival; (3) changes in the net lifetime reproductive returns of investing further in the mating relationship; (4) a probable decrease in the degree to which the unfaithful mate's mechanisms would value the victim of infidelity (the presence of an alternative mate would lower replacement costs); (5) a cue that the victim of the infidelity was likely to have been deceived about a range of past events, leading the victim to confront the likelihood that his or her memory was permeated with false information; and (6) a likelihood that the victim's status and reputation for being effective at defending his or her interests in general would plummet, inviting challenges in other arenas. These are just a few of the many factors that would constitute a list of elements associated in a probabilistic cluster, and that would constitute the evolutionary recurrent structure of a situation of sexual infidelity. The emotion of sexual jealousy evolved in response to these properties of the world, and there should be evidence of this in its computational design.

Emotion programs have evolved to take such elements into account, whether they can be perceived or not. Thus not only do cues of a situation trigger an emotion mode, but embedded in that emotion mode is a way of seeing the world and feeling about the world related to the ancestral cluster of associated elements. Depending on the intensity of the jealousy evoked, less and less evidence will be required for individuals to believe that these conditions apply to their personal situation. Individuals with morbid jealousy, for example, may hallucinate counterfactual but evolutionarily thematic contents, such as seeing their mates having sex with someone else (Mowat, 1966; Shepherd, 1961). This leads many to consider emotions "irrational," but this property was selected for because it allows emotional computation to go beyond the evidence given, producing correct responses (when averaged over evolutionary time).

To the extent that situations exhibited a structure repeated over evolutionary time, their statistical properties would be used as the basis for natural selection to build an emotion program whose detailed design features were tailored for that situation. This would be accomplished by selection acting over evolutionary time, differentially incorporating program components that dovetailed with individual items on the list of properties probabilistically associated with the situation.

For example, ancestrally a male's ability to inflict costs through violence (his "formidability") was associated with his status and reputation for defending his interests. Moreover, the fitness consequences of being cuckolded are great, and males have become motivated by design to resist this outcome. If a mate's mate is sexually unfaithful and this infidelity becomes public, this advertises a weakness previously unappreciated by those who know him best. This decrease in perceived formidability decreases his value to his male allies and increases the probability that he will be challenged by competitors in other domains of life. The sexual jealousy, anger, and shame systems have been shaped by the distillation of these (and other) payoff probabilities. Each of these recurrent subelements in a situation of sexual infidelity, and the adaptive circuits they require, can be added together to form a general theory of sexual jealousy, as well as a theory of the functional coactivation of linked programs (such as anger and shame).

Hence the emotion of sexual jealousy constitutes an organized mode of operation specifically designed to deploy the programs governing each psychological mechanism, so that each is poised to deal with the exposed infidelity. Physiological processes are prepared for such things as violence, sperm competition, and the withdrawal of investment; the goal of deterring, injuring, or murdering the rival emerges; the goal of punishing, deterring, or deserting the mate appears; the desire to make oneself more competitively attractive to alternative mates emerges; memory is activated to reanalyze the past; confident assessments of the past are transformed into doubts; the general estimate of the reliability and trustworthiness of the opposite sex (or indeed everyone) may decline; associated shame programs may be triggered to search for situations in which the individual can publicly demonstrate acts of violence or punishment that work to counteract an (imagined or real) social perception of weakness; and so on.

It is the relationship between the summed details of the ancestral condition and the detailed structure of the resulting emotion program that makes this approach so useful for emotion researchers. Each functionally distinct emotion state—fear of predators, guilt, sexual jealousy, rage, grief, and so on—will correspond to an integrated mode of operation that functions as a solution designed to take advantage of the particular structure of the recurrent situation or triggering condition to which that emotion corresponds. This approach can be used to create theories of each individual emotion, through four steps: (1) Reconstruct the clusters of properties of ancestral situations; (2) analyze what behavioral and somatic alterations would solve the adaptive problem posed by the recurrent situation (or minimize the damage it causes); (3) construct a provisional model of the program architecture of the emotion that could generate the necessary mechanism-, body-, and behavior-regulating outputs, including the cues used, the regulatory variables the emotion needs to track, and so on; and (4) design and conduct experiments and other investigations to test each hypothesized design feature of the proposed emotion program, revising them as necessary.

It is also important to understand that evolutionarily recurrent situations can be arrayed along a spectrum in terms of how rich or skeletal the set of probabilistically associated elements defining the recurrent situation is. Richly structured situations—such as sexual infidelity, exposure to potential disease vectors, or predator ambush—will support a richly substructured emotion program in response to the numerous ancestrally correlated features each manifests: Many detailed adjustments will be made to many psychological mechanisms as instructions for the mode of operation. In contrast, some recurrent situations have less structure (i.e., they share fewer properties), and so the emotion mode makes fewer highly specialized adjustments, imposes fewer specialized and compelling interpretations and behavioral inclinations, and so on. For example, surges of happiness or joy are an emotion program that evolved to respond to the recurrent situation of encountering unexpected positive events. The class of events captured by "unexpectedly positive" is extremely broad and general, and such events have only a few additional properties in common. Emotion programs at the most general and skeletal end of this spectrum correspond to what some call "mood" (happiness, sadness, excitement, anxiety, playfulness, homesickness, etc.).

HOW TO CHARACTERIZE AN EMOTION

To characterize an emotion adaptation, one must identify the following properties of environments and of mechanisms.

1. *An evolutionarily recurrent situation or condition*. A "situation" is a repeated structure of environmental and organismic properties, characterized as a complex statistical composite of how such properties covaried in the environment of evolutionary adaptedness. Examples of these situations are being in a depleted nutritional state, competing for maternal attention, being chased by a predator, being about to ambush an enemy, having few friends, experiencing the death of a spouse, being sick, having experienced a public success, having others act in a way that damages you without regard for your welfare, having injured a valued other through insufficient consideration of self–other behavioral tradeoffs, and having a baby.

2. *The adaptive problem*. Identifying the adaptive problem means identifying which organismic states and behavioral sequences will lead to the best average functional outcome for the remainder of the lifespan, given the situation or condition. For example, what is the best course of action when others take the products of your labor without your consent? What is the best course of action when you are in a depleted nutritional state? What is the best course of action when a sibling makes a sexual approach?

