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Adaptationism Carves Emotions at Their Functional Joints

Daniel Sznycer[a,b], Leda Cosmides[b,c], and John Tooby[b]

[a]Department of Psychology, Arizona State University, Tempe, Arizona; [b]Center for Evolutionary Psychology, University of California, Santa Barbara, California; [c]Department of Psychological & Brain Sciences, University of California, Santa Barbara, California

We appreciate Agnes Moors's (this issue) history of the debates among classical and constructionist emotion researchers and her attempt at integration. We have been pursuing an alternative perspective that emerges from evolutionary psychology, which integrates many aspects of the theories she discusses but embraces a universalism that Moors rejects.

An adaptationist approach to the emotions takes an engineering perspective: Each emotion was designed by selection to solve problems that arose in a particular domain. That is, the detailed architecture of the emotion (the problem solver) was engineered by natural selection so that its design features functionally engaged the detailed structure of its particular adaptive problem (i.e., fear of predators reflects the dangerous properties of predators; sexual jealousy reflects the decision structure of mate choice). This means that a theory of what computational circuits each emotion will embody can be derived from analyzing the nature and properties of the emotion's associated adaptive problem. For examples involving sexual jealousy, anger, shame, pride, gratitude, pathogen disgust, and sexual disgust, see Buss (2000); Fessler, (2001); Lieberman, Tooby, and Cosmides (2007); Lim (2012); Sell, Tooby, and Cosmides (2009); Sznycer Tooby, Cosmides, Porat, Shalvi, and Halperin (2016); Sznycer et al. (2016); Tooby, Cosmides, Sell, Lieberman, and Sznycer (2008); Tyber, Lieberman, Kurzban, and DeScioli (2013); and Weisfeld and Dillon (2012).

Paradoxically, this view has led us to make many of the same points that Moors raises (Cosmides & Tooby, 2000; Tooby & Cosmides, 1990a, 2008). But they flow from the view that emotion is a fruitful scientific concept, not a mishmash of folk notions ready for the dustbin of history. We highlight five examples here.

1. It is true: Folk concepts, such as "emotion," need not pick out natural kinds. That's why it is better to study the evolved design of the computational systems that generate behavior and regulate physiology. Arguing about criteria for classifying these systems as "emotions" is pointless; questions like "What is a concept?" and "What is an emotion?" are matters of discovery, not stipulation. The systems that give rise to anger, shame, pride, gratitude, fear, jealousy, love, lust (etc.) will not have a uniform architecture defined by necessary and sufficient features. The architecture of each evolved system should reflect the computational requirements of the adaptive problem that selected for its design. Discovering the design of systems that give rise to phenomena that people think of as emotions is valuable. A good theory does not reify common sense, it explains it.

Indeed, Moors's point about the infinite variety of colors can be turned on its head. Understanding the evolved design of rods and cones, the psychophysics of similarity for color, and the visual system's color constancy mechanisms illuminates why we see grass as green at both noon and sunset (when it is bathed in "red" [long wavelength] light); why red and violet—associated with the longest and shortest wavelengths of the visual spectrum—are seen as more similar than red and green; why we experience cherries and leaves as differing in color; and why it is easier to learn color labels for categories organized around focal colors (e.g., saturated red) than nonfocal ones (such as maroon or salmon). Universality and invariance are found at the level of evolved computational design. Folk ideas and experiences about color are thereby explained, not jettisoned as irrelevant to the psychology of color (Rosch, 1973; Shepard, 1992).

2. Verbal labels can indeed be misleading: Fear of predators and fear of losing a valued relationship are probably caused by distinct computational systems, each designed to solve a different ancestral adaptive problem. The odds of discovering this are low unless your research program is guided by theories of adaptive function.

By saying that different emotions may be activated by both threats, we are not suggesting that researchers should endlessly multiply emotions of fear by adding a new label for each stimulus that can elicit it. If both situations flip mechanisms regulating attention, perception, inference, memory, goals, learning, behavior, physiology (etc.) into the same configuration, it would be more sensible to invoke a single emotion—fear—that can be activated by two distinct monitoring systems: one that sifts for cues that you are in danger from predators and another that sifts for cues that your relationships are in jeopardy.

