Evolved to Learn: Emotions as Calibrational Adaptations

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Abstract

Emotion adaptations have evolved in response to eons of selection pressures characteristic of social and physical life over the history of our lineage. Cues relevant to these distinct selection pressures should reliably elicit relevant emotions and motivate efficacious behavioral responses. Selection likewise favors the strategic calibration of emotional processes to key contextual factors, such as fitness-relevant individual differences, situational factors, and culture. Here, we provide an overview of empirical and theoretical work on processes by which emotion adaptations calibrate to particularities of situation, self, and culture. Finally, we evaluate developmental processes as themselves potential adaptations, and sketch an outline of how developmental affect scientists might test such hypotheses. While acknowledging the fundamental role of ontogeny in the expression and calibration of evolved traits, we emphasize the design of flexible affective traits via selection.

Keywords: Natural selection, motivation, evolution, evolutionary development, cross-cultural differences, individual differences

Perhaps because they highlight the persisting effects of ancestral selection pressures on contemporary mental life, evolutionary perspectives on the emotions have often been misunderstood as entailing inflexible and invariant dynamics. This chapter will attempt to redress this confusion by briefly—and far from comprehensively—reviewing empirical and theoretical work on ways that emotion adaptations calibrate to particularities of the situation, the self and the socioecological environment. The focus of our discussion holds on the contingent flexibilities of mature emotion phenotypes, but we also consider the prospect that key developmental affective processes operative in early life themselves constitute adaptations.

Functionally Specialized Assemblages

In evolutionary biology, explanations at the level of ultimate function seek to clarify the benefits of traits with respect to reproduction and survival, whereas proximate explanations address how traits are mechanistically engineered and implemented (Mayr, 1961; Tinbergen, 1963). Ultimately, evolutionary affect scientists understand emotions as generating responses that would have, on average, effectively addressed distinct challenges that recurrently confronted the social and physical lives of individuals in our lineage. Cues relevant to these distinct challenges should reliably evoke correspondingly distinct emotion adaptations, much as keys are designed to fit particular locks (Cosmides & Tooby, 2000). Proximately, evolutionary affect scientists regard emotions as nested assemblages of myriad neural and somatic components orchestrated to produce coherent responses.

According to the prevailing view in evolutionary psychology, emotions are superordinate programs that recruit and entrain constellations of subordinate perceptual, motor, physiological and cognitive programs into characteristic patterns (Oatley & Johnson-Laird 1987; Nesse, 1990; Tooby & Cosmides 2008). Specialized, complex mental functions of various types emerge via interaction between subfunctions coalescing in the brain into hierarchical assemblages of networks and subnetworks (H. C. Barrett, 2017; also see Gkigkitzis, Haranas, & Kotsireas, 2017). In this integrative fashion, the emotions are thought to coordinate diverse processes relevant to their functional themes, including (but not limited to): attention, memory, focal goals, digestion, visual acuity, immune function, blood flow, information-seeking, sleep/wake cycling, inference, posture, energy levels, and so on. Importantly, no single element should be fixated on as the *sine qua non* of an emotion. In the brain, for example, amygdala activity has been closely linked with fear, but also supports attention and motivational functions relevant to multiple other emotions, including emotions of positive valence such as lust (e.g., Adolphs 2008; Lang & Bradley, 2013).

Functionally distinct emotions should be expected to efficiently share a significant degree of overlapping proximate mechanisms (see Anderson, 2010). For example, Bartels and Zeki (2004) compared the activation profiles of maternal love and romantic love in response to images of either romantic partners or babies, observing comparable anterior cingulate cortex reactivity consistent with approach motivation and attention-orienting, as well as comparable activation of reward regions (e.g., striatum, ventral tegmental area). Consistent with the distinct functions of maternal versus romantic love, unique activation patterns were also observed, such as periaqueductal grey reactivity in response to infants, but not romantic partners; periaqueductal grey is thought to help mediate maternal behavior (e.g., Lonstein & Stern 1998). Conversely, participants evinced hypothalamic reactivity to images of their partners, but not their infants, in a pattern likely related to the sexual aspect of romantic, but not maternal, love (Karama et al. 2002).