3. *Cues that signal the presence of the situation*. For example, low blood sugar signals a depleted nutritional state; the looming approach of a large, fanged animal signals the presence of a predator; seeing your mate having sex with another signals sexual infidelity; finding yourself often alone, rarely the recipient of beneficent acts, or actively avoided by others signals that you have few friends.

4. *Situation-detecting algorithms*. A multimodular mind must be full of "demons"—algorithms that detect situations. *The New Hacker's Dictionary* defines a "demon" as a "portion of a program that is not invoked explicitly, but that lies dormant waiting for some condition(s) to occur" (Raymond, 1991, p. 124). Situation-detecting subprograms lie dormant until they are activated by a specific constellation of cues that precipitates the analysis of whether a particular ancestral situation has arisen. If the assessment is positive, it sends the signal that activates the associated emotion program. Emotion demons need two kinds of subroutines:

a. *Algorithms that monitor for situation-defining cues*. These programs include perceptual mechanisms, proprioceptive mechanisms, and situation-representing mechanisms. They take the cues in point 3 above as input.

b. *Algorithms that detect situations*. These programs take the output of the monitoring algorithms and targeted memory registers in point a as input, and through integration, probabilistic weighting, and other decision criteria, identify situations as absent or present with some probability and with some index of the magnitude of the fitness consequences inherent in the situation.

The assignment of a situation interpretation to present circumstances involves a problem in signal detection theory (Tooby & Cosmides, 1990a; Swets, Tanner, & Birdsall, 1961; see also Gigerenzer & Murray, 1987). Animals should be designed to detect what situation they are in on the basis of cues, stored regulatory variables, and specialized interpretation algorithms. Selection will not shape decision rules so that they act solely on the basis of what is most likely to be true, but rather on the basis of the weighted consequences of acts, given that something is held to be true. Should you walk under a tree that might conceal a predator? Even if the algorithms assign a 51% (or even 98%) probability to the tree's being leopard-free, under most circumstances an evolutionarily well-engineered decision rule should cause you to avoid the tree—to act as if the leopard were in it. The benefits of calories saved via a shortcut, scaled by the probability that there is no leopard in the tree, must be weighed against the benefits of avoiding becoming catfood, scaled by the probability that there is a leopard in the tree. Because the costs and benefits of false alarms, misses, hits, and correct rejections are often unequal, the decision rules may still treat as true situations that are unlikely to be true. In the modern world, this behavior may look "irrational" (as is the case with many phobias), but we do it because such decision biases were adaptive under ancestral conditions, given ancestral payoff asymmetries. That is, they were "ecologically rational" (Tooby & Cosmides, 1990a; Haselton & Buss, 2003).

Situation-detecting algorithms can be of any degree of complexity, from demons that monitor single cues (e.g., "snake present") to algorithms that carry out more complex cognitive assessments of situations and conditions (LeDoux, 1995; Lazarus & Lazarus, 1994; Tooby & Cosmides, 1990a). Inherent in this approach is the expectation that the human mind has a series of evolved subsystems designed to represent events in terms of evolutionarily recurrent situations and situational subcomponents. The operations of these representational systems are not necessarily consciously accessible. By their structure, they impose an evolutionary organization on representational spaces that are updated by data inputs. When the representational space assumes certain configurations, an interpretation is triggered that activates the associated emotion program—corresponding approximately to what others have called a "cognitive appraisal" (see, e.g., Lazarus & Lazarus, 1994). It is important to recognize that the evolutionary past frames the experienced present, because these situation-detecting algorithms provide the dimensions and core elements out of which many cross-culturally recurring representations of the world are built. To some extent, the world we inhabit is shaped by the continuous interpretive background commentary provided by these mechanisms.

5. *Algorithms that assign priorities*. A given world state may correspond to more than one situation at a time; for example, you may be nutritionally depleted *and* in the presence of a predator. The prioritizing algorithms define which emotion modes are compatible (e.g., hunger[2] and boredom) and which are mutually exclusive (e.g., feeding and predator escape). Depending on the relative importance of the situations and the reliability of the cues, the prioritizing algorithms decide which emotion modes to activate and deactivate, and to what degree. Selection, through ancestral mutant experiments, would have sorted emotions based on the average importance of the consequences stemming from each, and the extent to which joint activation was mutually incompatible or facilitating. (Prioritizing algorithms can be thought of as a supervisory system operating over all of the emotions.)

6. *An internal communication system*. Given that a situation has been detected, the internal communication system sends a situation-specific signal to all relevant programs and mechanisms; the signal switches them into the appropriate adaptive emotion mode. In addition, information is fed back into the emotion program from other programs and systems that assess body states and other regulatory variables, which may govern the intensity, trajectory, supplantation, or termination of the emotion. Along with the sensorium and motivational systems, the emotions are embedded in and partly responsible for what might be called "feeling computation." In this view, the richly textured representations we experience as feeling constitute our conscious access to a high-bandwidth system of computational devices and program interfaces that amalgamate

valuation information with other representations to guide decision making and to recalibrate decisions in an ongoing way (see, e.g., Tooby et al., 2003).

Some modes of activation of the psychological architecture are accompanied by a characteristic feeling state, a certain quality of experience. The fact that we are capable of becoming aware of certain physiological states—our hearts thumping, bowels evacuating, stomachs tightening—is surely responsible for some of the *qualia* evoked by emotion states that entrain such responses. The fact that we are capable of becoming aware of certain mental states—such as the magnitude of certain regulatory variables or the retrieved memories of past events—is probably responsible for other *qualia*. In our view, the characteristic feeling state that accompanies an emotion mode results (in part) from mechanisms that allow us to sense the signal activating and deactivating the relevant programs, as well as signals communicating necessary parameters and variable magnitudes to the various programs. Such internal sensory mechanisms—analogous to proprioception—can be selected for if there are mechanisms requiring as input the information that a particular emotion mode has been activated. (This might be true, for example, of mechanisms designed to inhibit certain stimulus-driven actions when the conditions are not auspicious.)