In our view, *emotions are superordinate programs that evolved to solve problems of mechanism coordination* (Cosmides & Tooby, 2000; Tooby & Cosmides, 1990a, 2008). The mind is a crowded zoo of functionally specialized programs, many endowed with content-rich procedures that are good at solving one kind of adaptive problem, but useless or even counterproductive if activated in response to others. Visual attention includes a category-specific system that monitors the location and state of nonhuman animals (New, Cosmides, & Tooby,

CONTACT Daniel Sznycer dsznycer2@gmail.com Department of Psychology, Arizona State University, Tempe, AZ 85287-1104, USA.

2007), another for monitoring angry outgroup members (Ackerman et al., 2006), and others that select sexually attractive people for further processing (Maner et al., 2003). There are perceptual systems for recognizing faces (Duchaine, Yovel, Butterworth, & Nakayama, 2006) and parsing speech (Poeppel & Monahan, 2008), and spatial adaptations for foraging that are activated by resources with high caloric density (New, Krasnow, Truxaw, & Gaulin, 2007). Inference systems specialized for detecting cheaters in social exchange (Cosmides & Tooby, 2008) are useless for reasoning about object mechanics, which is governed by a different system (Baillargeon, Li, Gertner & Wu, 2011; Leslie, 1994; Spelke, 1990); both coexist alongside systems specialized for reasoning about precautionary rules (Boyer & Lienard, 2006; Fiddck, Cosmides, & Tooby, 2000; Szechtman & Woody, 2004), inferring mental states (Baron-Cohen, 1995), and learning which animals are dangerous (Barrett & Broesch, 2012). The mind has concepts that distinguish free riders from those who try but fail (Delton Cosmides, Guemo, Robertson, & Tooby, 2012); alternative sharing rules when resources acquired by luck versus effort (Aarøe & Petersen, 2014; Kaplan, Schniter, Smith & Wilson, 2012; Petersen, 2012; Petersen, Sznycer, Cosmides, & Tooby, 2012); and different cooperative strategies for collective action and dyadic trade (Baumard, 2016; Krasnow, Cosmides, Pedersen, & Tooby, 2012; Masclet, Noussair, Tucker, & Villeval, 2003; Robertson, Delton, Klein, Cosmides, & Tooby, 2014). And so on.

If there is a neurocognitive system that flips a large number of mechanisms (what Moors calls "components") into a configuration well-engineered for evading predators, we would call that an emotion: fear of predators. That emotion can be expected to hyperactivate the attention system that monitors animals and deactivate the ones that monitor angry outgroup members and potential sexual partners; it should shift auditory signal detection thresholds and activate inference systems for distinguishing wind in the grass from a stalking lion; mechanisms that scan the landscape for escape routes should be activated; conceptual frameworks that tag locations as safe or dangerous should come online; search engines should retrieve data from memory about dangerous animals; cortisol should facilitate glucose release; physiology should shift in ways that promote escape or, failing that, attack. Mechanisms that activate courtship activities, promote efficient foraging, or cause you to fall asleep should be deactivated by that emotion because they will interfere with efficient predator evasion.

The fitness cost of failing to evade predators is high; to successfully solve this problem, the mind's many subprograms need to be orchestrated so that their joint product is functionally coordinated rather than cacophonous and self-defeating. Predator fear is the emotion that solves this coordination problem. It entrains many different "components," adjusting their thresholds and parameters, and shuts off others. This configuration—this particular mode of activation of the cognitive system—can be recognized as predator fear because its computational architecture is very well engineered for detecting and evading predators. That is the ancestral adaptive problem that selected for its design.

Let's assume for the moment that the configuration of mechanisms that is the best-bet solution for avoiding predators is ill-suited for preventing the imminent loss of a friend. Assume further that preventing that loss requires the coordinated activation of many mechanisms: stronger activation of the mind-reading system in her presence, heightened vigilance to social cues, an appetite for gossip about who else she is spending time with, search engines scouring memory for episodes in which you sacrificed for her benefit (or failed to), the up-regulation of variables regulating how much weight to put on her welfare in future decisions, increased motivation to help her, deactivation of programs motivating courtship and dominance striving (etc.). If that configuration is different from the one elicited by cues that you are in danger of becoming prey, then the superordinate program generating this configuration would be a distinct emotion: fear of losing a cooperative partner.

