

Title: Adaptation, co-optation, variation: Emotions in evolutionary context

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“It will be universally admitted that instincts are as important as corporeal structures for the welfare of each species... I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that was profitable. It is thus, as I believe, that all the most complex and wonderful instincts have originated.” - Charles Darwin (1859: 264)

From ‘Instincts’ to ‘Programs’

Darwin (1859) recognized that motivation systems are no less subject to the inexorable force of natural selection than are physical attributes such as eyes, livers, or talons.

Unfortunately, although he produced a study of human emotion expressions (1872), Darwin never fleshed out an account of emotions as motivational adaptations, nor explained how the heritable components of emotions interdigitate with social experience. William James (1890) largely embraced Darwinian theory in his seminal discussion of the emotions (e.g., fear, jealousy, or parental love), and even coined the term *evolutionary psychology*. For example, James compared the imagined delight of a fly toward dung to the attraction a man might feel toward a beautiful woman as equivalently produced via natural selection. However, in a stark departure from evolutionary thinking, James conceptually distinguished emotion from bodily behavior, identifying the former with subjective qualia (e.g., the feeling of being afraid) and the latter with instinct (e.g., running from a bear).

Whereas James defined emotion in terms of subjective feeling, William McDougall (1928) conceived of emotions as thematically related cognitive, physiological and behavioral processes, in a general approach to emotion which may be regarded as an early precursor to modern evolutionary affective science. McDougall postulated the core of the human affective system as a set of instincts (i.e., emotion adaptations) engineered by natural selection to solve

particular adaptive problems by coordinating problem-relevant responses. On McDougall's account, emotional responses produce a set of action tendencies (e.g., the flight response to threat) which incorporate modulating effects of experience, such that individually and culturally acquired knowledge determines which events elicit emotions and which contextually calibrated actions they produce.

During the mid-twentieth century, Magda Arnold elaborated McDougall's model by emphasizing the role of informational appraisals in eliciting emotions, and related action tendencies, evolved to address particular threats or opportunities (Arnold 1960; see Reisenzein 2006). Arnold posited emotion-relevant informational appraisal processes as both reflexive and reflective. In the aftermath of reflexive responses, which she attributed to natural selection, Arnold proposed that a process of reflective appraisal associated with higher cortical brain structures modulates affective intensity and context-relevant behavioral outcomes. Whereas Arnold regarded the reflective mode of cognitive appraisal to be somewhat divorced from the evolved aspects of emotional responses, later evolutionary theorists would encompass both sorts of information-processing into emotion adaptations.

Richard Lazarus, deeply influenced by Arnold's work, popularized the notion that cognitive appraisals are integral to emotion while emphasizing threat-related responses and what Arnold would term the reflective mode. Lazarus (1991) viewed emotions as multilevel syndromes of subjective experience, physiological states, and behavioral tendencies operating in concert with cognitive appraisals of the personal relevance of, and ability to cope with, eliciting events. Robert Plutchik's "psychoevolutionary approach" (1982) similarly framed emotions as functional mechanisms designed to evoke adaptive responses, and argued that uniquely human, complex emotions (e.g., disappointment) arise through blendings of emotions shared with

nonhuman animals (e.g., sadness and surprise). Like Lazarus and Arnold, Plutchik focused on the importance of appraisals of events in triggering particular emotions. Although his blending model has been widely discounted by evolutionists, Plutchik's contention that cognitive capacities such as categorization, inference, counterfactual reasoning and planning evolved in service of emotional drives to address fitness challenges sits easily alongside current perspectives.

Paul Ekman (1992) advanced his basic emotions model during roughly the same period as Lazarus and Plutchik. According to Ekman, evolved emotions carry distinctive, cross-culturally universal signals shared by other primates, among a number of other criteria. Evolutionary affective scientists have generally discounted this stance on the grounds that i) human emotion adaptations should theoretically be tailored to address fitness challenges unique to our species, and that ii) some evolved emotions should not be expected to possess distinct facial expressions, as the detection of these states via facial signals or cues would be orthogonal or contrary to the emotions' functions (e.g., jealousy, Buss 2013; also see Tooby and Cosmides 2008; Al-Shawaf, Conroy-Beam, Asao, and Buss 2016).