More recent neuroimaging efforts have provided extensive further support for construing emotions as superordinate orchestrations of overlapping submechanisms into nonetheless distinguishable functional assemblages. For example, although divergent emotions draw on common brain regions (e.g., shared cortical midline and frontal areas), a meta-analysis of 83 neuroimaging studies reported distinguishable activation patterns for anger, disgust, fear, sadness, and happiness (Vytal & Hamann, 2010). State feelings of sadness, fear, shame, anger, pride, disgust, envy, happiness, and lust aroused while in the scanner have been similarly classified by a machine learning algorithm (Kassam, Markey, Cherkassky, Loewenstein, & Just, 2013). In a particularly compelling recent study, Saarimäki and colleagues (2016) induced disgust, fear, happiness and sadness via both brief film clips and mental imagery, then were able to correctly classify each distinct emotion using whole-brain multivoxel pattern analysis (also see Sitaram et al., 2011). Not only were the classifications accurate across induction modality (film vs. imagery), but they also generalized across individual participants, in characteristic neural signatures comprised of cortical and subcortical circuits. Subjective self-reports of the experience of each emotion were correlated with the extent to which the signature neural patterns were activated, suggesting a connection between emotional experience and activity in those regions. In sum, consistent with evolutionary reasoning (e.g., H. C. Barrett, 2012; Tooby & Cosmides, 2008), emotions appear to be proximately implemented via distributed assemblages of neural and somatic components identifiable in terms of holistic profiles of activation and deactivation, and including higher cortical regions which have sometimes been regarded as distinct from emotion.

The argument that emotions possess characteristic neural signatures remains somewhat controversial at the time of writing. *Psychological constructionists* have previously argued against the putative existence of distinct neural signatures, going so far as to claim that discrete emotions do not exist in any recognizable inter-individual way even within a shared culture – to say nothing of the prospect of similar emotions emerging across societies (e.g., L. F. Barrett, 2013; Lindquist, 2013; Raz et al. 2016). From this perspective, discrete emotions are folk concepts shaping intuitive understanding of individuals' valence, arousal and behavior, indexing culturally acquired categories of experience that do not actually exist in the mind as natural kinds. The primary evidence for psychological constructionism has been that distinctly lexicalized emotions are associated with common proximate mechanisms and exhibit individual and cultural variation (e.g., L.F. Barrett, 2006; L. F. Barrett, Gendron, & Huang 2009).

Consistent with their claim that discrete emotions are, like 'mermaids', essentially culturally transmitted fairytales lacking real-world referents to be studied, constructionists initially predicted that dissociable neural activation patterns correspondent with discrete emotions would not exist (e.g., L.F. Barrett et al. 2009; Lindquist & Barrett, 2012). Yet, as discussed above, such patterns have been detected, by multiple labs, using convergent techniques afforded by refinements in methods and analytic tools. In light of this new evidence, constructionists have changed course to acknowledge the existence of unique neural signatures linked with discrete emotional experiences (Wager et al. 2015). As newly formulated, constructionism is presented as not only anticipating the existence of distinct signatures, but as providing a uniquely effective theoretical way of understanding how regions from multiple systems, including cortical and subcortical areas, might interact to construct emotions (L. F. Barrett & Russell, 2015; Wager et al. 2015), the basic idea being that culturally acquired emotion concepts, associated with higher regions, interact with limbic regions to create classifiable assemblages. We have no objection to scientists refining their theoretical approaches on the basis of contradictory evidence, but note that evolutionary accounts have long offered an alternative theoretical framework for understanding the distributed, highly multifaceted cortical and subcortical nature of emotion networks, and that this framework is anchored in well-established ways of thinking about biological motivation systems in humans and other species.

Contextual Contingency

At the proximate level of analysis, because emotions are partially comprised of higher cortical mechanisms related to behavioral flexibility and learning, emotion elicitors and output behaviors should be expected to display context-sensitive variation in response to local circumstances, including culturally acquired norms. At the ultimate level of analysis, selection favors the evolution of capacities for contextually appropriate, individually and culturally contingent emotional performance. Indeed, not only is contextual variability consistent with evolutionary perspectives on the emotions, but observations of the strategic modulation of emotional responses to align with fitness incentives constitute the strongest evidence of adaptive design.