That some people use the word "fear" to refer to both of these emotions is irrelevant. This folk use could represent a conceptual metaphor (Pinker, 2010)—both emotions are systems designed to avoid a bad situation—or reflect the fact that a few of the same components are activated and deactivated by both emotions, generating some similarities in felt experience.

3. In rejecting the scientific status of emotion, Moors reviews evidence against the claim that there is an invariant relationship between the activation of an emotion and a specific facial expression. We agree that facial expressions can be a misleading way of deciding what counts as an emotion, but for the same reason that verbal labels are misleading.

Discovering that a lover has been unfaithful and discovering that a friend failed to reciprocate a favor may both elicit an anger expression, but sexual jealousy activates a different *constellation* of cognitive systems than social exchange (Buss, 2000; Cosmides & Tooby, 2008, 2015). Anger expressions can occur in both cases because they communicate the implicit threat to impose harm or withdraw benefits—bargaining tactics designed to continue the relationship but on better terms (Sell, 2005; Sell, Cosmides, & Tooby, 2014; Sell et al., 2009). If no apologies ensue—if the friend or lover wants to discontinue the relationship—your face may wear an expression of sadness or no expression at all.

Other emotions, such as guilt or malaise, may have no associated facial expression. Note that malaise counts as an emotion in our view: It reflects the operation of a superordinate program that coordinates many mechanisms to fight infection or promote tissue repair. "Feeling sick" is a computational state: Social motivations are deactivated, movement is effortful (despite adequate energy reserves), libido is low, testosterone decreases (in men), glucose is rerouted to immune function, and so on.

Robotic invariance in facial expressions of emotion is not expected on an evolutionary view, nor is it necessary for emotion to be a fruitful scientific concept. Facial expressions of emotion have an evolved function: They provide information to others about the sender's internal states, values, or intentions (Darwin, 1872). They should be elicited by situations in which the average fitness consequences of providing this information would have benefited the sender (Fridlund, 1994). For this reason, selection should have designed mechanisms that regulate when these expressions appear on the face, in a way that is not easily captured by terms like "automatic" versus "controlled" (German & Cohen, 2012).

For example, leaking information about what you value through spontaneous expressions is beneficial when you are surrounded by kin and cooperators (individuals who have an interest in your welfare) but not around antagonists (who could use the information to harm you). Producing a shame display may have been the best-bet response when facing people who have learned you did something disreputable, but when you are taking that action alone and then hear others approaching, the shame display risks advertising damaging information about yourself. The shame display may be a spontaneous, even automatic response to the first context; in the second context, the "automatic" response should be to *not* produce it (de Jong, Peters, & De Cremer, 2003; Sznycer, 2010).

4. Feeling states are neither necessary nor sufficient for a computational system to be considered an emotion, but there are cases in which the phenomenology of emotion may be as functional as the phenomenology of color. The design of some emotions may require distinct qualia—consider the internal experience of shame versus anger, or shame versus pride. Just as black-and-white images cannot represent distinctions between shades of red versus green, valence and arousal cannot represent distinctions that may be computationally important. Other qualia associated with emotions will not be unique. A thumping heart will feel similar whether it is caused by anger, fear, or lust; that felt experience is a secondary consequence of the physiological response these emotions entrain. When grief activates episodic memories of the person lost, the particular memories retrieved can color phenomenology in ways that differ from person to person (which may be important for reknitting the fabric of your social relationships). Yet other computational states that we would consider emotions have no associated feeling state at all (e.g., coma).

These are not reasons to jettison the "experience component" from theories of emotion. Just as sweetness and richness represent the concentrations of sugars and fats in food, some feeling states may represent the magnitude of a regulatory variable or the costs associated with a situation (Tooby et al., 2008). Distinctive qualia may evolve when one function of an emotion program is to evaluate alternative courses of action prior to making choices—prospection.

It matters, for example, whether a given action would lead others to evaluate you more negatively or more positively; these judgments can affect how much weight they will put on your welfare in making future decisions. Now consider the possibility that shame evolved as a defense against being devalued by others (Sznycer, 2010; Sznycer et al., 2016). If this is correct, then one function of shame is to deter the individual from taking courses of action that would cost more in terms of social devaluation than the payoffs the action would otherwise yield. Imagine eating your coworker's lunch; is the convenience worth the negative evaluations of those who might find out? Making this trade-off requires internal representations of (estimated) value; that value representation can be a feeling.