In a hugely influential paper, the biologist Robert Trivers (1971) posited emotions related to moralized behavior as adaptations for promoting mutualistic exchange. For example, Trivers argued that gratitude (encouraging continued cooperation) and guilt (prompting relationship-reparative acts) evolved to bolster and maintain fitness-enhancing processes of reciprocal cooperation. Trivers' proposals demonstrated not only the adaptive utility of moral emotions, but also a way in which emotion might theoretically resolve previously longstanding puzzles such as cooperation between genetically unrelated individuals. The economist Robert Frank (1988) adopted and extended Trivers' insights, arguing that emotions such as guilt and love

function as commitment devices that help to motivate individuals not to defect in pursuit of short-term payoffs, and thereby reap greater benefits via long-term cooperation.

Much as Trivers and Frank theoretically bridged theories of emotion and cooperation, the psychiatrist Randolph Nesse extended evolutionary views of emotion to clinical psychology, framing stress-related affective disorders as rooted in functional design. Nesse delineated clinical disorders rooted in malfunctioning affective adaptations from subjectively unpleasant, yet adaptively functional, affective defenses. For example, Nesse (1990) argued that depression may help individuals to adaptively cope with unpropitious environments under some circumstances (e.g., by conserving personal resources), and reframed phobias as hypertrophic expressions of domain-specific mechanisms for managing subtypes of threat (Marks and Nesse 1994).

As the twentieth century drew to a close, the Darwinian view of emotions was increasingly synthesized with the computational concepts of the ascendant field of cognitive science (e.g., Pinker 1997). As Nesse observed, “emotions provide for the mind what software programs provide for the computer... [they] adjust its various parameters to the needs of a particular task” (1990: 269). Over the last three decades, Leda Cosmides and John Tooby have vigorously promulgated this computational approach, and in so doing have largely set the parameters within which most evolutionary psychologists think about emotion today (e.g., Tooby and Cosmides 1990; Tooby and Cosmides 2008; Cosmides and Tooby 2000).

Emotions as Superordinate Programs

From an adaptationist perspective, human emotions arose over eons of distinct, recurrent selection pressures characteristic of hominid social and physical life. Accordingly, cues relevant to these distinct challenges should constitute reliable emotion elicitors, and the behavioral

responses evoked should constitute biologically adaptive solutions to those challenges, in a manner akin to keys fitting specific locks (Cosmides and Tooby 2000).

How, then, do emotions marshal adaptive behavioral responses? Evolutionary psychologists generally conceptualize emotions as *superordinate* information-processing programs that entrain constellations of subordinate cognitive, perceptual, motor and physiological processes (Gervais and Fessler 2016; LeDoux 2003; Oatley and Johnson-Laird 1987; Nesse 1990; Tooby and Cosmides 2008). Emotions thus orchestrate diverse functions, including attention, memory, focal goals, information-seeking, diurnal sleep/wake cycling, categorization, inference, energy and effort levels, and so on, and cannot be reduced to any subcomponent(s).

By updating cognitive parameters, including representations of the self, evolved emotions are thought to produce contextually appropriate responses. For example, a sexually jealous person who represents themselves as of lower mate-value but higher fighting ability than their rival may be inclined toward a relatively physically aggressive form of deterrence; conversely, a sexually jealous person who represents themselves as of greater mate-value than their rival may be inclined to deter infidelity by advising their partner that extra-pair romantic activities would end the relationship. Culturally variable information similarly modulates emotion. For instance, offering to shake with one's left hand in Hindu societies constitutes an insult. The intensity of the anger, and the particular responses potentiated, should be further contingent on contextual factors such as the identity of the offending individual (e.g., a relative versus a stranger), their apparent intentions (e.g., a Westerner may be unfamiliar with local taboos), and social contexts relevant to the costs of punishing the individual (e.g., whether the individual is a business associate). Far from denying the role of cultural learning or contextual contingency in the

operation of the emotions, evolutionists embrace such variability as indispensable to the computational processes yielding adaptive behavior.