Research on anger and disgust provides ready illustrations of adaptive contextual variability with regard to the particular individuals involved in eliciting incidents. For example, the degree of anger triggered by transgressions has been found to be contingent on the fitness costs entailed by the identity of the person harmed, such that harm to the self elicits greater anger and direct aggression than does harm to acquaintances (Molho et al., 2017) or strangers (Pedersen, McCauliffe & McCullough, 2018), with a similar pattern of heightened anger and aggression obtaining when harm befalls siblings (Lopez et al., under review). These findings make functional sense given the fitness costs inherent to aggressive confrontation (e.g., potential physical and/or reputational harm), which de-incentivize confrontation unless outweighed by the benefits of deterring substantial future harm (e.g., to self or kin). Anger and related inclinations toward punishment are moderated by the identity of transgressors as well as victims, such that kin or allies evoke both relatively muted feelings of anger and heightened inclinations to forgive (McCullough, Kurzban & Tabak, 2013). Pathogen disgust appears similarly modulated by contextual factors. For example, pathogenic olfactory cues associated with kin elicit less disgust than do the smells of sick strangers (Stevenson & Repacholi, 2005), and mothers find the smell of their own babies' feces less disgusting than the smell of other babies' feces—even when the soiled diapers are unlabeled or mislabeled (Case, Repacholi, & Stevenson, 2006). These target-contingent shifts in pathogen disgust are readily interpretable in light of the fitness benefits of providing care to sick kin or offspring offsetting the costs of pathogen exposure (Tybur et al. 2013; Tybur & Lieberman, 2016).

Trait differences in the ability to inflict costs (relevant to anger) or to withstand pathogens (relevant to disgust) also appear to functionally moderate responses. With regard to anger, physically strong individuals are more prone to experience anger and to resolve conflicts through force (Sell, Tooby, & Cosmides, 2009; Archer & Thanzami, 2009; also see Fessler, Holbrook, & Gervais, 2014). With regard to disgust, individuals who are more vulnerable to infection (e.g., due to higher progesterone levels) have been found higher in trait disgust and more prone to engage in behavioral precautions against pathogen-transmission (Conway et al., 2007; Żelaźniewicz, Borkowska, Nowak, & Pawłowski, 2016). Relatedly, disgust-sensitivity appears to systematically increase and decrease in a pattern tracking shifts in immune vulnerability related to female reproductive physiology (Fessler et al., 2005; Fleischman & Fessler, 2011; Jones et al., 2005). With regard to both anger and disgust, natural selection favored greater risk-taking in human males due to the greater variance in reproductive success among males than females, leading to higher-stakes competition—and hence larger 'gambles' with regard to incurring potential costs (e.g., injury or death from combat or illness) in exchange for the chance of obtaining greater reproductive rewards (for a detailed argument, see Sparks, Fessler, Chan, Ashokkumar, & Holbrook, 2018). Consistent with the sex difference in fitness incentives to engage in risky behavior, men are more prone to anger and violence than women (Archer, 2004; Fessler et al., 2004; Sell et al., 2009), and a large-scale meta-analysis confirms that men are substantially less disgust-prone than women (Sparks et al., 2018), a pattern observed worldwide in a cross-cultural study spanning 30 societies (Tybur et al., 2016).

Recent work on the positively valenced, prosocial emotion of *elevation* reveals a similar propensity to adaptively adjust to social and situational cues of the prevalence of cooperation versus exploitation. A sizable literature has documented that individuals experience elevation, characterized by warm feelings (e.g., of being “uplifted”) and motivation to help others, upon witnessing exemplary acts of prosociality (e.g., Algoe & Haidt, 2009; Schnall, Roper, & Fessler, 2010; for a recent review, see Thomson & Siegel, 2017). The tendency to facultatively adjust one’s prosocial inclinations according to prevailing levels of prosociality in one’s social environment has been theorized to maximize social benefits (i.e., through direct or indirect reciprocity, reputation enhancement, and/or inclusion in cooperative endeavors), and to minimize costs entailed by engaging in antisocial behavior in highly prosocial contexts wherein others are more likely to penalize selfish actors (Fessler, Sparks, Samore, & Holbrook, 2019). According to this functional logic, when individuals are embedded in a predominantly antisocial, exploitative social environment, it would be maladaptive to engage in overtly prosocial behavior, and hence feelings of elevation should be reduced. Consistent with this account, in a recent series of studies, participants reported significantly less elevation when a prosocial exemplar was depicted as being exploited by others in his community (Fessler et al., 2019). In convergent support of this evolutionary account of the determinants of elevation, trait differences in expectations regarding the prosociality of others have also been reliably observed to moderate responses to witnessing prosociality, such that individuals whose experiences with others have been generally noncooperative and exploitative find cues of prosociality less evocative of elevation, and are consequently less inclined to engage in behavioral measures of helping (Sparks, Fessler, & Holbrook, under review).