If the felt experience of shame evolved to represent a particular cost—the cost of being devalued by others—then the intensity of shame felt when imagining different acts should closely track how negatively other people evaluate individuals who take that action. We found that it does, both within and across cultures (Sznycer et al., 2016). Intensities of shame uniquely predicted how negatively others viewed these acts, but anxiety and sadness did not. Shame, anxiety, and sadness all have a negative valence, all three can cause arousal, and feelings of sadness and anxiety often coactivate with shame. But decision systems need to distinguish the felt experience of shame from other negative qualia—and register its intensity—if the function of shame qualia is to represent the magnitude of devaluation that an action is likely to cause.

5. Behavior varies across individuals and situations, as Moor says, but that does not undercut the concept of emotion. The functional architecture of many computational systems—including emotions—should reliably develop in all individuals of a given age and sex when they are exposed to the envelope of environmental conditions our ancestors routinely faced (Tooby & Cosmides, 1990b). But evolved computational systems exist *to generate behavior that is sensitively contingent on information from the internal and external environment*. There should be universal mechanisms, not universal behaviors (Tooby & Cosmides, 1992).

To flee or fight, to scowl or remain impassive—these behaviors are generated by computational systems that are designed to assess and use many kinds of information in making decisions. Am I strong enough to fight this adversary? Is the risk of injury worth it when an escape route exists? Will expressing anger escalate a dangerous interaction, risking costs beyond any potential benefits? Because a man's upper body strength predicted his ability to inflict harm and resist injury ancestrally, that variable should be accessed by the computational design of many systems that regulate behavior. It is. Based on the hypothesis that anger evolved as a bargaining system, we predicted and found that a man's upper body strength regulates how easily and frequently he angers, how entitled he feels to better treatment, how successfully he resolves conflicts of interest in his favor, and his attitudes about taking versus defending resources (Petersen, Sznycer, Sell, Cosmides, & Tooby, 2013; Sell et al., 2009). Behavioral choices should vary in principled ways across individuals and cultures. Invariances should emerge at the level of evolved computational systems when they are correctly described.

"Goal-Directed Mechanism" Is Not a Fruitful Concept

Based on the considerations just listed, Moors (this issue) rejects the scientific status of "emotions" and emotional episodes. She argues that these are not scientifically fruitful concepts: Because they do not "share deep features such as a common causal mechanism or a common deep structure" they do not "allow for scientific extrapolation, that is, the generalization from one exemplar to the other exemplars in the set" (p. 14). Moors suggests, instead, that the phenomena people refer to as emotional are best described by a "goal-directed mechanism" that is common to all behavior.

> The goal-directed mechanism assesses the utility of one or more action options. The utility of an action option is based on the values of the outcomes of the action and on the contingencies between the action and the outcomes, also called the expectancies that the action will lead to the outcomes. Defined at the mental level of analysis, the goal-directed mechanism is one that is mediated by representations of values and expectancies of one or more action options. The action option with the highest utility activates its corresponding action tendency, and this action tendency may translate in overt behavior. (p. 9)

Elements of the folk concept of emotion—heat, fast onset, action tendencies that are difficult to counteract—are handled by the position of a goal in a person's goal hierarchy:

> …if one adopts appraisal theory's proposal that emotional behavior is caused by action tendencies with high control precedence because they are at the service of highly valued goals, the heat is amply preserved. … Highly valued goals often require a more urgent fulfillment, hence the fast onset of emotional behavior. In addition, if a goal is high in a person's goal hierarchy, behavior at the service of this goal is more difficult to counteract because there are not many goals that can top it. Fleeing may be difficult to suppress if it is to save one's skin. (p. 11)

Sure. At a certain level of abstraction, emotions are goal-directed mechanisms: They evolved to solve adaptive problems. But that is true of all adaptations—hemoglobin, the suffocation alarm response, inflammatory processes—most of which accomplish their evolved function without representing goals or computing the utility of alternative courses of action.