The Case of Disgust

Disgust compellingly illustrates functional adaptation. Pathogens exert intense selection pressures (Fumagalli et al. 2011), leading humans and many other species to evolve physiological, cognitive, and behavioral defenses (Curtis et al. 2011). Visual cues of potential pathogens include color, viscosity (e.g., of rotten fruit or blood) and the presence of organisms (e.g., maggots) which colonize animals deceased long enough to be contaminated—correspondingly, all of these stimuli elicit *pathogen disgust* (Tybur, Lieberman, Kurzban and DeScioli 2013). Pathogen disgust similarly relies on contagion-detection mechanisms sensitive to olfactory cues such as chemical compounds present in feces (Wicker et al. 2003) or gustatory cues such as lactic acid (DeSimone, Lyall, Heck, and Feldman 2001).

Once elicited, the computational architecture of pathogen disgust must estimate the likelihood and severity of pathogen presence, and further calibrate the intensity of prophylactic responses by integrating the modulatory inputs of relevant contextual factors (Tybur et al. 2013; Tybur and Lieberman 2016). For example, the risk of contracting food pathogens should be offset by the benefits of acquiring nutritional resources, just as the risk of contracting a disease from one's ill child or sibling should be offset by the inclusive fitness benefits of providing close-proximity care to kin, which presumably explains why pathogenic scents evoke less disgust when associated with kin than with strangers (Stevenson and Repacholi 2005). Theoretically, social contexts such as status differentials should similarly modulate disgust reactions. For example, an American might be less disgusted when offered basashi (i.e., raw

horse meat) by their wealthy Japanese employer than by a subordinate, given the fitness benefits of affiliating with a prestigious resource-holder.

The primary behavioral output potentiated by disgust is withdrawal from the eliciting stimulus (e.g., Roseman, Wiest, and Swartz 1994), including individuals who possess cues of likely illness (Oaten et al. 2011). Beyond general avoidance, pathogen disgust triggers physiological changes that evince design to combat pathogens. For example, disgust is frequently linked with low appetite or nausea (detering pathogen ingestion), and at intense levels can even lead to the expulsion of pathogens—or of food identified as likely to harbor pathogens—via vomiting (Rozin et al., 2008). The prototypical disgust face, characterized by restricted nasal passages, narrowed eyes, and a closed mouth, also evinces design to minimize avenues by which pathogens might enter the body (Fessler and Haley 2006). With respect to the coordination of cognitive processes, pathogen disgust is thought to enhance memory of likely sources of contamination (e.g., observing insects near a restaurants' kitchen), mobilize action-planning to avoid future contact, shift conceptual schemas to emphasize elements pertinent to cleanliness or illness, and so on (see Tybur et al. 2013).

Importantly, behavioral and physiological responses associated with pathogen disgust have been experimentally dissociated from responses to non-pathogenic threats. For instance, physiological increases in oral immune function are triggered upon viewing images related to infectious disease (e.g., dirty toilets) relative to control images pertaining to threats of aggression (Stevenson, Hodgson, Oaten, Barouel, and Case 2011), and viewing images of sneezing or diseased faces likewise heightens production of pro-inflammatory cytokines that resist infection (Schaller, Miller, Gervais, Yager, and Chen 2010). At the level of social motivation, the same sort of pathogen image manipulation intensifies the negative association between trait germ

aversion and inclinations toward sexual promiscuity relative to images of potential aggression (Murray, Jones, and Schaller 2013). Complementarily, priming experiences of close proximity to diseased individuals increases the value ascribed to physical attractiveness—a cue of health—relative to primes of violent threat (White, Kenrick, and Neuberg 2013). Behaviorally, disease primes also induce physical withdrawal from others (Mortensen, Becker, Ackerman, Neuberg, and Kenrick 2010). By contrast, reminders of death increase tendencies to approach others (Wisman and Koole 2003), possibly reflecting functional motivation to affiliate during times of peril or adversity (Kirkpatrick and Navarrete 2006). Taken together, these convergent findings indicate that, consistent with an evolutionary perspective, disease cues activate a suite of responses specifically designed to minimize risk of contagion (Neuberg, Kenrick, and Schaller 2011).