In a complementary set of findings obtained among the Tsimane' people of lowland Bolivia, tendencies to pursue prosocial, affiliative leadership roles (i.e., initiating cooperative ventures), and to present a gregarious and warm interpersonal affective style, correlate with individual differences in physical strength (von Rueden, Lukaszewski, & Gurven, 2015). This association was hypothesized given that Tsimane' individuals of greater physical strength are more capable of protecting others, meting out punishment of those who shirk their obligations or attempt to exploit the group (von Rueden et al. 2014), and are also more capable of successfully extracting resources (Hess et al., 2010; Sell et al., 2012). Accordingly, physical strength mitigates the costs inherent to seeking leadership insofar as coordinating group endeavors requires a greater investment of time and effort on the part of the leader which only pays off in the event of successful outcomes, and insofar as failures in attempts to assert leadership may lead to reputational costs or other forms of interpersonal conflict in the aftermath (von Reuden & Gurven, 2012). This work not only demonstrates an adaptive logic relating individual differences in strength to variation in affiliativeness and status-seeking, but broadly replicates comparable findings obtained in modern postindustrial societies (e.g., linking strength and extraversion in men, see Lukaszewski, 2013) in a small-scale subsistence culture more faithful to the ancestral world.

Broadly speaking, phenotypes can be calibrated by early environmental inputs to improve the fit between organisms and their environments (Belsky, 1997; Bonner, 1965; Stearns, Allal, & Mace, 2008; Wolf, Van Doorn, Leimar, & Weissing, 2007), and decades of research in both nonhuman animals and humans provide support for the developmental plasticity of affective phenotypes (for reviews, see Davis, Glynn, Waffarn, & Sandman, 2011; Hostinar & Gunnar, 2013; Lyons, Parker, & Schatzberg, 2010; Pechtel & Pizzagalli, 2011). For example, exposing rodent pups to frequent and unpredictable signals that they live in a dangerous environment (e.g., by administering electric shocks, forced swimming, or separation from caregivers) causes changes in brain and endocrine vigilance systems that lead to more fearful phenotypes in adulthood (Ishikawa, Nishimura, & Ishikawa, 2015). Similarly, humans exposed to violence or trauma in early life are more likely to experience anxiety in adulthood (Saleh et al., 2017), a shift which, while unpleasant at the level of proximate experience, may reflect an affective strategy which yielded aggregate ultimate fitness benefits in facilitating responsiveness to dangerous environments (for discussion of the adaptive logic of ‘negative’ emotions, see Nesse, 1990). Much as differences in early experience may guide the later development of emotions over the lifespan in ways that track challenges within local environments, so may cultural differences guide the emergence of the emotions in ways that track the socioecological challenges of particular societies.

Cultural Contingency

Cultural differences in emotion are sometimes discussed as though such variation were at odds with evolutionary accounts (e.g., L.F. Barrett, 2006; 2013). In truth, culturally acquired norms and ideas should be expected to influence emotion elicitation and output behaviors, just as the situational and individual trait determinants discussed in the preceding section have been hypothesized and observed to.