7. *Each program and physiological mechanism entrained by an emotion program must have associated algorithms that regulate how it responds to each emotion signal*. These algorithms determine whether the mechanism should switch on or switch off, and if on, what emotion-specialized performance it will implement. For example, there should be algorithms in the auditory system that, upon detecting the fear signal (see point 6), reset signal detection thresholds, increasing acuity for predator-relevant sounds.

WHAT KINDS OF PROGRAMS CAN EMOTIONS MOBILIZE?

Any controllable biological or neurocomputational process that, by shifting its performance in a specifiable way, would lead to enhanced average fitness outcomes should have come to be partially governed by emotional state (see point 7 above). Some such processes are discussed in this section.

Goals

The cognitive mechanisms that define goal states and choose among goals in a planning process should be influenced by emotions. For example, vindictiveness—a specialized subcategory of anger—may define "injuring the offending party" as a goal state to be achieved. (Although the evolved functional logic of this process is deterrence, this function need not be represented, either consciously or unconsciously, by the mechanisms that generate the vindictive behavior.)

Motivational Priorities

Mechanisms involved in hierarchically ranking goals or calibrating other kinds of motivational and reward systems should be emotion-dependent. What may be extremely unpleasant in one state, such as harming another, may seem satisfying in another state (e.g., aggressive competition may facilitate counterempathy). Different evolutionarily recurrent situations predict the presence—visible or invisible—of different opportunities, risks, and payoffs, so motivational thresholds and valences should be entrained. For example, a loss of face should increase the motivation to take advantage of opportunities for status advancement, and should decrease attention to attendant costs.

Information-Gathering Motivations

Because establishing which situation one is in has enormous consequences for the appropriateness of behavior, the process of detection should in fact involve specialized inference procedures and specialized motivations to discover whether certain suspected facts are true or false. What one is curious about, what one finds interesting, and what one is obsessed with discovering should all be emotion-specific.

Imposed Conceptual Frameworks

Emotions should prompt construals of the world in terms of concepts that are appropriate to the decisions that must be made. When one is angry, domain-specific concepts such as social agency, fault, responsibility, and punishment will be assigned to elements in the situation. When one is hungry, the food–nonfood distinction will seem salient. When one is endangered, safety categorization frames will appear. The world will be carved up into categories based partly on what emotional state an individual is in.

Perceptual Mechanisms

Perceptual systems may enter emotion-specific modes of operation. When one is fearful, acuity of hearing may increase. Specialized perceptual inference systems may be mobilized as well: If you've heard rustling in the bushes at night, human and predator figure detection may be particularly boosted, and not simply visual acuity in general. In fact, nonthreat interpretations may be depressed, and the same set of shadows will "look threatening"—that is, given a specific threatening interpretation such as "a man with a knife"—or not, depending on emotion state.

Memory

The ability to call up particularly appropriate kinds of information out of long-term memory ought to be influenced. A woman who has just found strong evidence that her husband has been unfaithful may find herself flooded by a torrent of memories about small details that seemed meaningless at the time but that now fit into an interpretation of covert activity. We also expect that what is stored about present experience will also be differentially regulated. Important or shocking events, for example, may be stored in great detail (as has been claimed about "flashbulb memories"), but other, more moderate emotion-specific effects may occur as well.

Attention

The entire structure of attention, from perceptual systems to the contents of high-level reasoning processes, should be regulated by emotional state. If you are worried that your spouse is late and might have been injured, it is hard to concentrate on other ongoing tasks (Derryberry & Tucker, 1994), but easy to concentrate on danger scenarios. Positive emotions may broaden attentional focus (Fredrickson, 1998).

Physiology

Each organ system, tissue, or process is a potential candidate for emotion-specific regulation, and "arousal" is insufficiently specific to capture the detailed coordination involved. Each emotion program should send out a different pattern of instructions (to the face and limb muscles, the autonomic system, etc.), to the extent that the problems embedded in the associated situations differ. This leads to an expectation that different constellations of effects will be diagnostic of different emotion states (Ekman, Levenson, & Friesen, 1983). Changes in circulatory, respiratory, and gastrointestinal functioning are well known and documented, as are changes in endocrinological function. We expect thresholds regulating the contraction of various muscle groups to change with certain emotion states, reflecting the probability that they will need to be employed. Similarly, immune allocation and targeting may vary with disgust, with the potential for injury, or with the demands of extreme physical exertion.

Communication and Emotional Expressions

Emotion programs are expected to mobilize many emotion-specific effects on the subcomponents of the human psychological architecture relevant to communication. Most notably, many emotion programs produce characteristic species-typical displays that broadcast to others the emotion state of an individual (Ekman, 1982). Ekman and his colleagues have established in a careful series of landmark studies that many emotional expressions are human universals, both generated and recognized reliably by humans everywhere they have been tested (Ekman, 1994). Indeed, many emotional expressions appear to be designed to be informative, and these have been so reliably informative that humans have coevolved automated interpreters of facial displays of emotion, which decode these public displays into knowledge of others' mental states.

Two things are communicated by an authentic emotional expression:[3] (1) that the associated emotion program has been activated in an individual, providing observers with information about the state of that individual's mental programs and physiology (e.g., "I am afraid"); and (2) the identity of the evolutionarily recurrent situation being faced, in the estimation of the signaler (e.g., the local world holds a danger). Both are highly informative, and emotional expressions provide a continuous commentary on the underlying meaning of things to companions. This provokes the question: Why did selection build facial, vocal, and postural expressions at all? More puzzlingly, why are they often experienced as automatic and involuntary? The apparent selective disadvantages of honestly and automatically broadcasting one's emotional state have led Fridlund (1994), for example, to argue that expressions must be voluntary and intentional communications largely unconnected to emotion state. But even when people deliberately lie, microexpressions of face and voice often leak out (Ekman, 1985), suggesting that certain emotion programs do in fact create involuntarily emitted signals that reliably broadcast the person's emotion state and that are difficult to override. Why?