Adaptation via Co-optation: The Case of Sexual Disgust

Selection appears to have copied and modified pathogen disgust to create a distinct adaptation, *sexual disgust*, illustrating the efficient manner by which selection can generate psychological adaptations by co-opting existing mechanisms. This evolutionary re-use process is generally termed *homology*. 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 alongside the conserved antecedent trait. Serial psychological homologues of complex traits such as emotions are hypothesized to be instantiated in patterns of activation and de-activation which, though distinct, draw on significantly overlapping neural and somatic elements (Clark 2010; Holbrook 2016; Holbrook, Fessler, and Navarrete 2016). For example, neural mechanisms that originally evolved for spatial reasoning appear to have been co-opted to represent social relations (e.g., “social distance”; Parkinson and Wheatley 2013). Serial

homology provides a plausible avenue by which the unifying traits shared across cognate emotions may be reconciled with the specializations that differentiate them (Clark 2010; Moore 2013; Holbrook and Fessler 2015).

Sexual intimacy risks pathogen transmission via fluid exchange, in addition to non-pathogenic fitness costs related to the expenditure of time and effort in courtship and child-rearing rather than pursuit of additional mating opportunities or other adaptive goals. Accordingly, selection may be expected to have designed a motivational adaptation guiding individuals to seek or avoid sexual coupling contingent on cost/benefit tradeoffs (Tybur et al. 2013). Sexual disgust should therefore deter sexual activities yielding zero or negligible benefits to genetic fitness, such as intercourse with close kin or non-reproductively viable individuals (e.g., children, the elderly, or members of other species). Space prohibits a full presentation of the intricate mate-quality assessment algorithms (e.g., related to kin-detection, immunological compatibility, or indirect cues of genetic quality) that have been linked with sexual disgust (for a review, see Tybur et al. 2013). Rather, it is the striking degree of overlap between sexual and pathogen disgust that is of focal interest here.

Both pathogen and sexual disgust motivate avoidance of physical contact with potentially harmful bodily fluids. Pathogen disgust thus appears to have presented an excellent preadaptation from which to derive sexual disgust insofar as pathogen disgust should be elicited by sexual fluids and bodily openings. Pathogen disgust plausibly deterred sexual arousal (and vice versa) prior to the elaboration, via serial homology, of a complex sexual disgust adaptation designed to incorporate fitness-relevant variables such as relatedness, age, alternative mating options, reputational costs, etc. (Clark and Fessler in preparation). Finally, it is also telling that sexual disgust can evoke nausea (e.g., imagine graphic sex with your grandparents). Sexual nausea appears to be a by-product of the antecedent emotion of pathogen disgust, illustrating the explanatory utility of considering the

phylogenetic contexts in which new traits emerge.

Moral Disgust: Phylogenetic or Ontogenetic Co-optation?

A number of investigations have implicated feelings of disgust in processes of moral condemnation. Although some researchers characterize disapproval of counternormative acts involving potential pathogen contact (e.g., eating a dead pet) or sexual behavior (e.g., incest) as involving a form of moral disgust (e.g., Haidt 2001), such evaluations are more parsimoniously explicable in terms of pathogen disgust or sexual disgust. However, counter-normative acts which do not involve pathogenic or sexual contact also appear to elicit feelings of disgust which potentiate a novel output: moral condemnation. For example, the levator labii muscle responsible for raising the upper lip in disgust expressions has been shown to correlate with self-reports of subjective disgust, and this action increases as offers grow increasingly unfair in an economic game (Chapman, Kim, Susskind, and Anderson 2009). A parallel pattern of levator labii activity tracks reading about either unfair behaviors or behaviors involving risk of pathogen exposure (Cannon, Schnall, & White 2011). Why should non-pathogenic or non-sexual transgressions elicit disgust? *Moral disgust* may constitute another serial homologue of pathogen disgust, alongside and conceivably deriving some structure from sexual disgust, designed to monitor certain norm violations and to facilitate both literal physical withdrawal and social “distancing” (for a more detailed adaptationist proposal linking moral disgust with social coordination, see Tybur et al. 2013). Alternatively, moral disgust may emerge over ontogeny, as a developmental homologue, via interaction between non-disgust processes of moral judgment and extant pathogen and/or sexual disgust adaptations, much as visual word recognition mechanisms emerge in literate societies from the recycling of neural structures that originally evolved for object recognition (Dehaene and Cohen, 2007; see Barrett, 2012). Theoretically,

homologues produced via selection should have been relatively optimized over deep time, and hence possess the sort of intricate functional circuitry evinced by pathogen or sexual disgust. Hence, future work might assess the extent to which moral disgust evinces distinct moderators from those associated with pathogen or sexual disgust, or whether the fit between norm violations, disgust elicitation, and condemnation is relatively coarse.