Attempts to elucidate the interplay between culture and emotion can be muddled by the presence of folk emotion concepts, which must be disambiguated from the actual emotions which may exist (Fessler, 2004). Although evolutionary accounts broadly disagree with the constructionist claim that apparently discrete emotions are created by folk emotion concepts as a kind of collective delusion, folk concepts about emotions should exert some relevant degree of influence. The emotions have been hypothesized to incorporate culturally transmitted knowledge and concepts—presumably including folk emotion concepts and cultural emotion norms—to calibrate emotion elicitors, regulation tendencies, event appraisals, selection of appropriate behavioral responses, and so on (e.g., Markus & Kitayama, 1994; Tooby & Cosmides, 2008). As such, folk emotion concepts thus appear likely to both influence and be influenced by emotions which are nonetheless heritable in a panhuman sense (Gervais & Fessler, 2016).

Another issue complicating the interplay between culture and emotion is that emotions should be anticipated to require extensive social experience to develop (e.g., to learn about local hazards or resources, modes of status-striving, access to allies or mates, locally prescribed levels of cooperation, etc., for a fuller account, see Tooby & Cosmides, 2008). Many adaptations are designed to develop differently in responses to varying environments, according to genetically specified *reaction norms* (e.g., H. C. Barrett, 2012), raising the possibility that at least some variation in the expression (or even existence) of emotions may owe to reaction norms responsive to certain cultural or ecological factors varying across societies. In other words, selection is likely to have evolved conditional developmental rules of the form, ‘Given condition X, pursue emotion variant A; given condition Y, pursue emotion variant B; etc.’. Consider the

American eel (Anguilla rostrata), which matures at a slower rate and to larger size in freshwater than in saltwater (Côté et al., 2013); might particular human emotions be designed with reaction norms sensitive to differences in factors such as collectivism, food or mate availability, population density, intragroup cooperation, intergroup conflict, disease-prevalence, status hierarchy, and so on? Even should such reaction norms be identified, some portion of cultural variation in emotion will almost certainly be due to mismatches between ancestral environments and developmental environments that alter otherwise typical emotion development as the by-product outcome of a surfeit, paucity, or novel combination of environmental cues, rather than according to inherited reaction norms sensitive to those cues. Thus, we are not confronted by a false choice between nature and nurture, but by a set of related questions entwining both:

i) Which culturally contingent emotion phenotypes emerge due to naturally selected reaction norms—and which specific factors are these reaction norms attuned to?
ii) Which culturally contingent emotion phenotypes emerge due to by-product effects rather than reaction norms?
iii) Which emotions, if any, are essentially unaffected by cultural differences—and why?

To address these open questions, affect scientists will require far more complete and systematic descriptive data on cultural variation in emotion than currently exists. Previous cross-cultural emotion research has been conducted in a piecemeal manner which has largely overlooked small-scale societies, and is therefore insufficient to ascertain the actual range of human emotion phenotypes, let alone correlate them with potentially relevant societal and ecological variables. However, in light of the close association between emotion-propensity and personality traits, recent findings concerning the cultural and environmental determinants of personality structure may provide a useful proof-of-concept.

According to Lukaszewski and colleagues' (2017) *socioecological complexity hypothesis*, the extent to which personality traits covary in a given society should be inversely correlated with the number and specificity of niches available within that society, because selection favors phenotypic specialization over development to optimize performance within one's social and physical environment, and personality traits are directly relevant to successful performance within differing niches. Thus, individuals who find themselves embedded within complex societies may pursue fitness-enhancing outcomes (e.g., status-seeking, alliance-formation, mate-finding, offspring provisioning) via a variety of niches suited to a variety of personality profiles. For example, the personality profile of an elementary school teacher may not be well-suited to that of a homicide detective, or vice versa, but both niches are viable in a complex society. By contrast, within less complex societies, individuals are confronted with a more constrained set of social and material challenges, leading people to engage in a relatively homogenous range of social interactions and subsistence tasks (Gurven et al., 2009) that not only can be adequately navigated according to a less complex and varied range of personality profiles than found in postindustrial societies, but might actually be more successfully served by having fewer dissociations in personality structure.