First, natural selection has shaped emotion programs to signal their activation, or not, on an emotion-by-emotion basis. For each emotion program considered by itself (jealousy, loneliness, disgust, predatoriness, parental love, sexual attraction, gratitude, fear), there was a net benefit or cost to having others know that mental state, averaged across individuals over evolutionary time. For those recurrent situations in which, on average, it was beneficial to share one's emotion state (and hence assessment of the situation) with those one was with, species-typical facial and other expressions of emotion were constructed by selection. For example, fear was plausibly beneficial to signal, because it signaled the presence of a danger that might menace one's kin and cooperators as well, and it also informed others in a way that might recruit assistance. Guilt was not selected to cause a presentation with an unambiguous, distinctive signal.

Nevertheless, averaged over evolutionary time, it was functional for the organism to signal the activation of only *some* emotion states. The conditions favoring signaling an emotion are hard to meet (for conditions and discussion, see Tooby & Cosmides, 1996b; Cosmides & Tooby, 2000a). Consequently, only some emotions out of the total species-typical set are associated with distinctive, species-typical facial expressions. There should be a larger set of emotions that have no automatic display. Moreover, emotions that lack a display are not necessarily less fundamental or less anchored in the evolved architecture of the human mind. For this reason, the existence of a distinctive expression is not a necessary aspect of an emotion, nor should it be part of its definition. Jealousy and guilt are both genuine emotions lacking distinctive signals.

Precisely because we are designed to monitor broadcast emotions, our attention goes disproportionately to the subset of emotions that do come equipped with emotional expressions. We think it likely that this has had an impact on the history of emotion research—specifically, that the emotions associated with distinctive expressions have been unnecessarily considered "primary" or "fundamental."

Finally, many features of facial expressions may not just be arbitrary, but may be reliable indicators of an emotion state. Many seem to be functional concomitants of the activity associated with the emotion (such as eyes widening or hyperventilation). Others may be signals that are nonarbitrary; that is, they remove barriers to the correct assessment of aspects of the phenotype that the organism benefits by demonstrating. For example, the anger expression may be designed to maximize the perception of strength—an advertisement of a property relevant to the negotiation, and not just an arbitrary signal to others that one is angry (Sell, Tooby, & Cosmides, in press-b). That is, there may be functional reasons why the anger face has the characteristics it does, rather than consisting of ear flapping or nose twitching. Similarly, the baring of teeth may be combat preparation and advertisement (Archer, 1988); the narrowing of the pupil may be preparation for the detection of fast motion; and so on.

Behavior

All psychological mechanisms are involved in the generation and regulation of behavior, so obviously behavior will be regulated by emotion state. More specifically, however, mechanisms proximately involved in the generation of actions (as opposed to such processes as face recognition, which are only distally regulatory) should be very sensitive to emotion state. Not only may highly stereotyped behaviors of certain kinds be released (as during sexual arousal or rage, or as with species-typical facial expressions and body language), but more complex action generation mechanisms should be regulated as well. Specific acts and courses of action will be more available as responses in some states than in others, and more likely to be implemented. Emotion mode should govern the construction of organized behavioral sequences that solve adaptive problems.

Biologists, psychologists, and economists who adopt an evolutionary perspective have recognized that game theory can be used to model many forms of social interactions (Maynard Smith, 1982). If the EEA imposes certain evolutionarily repeated games, then the "strategies" (the evolved cognitive programs that govern behavior in those contexts) should evolve in the direction of choices that lead to the best expected fitness payoffs. The strategy activated in the individual should match the game (e.g., exchange) and the state of play in the game (e.g., having just been cheated)—a process that requires the system of cues, situation detection, and so on, already discussed. So different emotion and inference programs or subprograms may have evolved to correspond to various evolved games, including zero-sum competitive games, positive-sum exchange games, coalitional lottery games, games of aggressive competition corresponding to "chicken," and so on (for exchange, see Cosmides, 1989; Cosmides & Tooby, 1992). Corresponding emotion programs guide the individual into the appropriate interactive strategy for the social "game" being played, given the state of play. Surprisingly, for some games, rigid obligatory adherence to a prior strategy throughout the game is better than the ability to revise and change strategies ("voluntarily") in the light of events. If an individual contemplating a course of action detrimental to you knows you will take revenge, regardless of the magnitude of the punishment to you that this might unleash, then that individual will be less likely to take such harmful action. This may translate into emotion programs in which the desire to attempt certain actions should be overwhelming, to the point where the actions are experienced as compulsory. In the grip of such programs, competing programs, including the normal integration of prudential concerns and social consequences, are muted or terminated. For example, the desire to avenge a murder or an infidelity is often experienced in this way, and crimes resulting from this desire are even culturally recognized as "crimes of passion" (Daly & Wilson, 1988). In modern state societies, where there are police who are paid to punish and otherwise enforce agreements, it is easy to underestimate the importance that deterrence based on the actions of oneself and one's coalition had in the Pleistocene (Chagnon, 1983). Hirshleifer (1987) and Frank (1988) are evolutionary economists who have pursued this logic the furthest, arguing that many social behaviors are the result of such "commitment problems."

Specialized Inference

Research in evolutionary psychology has shown that "thinking" or reasoning is not a unitary category, but is carried out by a variety of specialized mechanisms. So, instead of emotion's activating or depressing "thinking" in general, the specific emotion program activated should *selectively* activate appropriate specialized inferential systems, such as cheater detection (Cosmides, 1989; Cosmides & Tooby, 1989, 1992), bluff detection (Cosmides & Tooby, 1989), precaution detection (Fiddick, Cosmides, & Tooby, 2000), attributions of blame and responsibility, and so on. For example, fear could influence precautionary reasoning (Boyer & Liénard, 2006), competitive loss could regulate bluff detection, and so on.

Reflexes

Muscular coordination, tendency to blink, threshold for vomiting, shaking, and many other reflexes are expected to be regulated by emotion programs to reflect the demands of the evolved situation.