Neurocognitive Correlates of Homologous Emotions: The Same, Only Different

Arguably, the most direct assessment of the degree of shared architecture linking pathogen, sexual, and moral disgust homologues would involve neuroimaging. Unfortunately, to date no such neuroscientific comparison has been conducted. However, neuroimaging has been employed to contrast another set of likely serial emotion homologues in humans: *parental love* and *romantic love*. Bartels and Zeki (2004) compared the activation profiles of parental and romantic attachment, noting common recruitment of reward regions (e.g., striatum, ventral tegmental area), as well as comparable anterior cingulate cortex reactivity to images of either the participants' infants or romantic partners indicative of approach and attention-orienting. As expected, parental and romantic love also evinced unique activation patterns. For example, the hypothalamus activated in response to images of romantic partners but not children, evidently reflecting the erotic component of romantic love (Karama et al. 2002). By contrast, periaqueductal grey reactivity was associated with maternal—but not romantic—love, consistent with prior literature correlating this region with maternal behavior (e.g., Lonstein and Stern 1998). With regard to functional cognitive differences, Griskevicius and colleagues (2010) primed participants with memories of attachment partners versus nurturant caregiving, then assessed acceptance of weak persuasive messages. The investigators reasoned, and found, that the prime associated with romantic love would heighten trust and acceptance, thereby reducing critical skepticism; conversely, in line with the need for vigilant

evaluation of potential threats to vulnerable offspring (Fessler, Holbrook, Pollack, and Hahn-Holbrook 2014), the prime associated with parental love heightened critical skepticism toward dubious claims. Further supporting the distinct adaptive functions of parental versus romantic love, parental love is associated with vigilance toward precisely those threats which most reliably killed young children in the ancestral past (e.g., disease, assault by unrelated males; for a review, see Hahn-Holbrook, Holbrook, and Haselton 2011), with no parallel preoccupation syndrome associated with romantic love.

Common Misunderstandings

“Many instincts are so wonderful that their development will probably appear to the reader a difficulty sufficient to overthrow my whole theory.” - Charles Darwin (1859: 317)

Over a century and a half since Darwin proposed biology’s foundational metatheory, it is a strange and remarkable fact that many researchers who study human affective systems minimize, disregard, or even deny the relevance of natural selection. Some of the reluctance to integrate affective and evolutionary science may stem from the interminable debates that dichotomize nature from nurture. In reality, we are uniquely cultural, highly encephalized apes. Culture both structures and is structured by the expression of the human genome. Dismissing the role of culture or learning in studying human emotion adaptations would be like dismissing the importance of aerodynamics in studying adaptations for flight. Contemporary evolutionary psychologists do not equate human emotions with those of nonhuman primates or any other species, nor do they deny the essential role of culture and of learning in the algorithms of the emotions. However, evolutionary psychologists also recognize natural selection as the most compelling explanation of complex, organized behavior, and regard the processes enabling cultural plasticity as themselves evolved specializations for learning in particular domains (e.g.,

Barrett 2012).

Beyond caricaturing evolutionary approaches as positing entirely ‘hardwired’ emotions, there are a number of other common misunderstandings. First, evolutionists do not claim that emotional behavior will increase fitness in every instance, but rather that such tendencies would have increased fitness in the ancestral past when considered in statistical aggregate. Second, claims that emotional behaviors were selected for in the ancestral past should not be taken as claims regarding modern outcomes, which can differ significantly from the environments in which our species evolved (e.g., cravings for salt, sugar and fat are generally maladaptive in resource-rich modern societies). Third, the concept of adaptive fitness should not be conflated with subjective well-being – emotions such as sorrow, anger, shame, or jealousy are all biologically adaptive to the extent that they contribute to the successful transmission of genes across generations. Fourth, whereas researchers often assume that evolved components of emotional responses must be automatic, evolved emotional responses can theoretically include conscious reflection and planning in conjunction with automatic shifts. Finally, an evolutionary approach to the emotions does not predict discrete modularity at the level of psychophysiological implementation, but rather assumes an extensive degree of efficient co-optation. Nevertheless, proponents of *psychological constructionism* have aggressively argued as though Darwinian approaches to emotion are incompatible with either mechanistic co-optation or contextual variation.