Moors's analysis is so general that it applies to most cognitive processes that regulate behavior. As a result, the same reasoning that leads her to jettison the concept of emotions as not picking out a natural kind applies equally to her concept of a "goal-directed mechanism" combined with appraisals of situations as "goal in/congruent." Choosing bananas versus apples at the grocery store, terror when confronted by a lion, and the decision to punish free riders are ruled in; recalibrational emotions, like guilt and gratitude, are ruled out. Guilt and gratitude are not "goal-directed mechanisms"; they do not represent the value and probability of action options, choosing the one with the highest utility. Their function is to up- and down-regulate the magnitude of internal variables that represent properties of other individuals, such as their value to you as a cooperative partner, their formidability relative to yours, their mate value, their status, their health (Tooby et al., 2008). Variables like these are accessed by many decision systems, including ones that make welfare trade-offs—decisions about how much to sacrifice to help a given individual or avoid harming them (see next).

Detailed Hypotheses Follow from Adaptationist Theories

Assimilating emotions to the set of all goal-directed mechanisms lacks heuristic value. Research in cognitive science has not uncovered a "utility maximizing" system that operates across all domains, regardless of content. Formalisms like $S \rightarrow [S{:}R\text{-}O^{v}] \rightarrow R$ express a wish, not a cognitive process—that cognition will somehow be organized to produces decisions likely to have better outcomes over worse ones.

Yes, natural selection will favor decision rules that produce better rather than worse choices, that is, choices that were more likely to promote fitness under ancestral conditions. But what counts as adaptive behavior differs from domain to domain, in ways that cannot be deduced by a goal-directed mechanism that is domain-general (for detailed argument, see Tooby & Cosmides, 1992). Theories of adaptive function promote discovery and understanding because they start with a task analysis of a specific adaptive problem faced by our hunter–gatherer ancestors, including the environmental information that would have been available to a mechanism capable of solving it.

Evolutionary biology tells us, for example, that biological siblings should be targets of altruism but avoided as sexual partners. That implies there should be mechanisms for identifying which local children are siblings, based on cues that predicted genetic relatedness in ancestral social environments. By following this logic, Lieberman et al. (2007) found that the mind computes a computational variable—a kinship index—using two developmental cues: living with your mother when she gave birth to a (younger) child and how long you coresided with an older child during the first 18 years of your life. Through the kinship index, these cues regulate two motivational systems, even among people who know they are not genetically related: A higher kinship index predicts more disgust when imagining sex with that sibling and greater willingness to help them.

Evolutionary biologists have discovered and modeled a variety of different selection pressures ("games") that predict the conditions under which it would be adaptive to place weight on the welfare of another compared to oneself (i.e., to sacrifice one's own welfare for another). One can put no weight on another's welfare and act with total selfishness; or some weight, or great weight, or one can lay down one's life for another. In modeling specific social emotions (love, anger, gratitude, guilt, shame, compassion) one specific internal regulatory variable—what we call a welfare trade-off parameter—turns out to be a necessary feature of social decision making and is embedded in various social emotions (Tooby et al., 2008). Indeed, it helps to define the adaptive problems associated with each of these emotions. For example, anger appears to be an emotion that evolved to orchestrate bargaining during conflicts of interest and was predicted (and found) to be triggered when another person treats the actor in a way that puts too little weight on the actor's welfare (Sell, 2005; Sell et al., 2009).

In contrast, gratitude is typically triggered when another person expresses through action an unexpectedly high welfare trade-off toward the actor. A major function of gratitude is to promote increasing levels of mutual valuation in relationships, or maintain them over time against uncertainty and decay (Lim, 2012; Tooby et al., 2008). In contrast, ingratitude for an act of generosity may trigger anger and should recalibrate the donor's welfare trade-off parameter toward the partner down—wasting the opportunity to have a more mutually beneficial cooperative partnership. On detecting an increasing level of welfare trade-off from another, gratitude typically recalibrates the actor so that the actor values the other person more than previously. The program also motivates the actor to express gratitude, that is, to communicate that the actor noticed and appreciated the act expressing valuation in a way that consolidates the mutual prosocial relationship at a higher level; it motivates the actor to look for opportunities to reciprocate (so that the partner feels that their investment was repaid), and so on. The gratitude system recalibrates one's welfare trade-off parameter toward the kind other upward. Gratitude obviously plays a role in organizing human reciprocity. However, a related (possibly encompassing system) that is often called gratitude is a program that recalibrates one's valuation upward for people or other entities given new information indicating their value to the actor (e.g., near-loss, or reexposure to kindness). For example, friendships, long-term pair bonds, and other deep engagement relationships operate not off of reciprocity (at least not exclusively) but out of positive externalities that others give off (Conroy-Beam, Goetz, & Buss, 2015; Tooby & Cosmides, 1996, 2008). You may intensify the value placed on (feel gratitude for the existence of) a parent, a sibling, a friend—or even a horse, a car, or a job—in a way that is not based on reciprocity but on their value to you.