Learning

Emotion mode is expected to regulate learning mechanisms. What someone learns from stimuli will be greatly altered by emotion mode, because of attentional allocation, motivation, situation-specific inferential algorithms, and a host of other factors. Emotion mode will cause the present context to be divided up into situation-specific, functionally appropriate categories so that the same stimuli and the same environment may be interpreted in radically different ways, depending on emotion state. For example, which stimuli are considered similar should be different in different emotion states, distorting the shape of the individual's psychological "similarity space" (Shepard, 1987). Highly specialized learning mechanisms may be activated, such as those that control food aversions (Garcia, 1990), predator learning (Mineka & Cook, 1993), or fear conditioning (LeDoux, 1995). Happiness is expected to signal the energetic opportunity for play, and to allow other exploratory agendas to be expressed (Frederickson, 1998).

Mood, Energy Level, Effort Allocation and Depression

Overall metabolic budget will be regulated by emotion programs, as will specific allocations to various processes and facilitation or inhibition of specific activities. The effort that it takes to perform given tasks will shift accordingly, with things being easier or more effortful, depending on how appropriate they are to the situation reflected by the emotion (Tooby & Cosmides, 1990a). Thus fear will make it more difficult to attack an antagonist, whereas anger will make it easier. The confidence with which a situation has been identified (i.e., emotional clarity) should itself regulate the effortfulness of situation-appropriate activities. Confusion (itself an emotional state) should inhibit the expenditure of energy on costly behavioral responses and should motivate more information gathering and information analysis. Nesse (1991) has suggested that the function of mood is to reflect the propitiousness of the present environment for action—a hypothesis with many merits. We have hypothesized (Tooby & Cosmides, 1990a) a similar function of mood, based on recognizing that the action–reward ratio of the environment is not a function of the environment alone, but an interaction between the structure of the environment and the individual's present understanding of it. (By "understanding," we mean the correspondence between the structure of the environment, the structure of the algorithms, and the weightings and other information they use as parameters.) The phenomenon that should regulate this aspect of mood is a perceived discrepancy between expected and actual payoff. The suspension of behavioral activity accompanied by very intense cognitive activity in depressed people looks like an effort to reconstruct models of the world so that future action can lead to payoffs, in part through stripping away previous valuations that led to unwelcome outcomes. Depression should be precipitated by (1) a heavy investment in a behavioral enterprise that was expected to lead to large payoffs that either failed to materialize or were not large enough to justify the investment; or (2) insufficient investment in maintaining a highly valued person or condition that was subsequently lost (possibly as a consequence); or (3) gradual recognition by situation detectors that one's long-term pattern of effort and time expenditure has not led to a sufficient level of evolutionarily meaningful reward, when implicitly compared to alternative life paths (the condition of Dickens's Scrooge). Discrepancies between expected and actual payoff can occur in the other direction as well: Joy, or a precipitated surge of happiness, is an emotion program that evolved to respond to the condition of an unexpectedly good outcome. It functions to recalibrate previous value states that led to underinvestment in or underexpectation for the successful activities or choices. Moreover, energy reserves that were being sequestered under one assumption about future prospects can be released, given new, more accurate expectations about a more plentiful or advantageous future. Similarly, one can be informed of bad outcomes to choices not made: For example, one may find out that a company one almost invested in went bankrupt, or that the highway one almost took was snowed in. Information of this kind leads to a strengthening of the decision variables used (experienced as pleasure), which is sometimes mistaken for pleasure in the misfortune of others. Reciprocally, one can be informed of good outcomes to choices not made, which will be experienced as unpleasant.

Moreover, the functional definition of emotion given here invites the possibility that many well-known mental states should be recognized as emotion states—such as the malaise engendered by infectious illness, coma, shock, the appreciation of beauty, homesickness, sexual arousal, confusion, nausea, and so on. For example, when you are sick, initiating actions and going about your daily activities is more effortful than usual; your impulse is to stay home and lie still. Although you feel as if your energy reserves are depleted, at a physical level the same fat reserves and digestively delivered glucose are available. Malaise is a computational state, not a physical one, and is designed to cope with the adaptive problem of illness: It shunts energy from behavior to the immune system, and possibly signals the need for aid. Similarly, when situation-detecting algorithms detect the presence of a very grave internal injury, or the potential for one as indicated by a major blow, these may trigger a mode of operation of the psychological architecture that is designed to prevent *any* discretionary movement:

coma. The function of coma, in a world before hospitals, was to prevent further injury from being done, minimize blood loss and internal hemorrhaging, and allow the mobilization of the body's resources toward repair of immediate threats to life. Note that a coma is not a physically mandated state of paralysis; it is a computational state—technically, "a state of unconsciousness from which the patient cannot be roused" (Miller, 1976, p. 46), or "unarousable unresponsiveness" (Berkow, 1992, p. 1398). It can occur even when there has been no damage to the motor system.

INTERNAL REGULATORY VARIABLES AND FEELING COMPUTATION

We expect that the architecture of the human mind, by design, is full of registers for evolved variables whose function is to store summary magnitudes that are useful for regulating behavior and making inferences involving valuation. These are not explicit concepts, representations, goal states, beliefs, or desires, but rather indices that acquire their meaning via the evolved behavior-controlling and computation-controlling procedures that access them. That is, each has a location embedded in the input–output relations of our evolved programs, and their function inheres in the role they play in the decision flow of these the programs.

