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 favors the strategic calibration of emotional processes to key contextual factors, such as fitness-relevant individual, situational and/or cultural differences. Here, we provide an overview of empirical and theoretical work on processes by which emotion adaptations may attune to particularities of self, situation, and culture, integrating neuroscientific, anthropological, and psychological approaches. Finally, we evaluate developmental processes as themselves potential adaptations, and sketch an outline of how developmental affective scientists might test such hypotheses.

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

In a seemingly deathless confusion, evolutionary perspectives on the emotions are often misunderstood as entailing inflexibility and invariance. Here, we review convergent empirical and theoretical work indicating that emotion adaptations calibrate to particularities of the situation, the self and the socioecological environment. We also consider ways in which developmental affective processes operative in early life also constitute evolutionary adaptations, and provide suggestions for future work integrating evolutionary and developmental approaches.

Functional Specialization and Neural Co-optation

Evolutionary 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 affective scientists understand emotions as coordinating responses that would have, on average, effectively addressed distinct challenges that recurrently confronted the social and physical lives of individuals in our lineage (Cosmides & Tooby, 2000). Proximately, evolutionary affective scientists regard emotions as nested assemblages of myriad neural and somatic components orchestrated to produce coherent responses.

According to the prevailing evolutionary meta-theory of the emotions, emotions superordinately 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, upon detection of relevant eliciting cues, emotions 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, energy levels, inference, posture, 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; Sander, Grafman & Zalla, 2003).

Functionally distinct emotions can efficiently share significantly 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 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).

Convergent neuroimaging studies likewise depict emotions as distinguishable functional assemblages of overlapping submechanisms. 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 distinct 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 neural signatures comprised of cortical and subcortical circuits. Subjective self-reports 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, 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 sometimes regarded as distinct from emotion.

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. Ultimately, 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 inflicted on 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 when harm befalls siblings (Lopez, Moorman, Schneider, Baker, & Holbrook, 2019). 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 costs (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). The fitness benefits of caring for kin offset 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 more disgust-prone and more inclined to engage in behavioral precautions against pathogen-transmission (Conway et al., 2007; Żelaźniewicz, Borkowska, Nowak, & Pawłowski, 2016). Relatedly, disgust-sensitivity appears to systematically track shifts in immune vulnerability (Fessler et al., 2005; Fleischman & Fessler, 2011; Jones et al., 2005). With regard to both anger and disgust, 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. 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). Prosocial behavior is maladaptive when individuals are embedded in a predominantly antisocial, exploitative social environment, 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). 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, mediating diminished helping behavior (Sparks, Fessler, & Holbrook, 2019).

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 may reflect an affective strategy which yielded aggregate fitness benefits in facilitating responsiveness to dangerous environments (e.g., 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 influence emotion elicitation and output behaviors, much as the situational and individual trait determinants discussed in the preceding section have been hypothesized and observed to.

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 appear likely to both influence and be influenced by emotions which are nonetheless heritable in a panhuman sense (Fessler, 2004; Gervais & Fessler, 2016).

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 some variation in the expression of emotions may be due to reaction norms that are 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, affective scientists will require far more complete and systematic descriptive data on cultural variation 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 of niches available within that society, because selection favors phenotypic specialization during 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 elementary school teachers may not be well-suited to that of homicide detectives, 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 navigated by a less complex and varied range of personality profiles than found in postindustrial societies, but might actually be more successfully accomplished with fewer dissociations in personality structure.

Indeed, Gurven and colleagues (2013) note that the emphasis on collective, consensual community decision-making observed in 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 numbers of 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 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? From an adaptationist perspective, and in line with emerging results indicating societal variation in personality structure, emotions are likely to reflect the exigencies of societal and environmental niches.

Emotion, Serial Homology, and Culture

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" in affiliation 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 (Curtis et al., 2011), and 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). Once activated, pathogen disgust 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) in particular. Like pathogen disgust, sexual disgust motivates withdrawal from contact with potentially harmful bodily fluids, and intense feelings of sexual disgust can even arouse nausea, presumably due to shared underlying proximate mechanisms with pathogen disgust. Similarities suggestive of common circuitry aside, sexual disgust also displays distinct capacities from pathogen disgust, including intricate mate-quality assessment algorithms which moderate the intensity of reactions, taking into account relevant variables such as genetic relatedness, availability of alternative mating options, immunological compatibility, and indirect cues of genetic quality (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 phylogenetic adaptation optimized over eons of selection.

By contrast with phylogenetic homology, serial emotion homologues may also theoretically arise over ontogeny, as by-products of the affordances of antecedent emotions coupled with environmental inputs, much as visual word recognition can 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; 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 an adaptation evolved via natural selection. We raise this possibility solely for the sake of argument—moral disgust may well turn out to be an adaptation. If so, moral disgust should evince a profile as distinguishable from sexual disgust as sexual disgust is distinguishable from pathogen disgust, indicative of an optimized fit between its evident social function and fitness-relevant moderators to improve the costs/benefit tradeoffs of social distancing.

In this fashion, panhuman emotion adaptations may set the stage for ontogenetically emergent emotion homologues occurring in some societies, but not in others. If so, there may be societies which, due to parochial norms, institutions, socioecological specializations, or other factors, possess genuinely distinct emotion homologues which have heretofore not been recognized. 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 meaningfully distinct variants of love, pride, anger, fear, disgust, and so forth. By the same token, members of postindustrial nations 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 the expression—or even the existence—of certain emotions would not conflict with evolutionary approaches.

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. C. Barrett, 2007; West-Eberhard, 2003). As the renowned biologist Leigh van Valen put it (1973), "Evolution is the control of development by ecology." To 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 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) 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 benefit from investing time in further sampling.

In investigating whether and to what extent developmental systems are adapted to respond to information relevant to a given emotion, thereby generating contextual variability in the elicitation and expression of phenotypic trajectories, researchers might apply the following strategy:

i) Characterize the fitness challenge that the emotion theoretically addresses.

ii) Take into account the typical range of physical and social environments in which the emotion would have functioned.

iii) Identify the required design features (i.e., what endogenous and/or exogenous information would need to be considered to maximize fitness), including which points in the lifespan contain relevant calibratory information, and at what developmental stage the emotion 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.

Evolutionary approaches to emotion development emphasize the force of selective design, but do not assume that all calibrational contingencies that would be adaptive actually exist, nor that all those found to 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 a lack of available structures suitable for modification. Conversely, sometimes a useful trait turns 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, & H. C. 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 – and well into the twenty-first century! – some affective scientists still invert this fundamental idea, conjuring underspecified notions of 'hardwiredness'. In another persistent misunderstanding, evidence of overlapping proximate mechanisms is often 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. Beyond redressing these confusions, we hope to have introduced novel questions and integrative research of use to the next generation of developmental affective scientists.

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