Indeed, Gurven and colleagues (2013) note that the emphasis on collective, consensual community decision-making characteristic of many small-scale societies incentivizes linking traits such as extroversion with traits such as agreeableness and conscientiousness in order to improve cooperation and deter defection and attendant conflicts. As hypothesized, large-scale personality survey data collected from 55 countries varying in degree of economic development, urban living (associated with greater social and occupational niches), and variety of economic exports (a proxy for the number of distinct occupational sectors) revealed a strong negative association between socioecological complexity and the extent of positive correlation between the Big Five personality dimensions, such that individuals from less complex societies evinced less distinctly dissociable personality dimensions (Lukaszewski et al., 2017). In a complementary finding derived from assessing the Big Five Inventory in a small-scale society quite low in relative socioecological complexity, the Tsimane' hunter-horticulturalists of Bolivia appeared to possess a "Big Two" oriented around prosociality and industriousness (Gurven et al., 2013).

Although admittedly these findings regarding personality structure and niche complexity are only indirectly related to the questions posed above regarding the potential reactivity of emotions to socioecological factors, they are highly suggestive, particularly given the close link between personality and emotion. Could a similar dynamic apply to the structure of the emotions, such that socioecological environments characterized by more [less] specialized niches evoke more [less] variegated emotion categories? Take a highly speculative example, included merely as a possibility to illustrate the sorts of relationships which may obtain. The emotions of pride and happiness have been found unambiguously distinct in industrial Western cultures, such that pride is particularly elicited by indications of status-attainment via possession of socially valued achievements, knowledge or skills (e.g., Smith & Ellsworth, 1985; Willams & DeSteno, 2009; Holbrook, Piazza, & Fessler, 2014), and happiness is more generally elicited by turns of good fortune (e.g., acquisition of material rewards) which may or not be social or achievement-oriented in nature (e.g., Smith & Ellsworth, 1985). Might humans embedded in less socioecologically complex societies—particularly those emphasizing links between positive social relations, status and hedonic states—evince less clearly delineable distinctions between pride and happiness? From an adaptationist perspective, much as emerging results indicate with regard to societal variation in personality structure, emotions are likely to reflect the exigencies of societal and environmental niches.

Culturally Bounded Emotion Homologues?

Newly evolved structures derive from and exploit the functional affordances of older structures. For example, the limbs of whales, birds, and primates, despite their apparent physical and functional distinctiveness, are all homologues of a common ancestral trait (Wagner, 2014). In cases of *serial homology*, such as successive spinal vertebrae (Cartmill, 1987), an ancestral trait is duplicated with modification, producing either newly derived traits in place of the antecedent trait, or derived traits coincident with the conserved antecedent trait. Homology can also occur within psychological systems (Lorenz, 1958; Moore, 2013; Dehaene, 2005; Holbrook & Fessler, 2015). For example, the brain system enabling representation of metaphorical "social distance" appears to be a serial psychological homologue that elaborates an antecedent system originally evolved for literal spatial reasoning (Parkinson & Wheatley, 2013). Serial psychological homologues of complex traits, such as emotions, are thought to be instantiated in patterns of activation and de-activation which draw on significantly overlapping (but non-identical) assemblages of bodily and neural components (Clark, 2010; Holbrook, 2016).

To introduce the concept of serial emotion homologues, consider the progression from pathogen disgust to sexual disgust. Pathogen disgust appears to be the antecedent emotion adaptation, shaped by intense selection pressures to avoid pathogens (Curtis et al., 2011). Pathogen disgust is elicited by visual (Tybur, Lieberman, Kurzban & DeScioli 2013), olfactory (Wicker et al., 2003) or gustatory cues of the likely presence of pathogens (DeSimone, Lyall, Heck, & Feldman, 2001), and motivates withdrawal from the eliciting stimulus (Roseman, Wiest, & Swartz, 1994), physiological changes to deter contamination, such as nausea or vomiting (Rozin et al., 2008), and cognitive shifts such as enhanced memory of potential contamination sources (see Tybur et al., 2013). Sexual fluid exchange and close physical contact entail risk of pathogen exposure, in addition to costs such as the expenditure of time and effort in child-rearing over alternative mating opportunities or other fitness-relevant objectives. To maximize cost/benefit tradeoffs in sexual behavior, selection may have re-purposed elements of pathogen disgust to create a homologous sexual disgust emotion customized to deter detrimental sexual interactions (e.g., with close kin). Sexual and pathogen disgust both motivate withdrawal from contact with potentially harmful bodily fluids, and intense feelings of sexual disgust can even arouse nausea, presumably because sexual disgust co-opts from pathogen disgust and thus shares underlying proximate mechanisms. Similarities suggestive of common circuitry aside, sexual disgust also displays distinct capacities from pathogen disgust, including intricate mate-quality assessment algorithms which moderate sexual disgust reactions, taking into account relevant variables such as genetic relatedness, local availability of alternative mating options, immunological compatibility, indirect cues of genetic quality, and so on (for a review, see Tybur et al. 2013). Given the strong and enduring selection pressures related to mate-choice, and the evident algorithmic sophistication of the moderators, sexual disgust appears likely to be a phylogenetically ancient adaptation refined over eons of selection.