For example, in our recent mapping of the architecture of the human kin detection system, we have identified a series of regulatory variables needed to make the system work functionally and to explain the data (Lieberman et al., 2007). For example, for each familiar individual *i*, the system computes and updates a continuous variable, the "kinship index" (K_i), which corresponds to the system's pairwise estimate of genetic relatedness between self and *i*. When the kinship index is computed or updated for a given individual, the magnitude is taken as input to procedures that are designed to regulate kin-relevant behaviors in a fitness-promoting way. For the case of altruism, the kinship index is fed as one of many inputs to the "welfare tradeoff ratio estimator," whose function is to compute a magnitude, the "intrinsic welfare tradeoff ratio" ($_{int}WTR_i$), which regulates the extent to which the actor is intrinsically disposed to trade off his or her own welfare against that of individual *i*. A high kinship index up-regulates the weight put on *i*'s welfare, while a low kinship index has little effect on the disposition to treat *i* altruistically. This is one element that up-regulates the emotion of love, attachment, or caring. Independently, the kinship index is fed as one of many inputs into the "sexual value estimator." Its function is to compute a magnitude, "sexual value" (SV_i), which regulates the extent to which the actor is motivated to value or disvalue sexual contact with individual *i*. As with altruism, many factors (e.g., health, age, symmetry) affect sexual value, but a high kinship index renders sexual valuation strongly negative, while a low kinship index is expected to have little effect on sexual valuation. The system takes as input two cues, whose values must themselves be stored and updated as regulatory variables. The first is maternal perinatal association (i.e., whether an older sibling observes his or her mother caring for a younger sibling as an infant), and the second is duration of coresidence between birth and the end of the period of parental investment. These two cues are processed to set the value of the kinship index for each familiar childhood companion. This system was designed by natural selection to detect which familiar others were close genetic relatives; to create a magnitude corresponding to the degree of genetic relatedness; and then to deploy this information to motivate both a sexual aversion between brothers and sisters, and a disposition to behave altruistically toward siblings.

An internal regulatory variable like the kinship index or the welfare tradeoff ratio acquires its meaning and functional properties fromits relationship to the programs that compute it, and from the downstream decisions or processes that it regulates. The claim is not that such computations and their embedded variables are deliberate or consciously accessible. We think that they are usually nonconscious or implicit. Outputs of processes that access these variables may be consciously experienced—as disgust (at the prospect of sex with a sibling), affection for them, fear (on their behalf), grief (at their loss), and so on. Indeed, we think that it may be possible eventually to arrive at a precise description of computational understructure subserving the world of feeling, by considering feeling to be a special form of computation that evolved to deal with the world of valuation.

Because the computational mapping of motivational systems and emotion programs is a new enterprise, at present it is difficult to know the full range of internal regulatory variables that our psychological architecture is designed to compute and access. On adaptationist grounds, we suspect that the full set may include a surprising variety of registers for specialized magnitudes, corresponding to such things as these: how valuable a mate is, a child is, one's own life is, and so on; how stable or variable the food supply is over the long term; the distribution of condition-independent mortality in the habitat; one's expected future lifespan or period of efficacy; how good a friend someone has been to you; the extent of one's social support; the aggressive formidability for self or others (i.e., the ability to inflict costs); the sexual value of self and others; one's status, as well as the status of the coalition one belongs to; present energy stores; one's present health; the degree to which subsistence requires collective action; and so on. However, even focusing on one small set of internal regulatory variables, welfare tradeoff ratios, offers to clarify the functional architecture of several emotions, including anger, guilt, and gratitude.

ANGER AS AN EVOLVED REGULATORY PROGRAM

Consistent with the views of many other researchers, we have hypothesized that anger is an evolved emotion program with a special relationship to aggression. However, we think that it has an equal relationship to cooperation. In the evolutionary-psychological approach to the emotions, anger (in addition to being an experienced psychological state) is the expression of a functionally structured neurocomputational system whose design features and subcomponents evolved to regulate thinking, motivation, and behavior in the context of resolving conflicts of interest in favor of the angry individual (Sell, 2005; Sell, Tooby, & Cosmides, in press-a, in press-b). Two negotiating tools regulated by this system are the threat of inflicting costs (aggression) and the threat of withdrawing benefits (the down-regulation of cooperation). Humans differ from most other species in the number, intensity, and duration of close cooperative relationships, so traditional models of animal conflict must be modified to integrate the cooperative dimension more fully. Given its apparent functional logic, its universality across individuals and cultures (Ekman, 1973; Brown, 1991), and its early ontogenetic development (Stenberg, Campos, & Emde, 1983; Stenberg & Campos, 1990), it seems likely that anger is an adaptation designed by natural selection. If so, then its computational structure (i.e., what variables cause anger, what behavioral patterns are enacted by it, and what variables cause it to subside) might be usefully illuminated by testing predictions derived by reference to the selection pressures that designed them.

Humans evolved embedded in small-scale social networks involving both cooperation and conflict. In many situations, each individual has open to him or her a range of alternative behaviors that embody—as one dimension—a spectrum of possible tradeoffs between the individual's own welfare and the welfare of one or more others. By choosing one course of conduct, the individual is intentionally or unintentionally expressing what can be termed a welfare tradeoff ratio with respect to the affected party or parties. For example, an individual might act in a way that weights the welfare of another person slightly or not at all (e.g., being late, theft, marital abandonment, rape, burning down someone's house for the fun of it), in a way that balances the two, or in a way that minimizes one's own welfare by sacrificing one's life for the other party. In this view, humans have a system that, in each individual, computes the welfare tradeoff ratio expressed in the actions of that person toward another (individual *i* to *j*), and stores it as a summary characterization of *i*'s disposition toward *j* in the form of a regulatory variable—the welfare tradeoff ratio of *i* to *j* (WTR_{ij}). Indeed, there are at least two parallel, independent welfare tradeoff ratios: the intrinsic one ($_{int}WTR$), which guides an individual's behavior toward another, regardless of whether his or her actions are being observed; and the public one ($_{public}WTR$), which guides an individual's behavior when the recipient (or others) can observe the behavior. Some altruism is motivated through love, and some through fear, shame, or hope of reward—and the mechanisms involved are different.

If the human mind really contains welfare tradeoff ratios as regulatory variables that control how well one individual treats another, then evolution can build emotions whose function is to alter welfare tradeoff ratios in others toward oneself. Anger is conceptualized as a mechanism whose functional product is the recalibration in the mind of another of this other person's welfare tradeoff ratio with respect to oneself. That is, the goal of the system (rather than a conscious intention) is to change the targeted person's disposition to make welfare tradeoffs so that he or she more strongly favors the angered individual in the present and the future. As in animal contests, the target of anger may relinquish a contested resource, or may simply in the future be more careful to help or to avoid harming the angered individual. In cooperative relationships, where there is the expectation that the cooperative partner will spontaneously take the welfare of the individual into account, the primary threat from the angered person that potentially induces recalibration in the targeted individual is the signaled possibility of the withdrawal of future help and cooperation if the welfare tradeoff ratio is not modified. If the withdrawal of this cooperation would be more costly to the target of the anger than the burden of placing greater weight on the welfare of the angry individual, then the target should increase his or her welfare tradeoff ratio toward the angry individual, and so treat her or him better in the future.