Answering Psychological Constructionism

Psychological constructionists observe that emotions are composed of more basic elements that contribute to a variety of affective states (e.g., LF Barrett 2013; Lindquist, 2013; Raz et al. 2016). Evolutionists view emotions as superordinate programs orchestrating myriad

subordinate elements, and hence intrinsically agree. However, constructionists further contend that discrete panhuman emotions *do not exist*, but are rather folk concepts reinforced by language (e.g., ‘anger’ or ‘love’), on the grounds that distinctly lexicalized emotions derive from shared subcomponents and exhibit individual and cultural variation (LF Barrett 2006). As a consequence, constructionists have hypothesized the absence of clearly dissociable neural activation patterns delineating emotions (LF Barrett, Gendron, and Huang 2009; Lindquist and Barrett 2012).

Constructionists highlight the recurrent activation of neural regions commonly associated with any given discrete emotion in both other emotions and in cognitive processes that are conceptually dissociable from affect (e.g., LF Barrett and Wager 2006). For example, fear is widely associated with amygdala activity (LeDoux 2003), but the amygdala is also implicated in positive emotional experiences and in the detection of novelty, and has been generally characterized as functioning to orient attention (Adolphs 2008). Regions conventionally identified with other emotions (e.g., insula and disgust) have been similarly associated with multiple other emotions (e.g., Calder et al. 2001), and a set of cortical midline and frontal regions (e.g., medial prefrontal cortex, posterior cingulate cortex) appear to activate comparably during experiences of any of the emotions conventionally categorized as “basic” (Phan et al. 2002). An influential meta-analysis conducted by Murphy and colleagues (2003) provided some support for emotion-region pairings differentiating fear, disgust, and anger, but simultaneously failed to identify regions distinguishing happiness from sadness. Constructionists have cited such observations of the recurrent activation of particular regions as evidence against discrete emotions (e.g., LF Barrett et al. 2009). However, evolutionary psychologists envision emotions as instantiated in constellations of patterned activation distributed throughout the brain and body,

without one-to-one correspondences between localized brain regions, hormones, or any other single mechanism (e.g., Pinker 1997; Barrett and Kurzban 2006; Tooby & Cosmides 2008; Holbrook and Fessler 2015).

Analytical refinements in recent years have enabled researchers to successfully pair discrete emotions with discrete patterns of distributed brain activation. For example, Vytal and Hamann (2010) utilized activation likelihood estimation, a statistical technique enabling more spatially sensitive comparisons of neuroimaging data, in a meta-analysis of 83 studies, finding distinct, reliably discriminable patterns characteristic of fear, anger, disgust, sadness, and happiness. Saarimäki and colleagues (2016) experimentally induced the same emotions utilizing video stimuli or mental imagery, then analyzed neuroimaging data using a multivariate machine-learning approach well-suited to detect patterned activation of distributed regions (see Kragel and LaBar 2014). Contrary to prior constructionist predictions (e.g., LF Barrett, Gendron, and Huang 2009), Saarimäki et al. were able to discretely classify each emotion according to signature activation patterns, the classification pattern for each emotion generalized from one induction to another (i.e., video or mental imagery), and the emotions were generalizable across different participants. Compellingly, Saarimäki et al. also found that the relative similarity of subjective experiences reported to obtain between the emotions significantly predicted the degree of similarity between neural patterns for those emotions. In convergent support, Sitaram and colleagues (2011) obtained classifiable signatures of brain activity differentiating sadness, fear, and disgust using machine learning. Moreover, in a novel paradigm wherein method actors were asked to arouse feelings of anger, disgust, envy, fear, happiness, lust, pride, sadness, and shame while being scanned, all nine emotions were accurately classifiable by a pattern-matching machine learning algorithm (Kassam, Markey, Cherkassky, Loewenstein, and Just 2013).