Theoretically, serial emotion homologues may also arise over ontogeny as by-product effects of the affordances of antecedent emotions coupled with environmental inputs, much as visual word recognition capacities have been shown to emerge from the reuse of object recognition mechanisms when humans are raised in literate cultures (Dehaene & Cohen, 2007). In this manner, cultural evolutionary processes might plausibly exploit the affordances of phylogenetically evolved emotions to spawn culture-bound emotions within individual lifetimes.

For example, *moral disgust* has been found to facilitate both metaphorical and literal social distancing in response to norm violations (Cannon, Schnall, & White, 2011; Chapman, Kim, Susskind, & Anderson, 2009; Tybur et al., 2013; Molho et al., 2017). Moral disgust may conceivably be a developmental homologue arising via interplay between processes of deontic reasoning and extant disgust adaptations, rather than a true adaptation evolved via natural selection over evolutionary time. To be clear, this possibility is offered only as an illustrative example for the sake of argument—moral disgust may well be a genetically evolved homologue. If so, moral disgust should evince a profile as distinct from sexual disgust as sexual disgust is distinguishable from pathogen disgust, indicative of optimization and suggestive of a tight fit between its evident social function and fitness-relevant moderators to improve the costs/benefit tradeoffs of social distancing.

Just as panhuman object recognition capacities may set the stage for visual word recognition given exposure to cultures that provide formal literacy training (Dehaene, 2005), so may panhuman emotion adaptations set the stage for culturally bounded emotion homologues. There may be societies which, due to parochial norms, institutions, socioecological specializations, or other factors, create genuinely distinct emotion homologues which have heretofore not been recognized. If so, these culture-bound emotions, though distinct, would resemble the antecedent emotions from which they spawned. For example, members of some societies may experience derived yet functionally distinct variants of love, pride, anger, fear, disgust, and so forth. By the same token, members of postindustrial societies may presume some emotions to be panhuman which in actuality are evoked by experiences characteristic of modern upbringing and sociality. In either case, cross-cultural variation in not only the expression, but even in the very existence, of certain emotions would follow directly from evolutionary theory.

Developmental Processes as Potential Adaptations

Natural selection retains those developmental processes which best address the demands on reproductive fitness imposed by the organism's ecology; developmental systems may accordingly be regarded as the central units of evolution (H. S. Barrett, 2007; West-Eberhard, 2003). As the renowned biologist Leigh van Valen put it (1973), "Evolution is the control of development by ecology." As we close this chapter, we invite consideration of developmental dynamics as themselves potential adaptations.

Consider, for example, the capacity for developmental processes to actively sample their environments and select a phenotypic trajectory accordingly (e.g., Oyama et al. 2001). As some phenotypic specializations may take longer to construct effectively, early initiation of the process of specializing to particular environments (e.g., hazardous environments characterized by high mortality) carries the advantage of increasing the time available to generate a maximally adaptive phenotype. On the other hand, the developmental decision to specialize early requires a tradeoff in how long the organism is able to sample the environment to assess what the best adaptive phenotype may be, thus increasing the risk of investing in a phenotype which in the end will be a poor fit for the environment (Frankenhuis & Panchanathan, 2011). For instance, a phenotype suited to a violent world may modulate a number of threat-relevant affective parameters related to factors such as vigilance, risk-taking, or future discounting which would be adaptive within uncertain and dangerous environments, but maladaptive in stable and safe environments (Pepper & Nettle, 2013). And vice versa. How, then, should developmental systems optimally weigh the benefits of taking more and richer samples against the costs of delaying development of a phenotype that will be well-suited to the local environment?