Reciprocally, the program is designed to recalibrate the angry individual's own welfare tradeoff ratio toward the target of the anger for two functional reasons. This first is that it curtails the wasteful investment of cooperative effort in individuals who do not respond with a sufficient level of cooperation in return. The second is that the potential for this downward recalibration functions as leverage to increase the welfare tradeoff ratio of the target toward the angry individual. In the absence of cooperation, the primary threat is the infliction of damage. In the presence of cooperation, the primary threat is the withdrawal of cooperation. Concepts that are anchored in the internal regulatory variable ${}_{public}WTR$ include respect, consideration, deference, status, rank, and so on.

For example, ancestrally, one major cue that an individual would have been able to inflict costs to enforce welfare tradeoff ratios in his or her favor was the individual's physical strength (as noted earlier, we call the ability to inflict costs "formidability"). Consistent with this, in many species the degree to which an organism values a nonrelative is determined primarily by the relative strength of the two; thus animals with higher relative strength will, when other factors are held constant, fight more effectively for resources and have a higher expectation of gaining a larger share of disputed resources or social rank. Because strength was consistently one factor (out of several) relevant under ancestral conditions, and the nervous system had reliable access to the body, it seems plausible and worth investigating that the mind is designed to compute a strength self-assessment automatically and nonconsciously, and to use this self-assessment as an input regulating behavior. Thus the human brain should have evolved a set of programs that (1) evaluates one's own and other's formidabilities; (2) transforms each of these evaluations into a magnitude (a "formidability index") associated with each person; and, in situations where cooperation is not presumed, (3) implicitly expects or accords some level of deference based on relative formidability.

The approach briefly sketched above can be unpacked into a large number of empirical predictions derived from this analysis of the design features of the program regulating anger. For example, it is predicted that in humans, physical strength should be a partial cause of individual differences in the likelihood of experiencing and expressing anger. Other things being equal, stronger individuals are predicted to be more likely to experience anger and express anger; they should feel more entitled; they should expect others to give greater weight to their welfare, and become angrier when they do not. Although physical strength by no means exhausts the set of relevant variables, it offers an easily operationalizable and measurable gateway into a series of tests of this general model of the logic underlying the regulation of anger. Arguments precipitated by anger should reflect the underlying logic of the welfare tradeoff ratio: The complainant will emphasize the cost of the other's transgression to him or her, as well as the value of the complainant's cooperation to the transgressor, and will feel more aggrieved if the benefit the transgressor received (the justification) is small compared to the cost inflicted. A series of empirical studies supports both sets of predictions of this theory about the design of anger (Sell, 2005; Sell et al., in press-a, in press-b).

RECALIBRATIONAL EMOTIONS SUCH AS GUILT AND GRATITUDE

The EEA was full of event relationships (e.g., "Mother is dead") and psychophysical regularities (e.g., "Blood indicates injury") that cued reliable information about the functional meanings and properties of things, events, persons, and regulatory variables to the psychological architecture. For example, certain body proportions and motions indicated immaturity and need, activating the emotion program of experiencing cuteness (see Eibl-Ebesfeldt, 1970). Others indicated sexual attractiveness (Symons, 1979; Buss, 1994). To be moved with gratitude, to be glad to be home, to see someone desperately pleading, to hold one's newborn baby in one's arms for the first time, to see a family member leave on a long trip, to encounter someone desperate with hunger, to hear one's baby cry with distress, to be warm while it is storming outside—these all *mean* something to us. How does this happen? In addition to the situation-detecting algorithms associated with major emotion programs such as fear, anger, or jealousy, we believe that humans have a far larger set of evolved specializations, which we call "recalibrational releasing engines." These are activated by situation-detecting algorithms, and their function is to trigger appropriate recalibrations, including affective recalibrations, when certain evolutionarily recognizable situations are encountered.

We believe that the psychophysical or interpretive "front ends" of emotion programs use these cues not only to trigger the appropriate emotion, but to alter the weightings of regulatory variables embedded in decision rules. (For example, if you experience someone treating you disrespectfully, it makes you angry.) Indeed, most evolutionarily recurrent situations that selected for corresponding emotion programs bristle with information that allows the recomputation of one or more variables. Recalibration (which, when consciously accessible, appears to produce rich and distinct feeling states) is therefore a major functional component of most emotion programs. Jealousy, for example, involves several sets of recalibrations (e.g., diminution in estimate of one's own mate value, diminution of trust, lowering of the welfare tradeoff ratio toward the mate).

Indeed, from an evolutionary-psychological perspective, recalibrational emotion programs appear to be the dominant (but not the only) components of such emotions as guilt, grief, depression, shame, and gratitude. Their primary function is not to orchestrate any short-run behavioral response (as fear or anger do), but instead to carry out valuation recomputations in the light of the new information relevant to evolved regulatory variables that is provided by external or internal environments (Tooby & Cosmides, 1990a). An evolutionary viewpoint is a utilitarian one, which suggests that the time humans spend simply feeling—attending inwardly not to factual representations, but to something else—is doing something useful that will be reflected eventually in behavior. The hypothesis is that feeling is a form of computational activity that takes time and attention, that can compete with or preempt motivation to engage in other activities, and whose function is to recalculate and reweight the regulatory variables implicated by the newly encountered information. This approach has the potential to provide an account of the characteristics of emotions such as guilt or depression, which appear otherwise puzzling from a functional perspective. The feelings these emotion programs engender interfere with short-term utilitarian action that an active organism might be expected to engage in. If they were not useful, the capacity to feel them would have been selected out.