In something of a reversal, constructionists have recently joined the growing chorus demonstrating the unique neural signatures of discrete emotions (Wager et al. 2015). Rather than continuing to deny the existence of stably detectable brain signatures of discrete emotions, psychological constructionism has now been framed as providing a singular lens through which to understand how regions from multiple systems, including cortical areas conventionally associated with non-affective cognitive functions, might interactively construct emotions (LF Barrett and Russell 2015; Wager et al. 2015). It bears noting, however, that the distributed, highly multifaceted cortical and subcortical nature of emotion networks is perfectly compatible with the framework espoused within evolutionary affective science since before the turn of the century (e.g., Nesse 1990; Tooby and Cosmides 1990). Simply put, there is no contradiction between the existence of emotion adaptations and either mechanistic re-use or the involvement of cognitive regions.

Psychological constructionists have also taken evidence of cultural variation in emotional phenomena as evidence against evolved emotions (e.g., Barrett 2006; 2013). Without question, culturally contingent folk emotion concepts should be disambiguated from heritable emotions (Fessler 2004; Scarantino 2009). However, emotions are hypothesized to incorporate culturally transmitted knowledge and concepts to calibrate event appraisals, emotion regulation, and the selection of appropriate behavioral outputs (e.g., Markus and Kitayama 1994; Tooby and Cosmides 2008), and this dynamic presumably incorporates folk emotion concepts, including normative emotional behavior in a given society or subculture. Folk emotion concepts thus appear to interact with – and themselves be shaped by — evolved emotions (Gervais and Fessler 2016). In summary, longstanding constructionist objections citing the likely influence of folk emotion concepts on emotional experience, the distributed character of neural substrates, the

integral role of cognition, or the presence of contextual or cultural variability are actually consistent with an evolutionarily informed perspective.

Tree Thinkers and Key Thinkers

Natural selection produces well-engineered solutions to adaptive challenges, yet the evolution of new forms is constrained by existing forms. Evolutionary psychologists vary in the extent to which they foreground selection (e.g., Tooby and Cosmides 2008) versus phylogenetic constraint (e.g., Fessler and Gervais 2010). In his analysis of the descent of human emotion expressions, Darwin himself (1872) emphasized phylogeny over function, and interpreted panhuman aspects of emotion expression as by-products of ancestral traits. Such phylogenetic “tree thinking” generates different predictions than “key thinking” approaches centered on adaptations that fit particular fitness problems like keys in locks. Key thinking deprioritizes the messy details of biological implementation or phylogenetic context in favor of identifying design features. Consequently, predilections toward key versus tree thinking may account for varying tendencies to black box versus delve into the proximate mediators of emotion adaptations.

Future Trajectories of Evolutionary Affective Science

Many evolved traits respond plastically to varying environments (e.g., American eels mature faster and to smaller size in saltwater than in freshwater), in accordance with genetically specified reaction norms (e.g., Barrett 2012). Given that plasticity is heritable, which social or ecological factors interact with reaction norms to produce variation in human emotions? To what extent are the range of environmentally contingent emotion phenotypes by-products versus outcomes of natural selection? In my view, these are the foremost open questions in evolutionary affective science.

Continuing advances in neuroscience and genomics promise to illuminate the specialized

architecture of the human brain, eventually revealing how evolved emotion mechanisms integrate and derive structure from experiential inputs. However, a complete answer will require rich phenomic data on species-wide variation in emotion correspondent with differences in social structure and ecology. Prior cross-cultural work, while valuable, has proceeded in a piecemeal fashion inadequate to ascertain the actual range of emotion phenotypes – a global collaborative network of anthropologists, psychologists, and biologists is required. From an evolutionary perspective, emotion phenotypes should adaptively reflect the exigencies of social and environmental niches, much as emerging results indicate with regard to societal variation in personality structure (e.g., Lukaszewski, Gurven, Von Rueden, and Schmitt 2017). As Darwinian approaches increasingly embrace, mine, and make sense of the variable aspects of emotion, the inertia inhibiting some affective scientists from engaging with evolutionary theory will hopefully be dispersed.

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