Selection might operate on heritable settings of developmental systems which determine the frequency and duration of samples taken of the environment, or lead them to weigh environmental cues differentially (e.g., take cues of close kin mortality in early life as more or less diagnostic of the world as dangerous). Frankenhuis and Panchanathan (2011) further propose the intriguing possibility that selection may favor developmental information-sampling adaptations that equip organisms to update their sampling policies on the basis of how informationally consistent the early samples are. For example, organisms whose early samples appear clear and homogenous may safely pursue a strategy of committing to a long-term phenotypic trajectory early, whereas those whose early samples are varied and heterogeneous may be better off delaying choosing a trajectory and investing time in further sampling the environment. Note that the incentives favoring the evolution of such a sophisticated adaptation are not equal across types of environmental information. Some aspects of environments will be more or less stable across time and place, obviating or enhancing the need to adjust sample patterns based on degree of heterogeneity. In addition, some aspects of environments will have more or less bearing on fitness outcomes. Accordingly, for any given affect-relevant developmental process, the existence of plastically contingent phenotypic trajectories to be chosen between, the types and relative weights of environmental cues that are sampled, the duration of sampling, and the existence of adaptations sensitive to sample-heterogeneity, are all open to hypothesis-generation and empirical testing.

In investigating whether and to what extent developmental systems are adapted to respond to information relevant to a given emotion, including contextual variability in its elicitation and expression, the researcher might apply the following research strategy:

i) Formulate hypotheses regarding the fitness challenge that the emotion addresses.

ii) Take into account the typical range of physical and social environments in which the emotion would have been designed to function.

iii) Explicate the design features that would be required to perform the emotion’s function (i.e., what endogenous and/or exogenous factors would need to be considered to maximize fitness), including which points in the lifespan contain relevant calibratory information, and at what developmental stage the phenotypic trait should emerge.

iv) Consider the proximate mechanisms by which the emotion’s developmental process might integrate such factors.

v) Compare all of the above against evidence assessing how well the developmental process actually performs with regard to calibrating emotion outcomes

This sort of problem decomposition template can generate fruitful insights into how emotions develop, regardless of the particular empirical outcome. Evolutionary approaches to emotion emphasize the force of selective design, but do not assume that all calibrational contingencies that would be adaptive actually exist, nor that all those which do exist arose as adaptations. After all, selection is often constrained by factors such as the deleterious effects a new trait would have on existing structures, or by the lack of available structures suitable for modification. Conversely, sometimes a useful trait will turn out to be a fortuitous by-product of structures evolved for orthogonal reasons. By unveiling the details of how affect programs unfold, including those factors which do or do not determine varying phenotypic outcomes, developmentalists are uniquely well positioned to test adaptationist claims (Frankenhuis, Panchanathan, & Barrett, 2013).

Conclusion

One of the hallmarks of adaptation is contextual sensitivity to individual, situational, and environmental contingencies. Indeed, when people refer to evidence that a complex adaptation has been functionally optimized, what they generally mean is that there is evidence of design for adjusting to the contingent demands of an organism's circumstances, within the constraints imposed by existing traits and external structures (e.g., telepathy might be highly adaptive but not an available option). In short, strategic plasticity is a strong indication of adaptive design. Ironically – well into the twenty-first century! – some affect scientists still invert this fundamental idea, conjuring underspecified notions of 'hardwiredness'. In another stubbornly deathless confusion, evidence of overlapping proximate mechanisms is sometimes taken as contrary to the possibility that emotions are adaptations, when in reality, evolutionary approaches construe emotions as nested assemblages of many, often efficiently shared, components. Finally, developmental explanations are often framed as orthogonal or antagonistic to evolutionary explanations, despite the fact that developmental processes are themselves subject to selection, and critical for enabling adaptations to calibrate to their environments. More than redress these confusions, we hope to have introduced evolutionary concepts that invite novel questions and integrative research, particularly on the part of the next generation of researchers to map emotion development in early life and over the lifespan.

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