Consider guilt: We believe that guilt functions as an emotion mode specialized for recalibration of regulatory variables that control tradeoffs in welfare between self and other (Tooby & Cosmides, 1990a). Three important reasons why humans evolved to take the welfare of others into account are genetic relatedness toward relatives (Hamilton, 1964), the positive externalities others emit (Tooby & Cosmides, 1996a), and the maintenance of cooperative relationships (Trivers, 1971; Tooby & Cosmides, 1996a). The regulatory variable approach provides a clear framework for understanding why guilt evolved and what its underlying logic is. In this view, guilt involves the recalibration of regulatory variables considered when one is making decisions about tradeoffs in welfare between the self and others, based on new information about actual or potential harm arising from having placed too little weight on the other person's welfare in past actions. Kin selection would favor a mechanism designed to effect such recalibration toward those the kin detection mechanism identifies as close genetic relatives. Similarly, individuals have an intrinsic interest in the welfare of those whose existence benefits them, and with whom they share deep engagement relationships

(Tooby & Cosmides, 1996a). Third, reciprocal, exchange, or cooperative relationships need to be proximately motivated, so that benefit flows are appropriately titrated. Individuals who experienced guilt (and the associated modification of decision rules) would have been less likely to injure relationship partners repeatedly, and they would have had more success in maintaining beneficial cooperative relationships.

In the case of kin selection, we now have an empirical map of the architecture of the neurocomputational program that detects genetic relatedness and passes this information to the welfare tradeoff system (Lieberman et al., 2007). The theory of kin selection says nothing, however, about the procedures by which a mechanism could estimate the value of, say, a particular piece of food to oneself and one's kin. The fitness payoffs of such acts of assistance vary with circumstances. Consequently, each decision about where to allocate assistance depends on inferences about the relative weights of these variables. These nonconscious computations (however they are carried out) must be subject to error, selecting for feedback systems of correction.

Imagine a hunter–gatherer woman with a sister. The mechanisms in the woman's brain have been using the best information available to her to weight the relative values of the meat she has been acquiring to herself and her sister, leaving her reassured that it is safe to leave her sister for a while without provisioning her. The sudden discovery that her sister, since she was last contacted, has been starving and has become desperately sick functions as an information-dense situation allowing the recalibration of the algorithms weighting the relative values of the meat to self and sister (among other things). The sister's sickness functions as a cue that the previous allocation weighting was in error and that the variables need to be reweighted—including all of the weightings embedded in habitual action sequences that might be relevant to the sister's welfare. Guilt should be triggered when the individual receives (1) unanticipated information about the welfare of a valued other (or the increased value of the other), indicating that (2) the actor's actions or omissions caused or allowed the welfare of the valued individual to be damaged in a way that is inconsistent with the actor's ideal welfare tradeoff ratio, given (3) the actor's resources and potential for action. When guilt is triggered, the welfare tradeoff ratio is adjusted, as well as a variety of subsidiary variables expressing this ratio in action. As a result of this recalibration, the guilty individual's behavior should reflect this higher valuation. In cases where the effects were intentional and anticipated, there should be little recalibration.

Existing findings substantiate these predictions and explain some of their otherwise puzzling features. Unsurprisingly, when the valued other is negatively affected unexpectedly, subjects feel guiltier (Baumeister, Stillwell, & Heatherton, 1995, Kubany & Watson, 2003). More surprisingly, individuals feel guiltier when the harm was caused accidentally rather than anticipated, even though individuals are usually considered less responsible and culpable for the harm when it occurs accidentally (McGraw, 1987; Baumeister et al., 1995). If the function of guilt is, however, to recalibrate an improperly set welfare tradeoff ratio, then information that merely confirms the evaluation present in the decision requires no recalibration. If the effect was foreseen and chosen anyway in the light of the existing ratio, then no adjustment is necessary.

Gratitude is a recalibrational emotion program that is complementary to guilt. Guilt turns up the welfare tradeoff ratio toward an individual when one has evidence that one's own actions have expressed too low a valuation of the other. Gratitude is triggered by new information indicating that another places a higher value on one's welfare than one's system had previously estimated—again leading to an up-regulation of the WTR toward that person. Anger, guilt, and gratitude all play different roles in cooperation, and their computational structure reflects their recalibrational functions with respect to welfare tradeoff ratios and the choice points they involve.

The evolutionary-psychological stance motivating the investigation of the program architecture of the emotions suggests that the emotions are intricate, functionally organized, and sensitively related to the detailed structure of ancestral problems. In this view, the emotions are likely to be far more sophisticated engineering achievements than previously appreciated, and there are many decades of work ahead for emotion researchers before they are comprehensively mapped.

NOTES

1. Marks (1987, pp. 68–69) vividly conveys how many aspects of behavior and physiology may be entrained by certain kinds of fear:

> During extreme fear humans may be "scared stiff" or "frozen with fear." A paralyzed conscious state with abrupt onset and termination is reported by survivors of attacks by wild animals, by shell-shocked soldiers, and by more than 50% of rape victims (Suarez & Gallup, 1979). Similarities between tonic immobility and rape-induced paralysis were listed by Suarez & Gallup (features noted by rape victims are in parentheses): (1) profound motor inhibition (inability to move); (2) Parkinsonian-like tremors (body-shaking); (3) silence (inability to call out or scream); (4) no loss of consciousness testified by retention of conditioned reactions acquired during the immobility (recall of details of the attack); (5) apparent analgesia (numbness and insensitivity to pain); (6) reduced core temperature (sensation of feeling cold); (7) abrupt onset and termination (sudden onset and remission of paralysis); (8) aggressive reactions at termination (attack of the rapist after recovery); (9) frequent inhibition of attack by a predator . . .

2. We think that some emotion programs evolved in response to the situation cue provided by a strong drive state, such as hunger, when the motivational intensity reached a point that other mechanisms became dominated and entrained by the magnitude of the motivation. We see no principled reason for distinguishing strong drive states from other emotion programs, and suspect that this practice originated from outdated notions of natural selection that separated "survival-related" functions (hunger, thirst) from other functions, such as mate acquisition or reciprocity. Thus we propose that it is useful to model specialized motivational states as emotion programs, just as one would disgust, anger, or fear.
3. The evolutionary purpose of deceitful emotional expressions is to (falsely) communicate the same two things.

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