A theory of adaptive function not only predicts new design features, promoting discovery, but also explains why an emotion orchestrates its target systems in a particular pattern. Consider again the hypothesis that shame is a neurocognitive system that evolved as a defense against being devalued by others. If true, then shame should orchestrate cognition, motivation, physiology, and behavior in ways likely to (a) deter the individual from taking courses of action that would cost more in terms of social devaluation than the payoffs the action would otherwise yield; (b) limit the extent to which others learn about and spread potentially damaging information; (c) limit the degree and the costs of any ensuing social devaluation; and, if devaluation occurs, (d) mobilize the individual to respond adaptively to the new social landscape.

Many results in the literature make sense in light of this function. Shame motivates one to avoid behaviors that could cause devaluation and conceal damaging information (Sznycer, Schniter, Tooby, & Cosmides, 2015). When damaging information is discovered, the shamed individual withdraws (Tangney, Miller, Flicker, & Barlow, 1996), which protects him or her against acts immediately motivated by devaluation and may weaken the formation of common knowledge of the shameful act. Shame mobilizes physiology in preparation for negative sanctions from others, up-regulating cortisol (Gruenewald, Kemeny, Aziz, & Fahey, 2004) and proinflammatory cytokines that defend against infection (Dickerson, Gable, Irwin, Aziz, & Kemeny, 2009). Shame can elicit a stereotyped nonverbal display (Fessler, 1999; Keltner, 1995; Tracy & Robins, 2007; Weisfeld & Dillon, 2012). Behaviors mobilized by shame—accepting subordination (Gilbert, 2000; Wicker, Payne, & Morgan, 1983), acts of appeasement (Keltner, Young, & Buswell, 1997), and increasing cooperativeness (de Hooge, Breugelmans, & Zeelenberg, 2008; Masclet et al., 2003), can increase the value others place on the shamed individual. Shame may also be accompanied by aggression (Fessler, 2001; Tangney, Wagner, Fletcher, & Gramzow, 1992), which would be expected if social benefits are no longer as abundantly provided because of your value to others, but must instead be bargained for by threatening harm (Sell et al., 2009). Cross-cultural variation in shame tracks cross-cultural variation in negative evaluations of acts (Sznycer et al., 2016) and is higher in countries where relational mobility—how easy it is to switch cooperative groups—is low (Sznycer et al., 2012). The hypothesis that shame evolved to manage the threat of devaluation led to the prediction discussed above: The intensity of felt shame when imagining different acts will closely track how negatively others evaluate people who commit them. It also suggests new, untested hypotheses about the factors and situations that will make an individual more prone to feel shame. For example (and all else equal), (a) factors that make a person less vulnerable to devaluation by others (like strength, attractiveness, entrenched status) should make them less prone to shame, (b) shame intensity should vary with features of the audience (e.g., more shame will be provoked when the discrediting act is seen by more aggressively formidable individuals than weaker ones, or when the audience is composed of higher status individuals; Fessler, 2007; Gilbert, 2000), and (c) shame-proneness should be a function of the ease with which new relationships can be established to compensate for degraded relationships when devaluation occurs. The evolved defense theory predicts new features and makes sense of those that are already known.

Conclusion

When Moors argues that emotions should be described as computational systems, she is correct. But that is not enough to produce a scientifically fruitful approach to understanding emotions. It is easy to drown in particularities—everything about human emotions can be made to sound idiosyncratic and variable by choosing descriptive frameworks that are blind to function because, in the words of Dobzhansky (1973, p. 125), "nothing in biology makes sense except in the light of evolution." Discovering regularities depends on selecting the appropriate conceptual framework. The human brain is teeming with computational systems that were engineered by natural selection, but to see their functional organization we need to consider what adaptive problems each system was designed to solve. Theories of adaptive function are necessary to discover which emotions exist, what operations they carry out, and how those operations are functionally organized. Adaptationism is the conceptual framework that can carve emotions at their functional joints.

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