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Review

The Evolution of Well-Being: An Anthropology Based, Multidisciplinary Review

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Abstract: Evolutionary perspectives have generated many questions and some answers in the study of human health and disease. The field of evolutionary medicine, and related analytics of evolutionary psychiatry and evolutionary psychology have extended and expanded the way health disorders are viewed by searching for why humans, as a species, are vulnerable to certain pathological conditions. The search is organized into four domains that apply proximate and evolutionary explanations to human traits and developmental sequences. This framework opens inquiry to the ontogeny, phylogeny, mechanism, and adaptive significance of human health conditions. In this paper I argue that evolutionary medicine seems to parallel biomedicine in its primarily pathogenic focus. That is, conditions of pain, suffering, and disorder have received the most attention. Some work has used the architecture of evolutionary medicine to take a salutogenic approach, evaluating the proximate and evolutionary explanations of human well-being. I propose that an evolutionary understanding of human well-being requires a survey of emotions and their relationship with neurobiology, language, and culture. My anthropology based, multidisciplinary review of biopsychosocial processes reveals the way evolution has shaped modern human understanding of well-being through sociolinguistic learning processes and thereby our individual experiences of well-being. These insights have the power to contextualize human suffering and flourishing as we progress toward the goal of attenuating the former and expanding the latter.

Keywords: well-being; evolution; emotion; learning; language; motivation

1. Introduction: Evolution and Well-Being

Evolutionary perspectives have generated many questions and some answers in the study of human health and well-being. The field of evolutionary medicine, and related analytics of evolutionary psychiatry and evolutionary psychology have expanded the way health disorders are viewed by searching for why humans, as a species, are vulnerable to certain pathological conditions. Evolutionary medicine has paralleled biomedicine in its primarily pathogenic focus. That is, conditions of pain, suffering, and disorder have received the most attention. Some work has used the architecture of evolutionary medicine to take a salutogenic approach, evaluating the proximate and evolutionary explanations of human well-being. This paper provides an anthropology based, multidisciplinary review of evolutionary perspectives on human biopsychosocial [1] processes. My goal is to organize evolutionary insights to provide a conceptualization of human well-being that is both accurate and actionable.

I have organized the paper into two main topical sections. The first section provides an overview of evolutionary medicine, evolutionary psychiatry, and evolutionary psychology to show the ways these fields generate inquiries of temporal and biological depth regarding human well-being. I begin by drawing from the work of Randolph Nesse, a founder and leader of the evolutionary medicine and evolutionary psychiatry movements. I then provide an overview of the related field of evolutionary psychology, which is built on some overlapping tenets with evolutionary medicine, particularly in their

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shared analysis of the environment of evolutionary adaptedness and contemporary neuropsychological environmental mismatches.

The second section looks more closely at emotions. I review leading theories of emotion and emphasize evolutionary explanations. The relationship between emotion and motivation is discussed, as these phenomena are closely linked, especially when considering evolutionary and developmental contexts. Asking questions from the evolutionary medicine framework sheds light on the reasons we have feelings, good and bad. I close this section by connecting the evolution of emotion and motivation to learning. Humans, like other animals, learn how to interact with their environment through a variety of pathways that integrate emotion, motivation, language, and socialization. I connect and culminate the pieces of the paper by identifying how language and emotion, as evolved neuropsychological abilities, shape the way we interpret and transmit experiences of well-being at the individual and cultural levels. I conclude with the thesis that using a multidisciplinary evolutionary lens opens pathways of inquiry that advance understanding of emotional, motivational, and sociolinguistic experiences.

2. Evolutionary Perspectives in the Fields of Medicine and Psychology

Health and well-being have become the motivation and goal of professions, scholarship, and individuals the world around. The motivation for most human endeavors can be traced to achieving, maintaining, or supporting well-being, in one's own body and mind, or in others, individually or collectively. Vast portions of public and private resources are allocated to the ideal of well-being, often without pause or question because it is deemed as a universal and moral good. However, defining and understanding health and well-being has been elusive and often contradictory across and within disciplines. Most medical work and social research has taken a pathogenic approach, meaning that disease, suffering, their causes, and their remediation have been the focus. The fields of evolutionary medicine, evolutionary psychiatry, and evolutionary psychology have similarly emphasized pathology, using the timescales and principles of evolutionary biology to produce valuable insights on human health and disease. Increasingly, in these fields and across disciplines, more theories and methods are salutogenic, attempting to identify and explain human flourishing. Applying evolutionary theory to pathogenic and salutogenic questions of human well-being has been a discovery in itself. Perhaps most importantly, evolutionary questions begin to reconcile pathogenic and salutogenic approaches by revealing how biopsychosocial disorders and well-being share related evolutionary underpinnings.

2.1. The Architecture of Evolutionary Medicine

Evolutionary medicine is the enterprise of using evolutionary biology to address problems of medicine [2], including those of psychiatry. Randolph Nesse, a founder of the evolutionary medicine movement, and a psychiatrist by medical training, has developed a framework for applying evolutionary perspectives to human bodily and mental pathologies. Nesse [3] organizes Tinbergen's [4] four questions of ethology to create four domains that apply proximate and evolutionary explanations to single traits and developmental sequences. This framework channels inquiry into the ontogeny, phylogeny, mechanism, and adaptive significance of many human health conditions (figure 1). Importantly, these domains of inquiry are not alternatives, rather compliments. All four are needed for a complete biological explanation of why natural selection has left the human body with traits that make us vulnerable to disease [5, 6]

An analogy is helpful for understanding the benefit of the evolutionary perspective on health [7]: the usual questions of medicine are those of a mechanic (How does it work? What is broken? How do we fix it?), while questions of evolutionary medicine are that of the engineer (How did the body come to be this way? What forces and processes shaped the current form?). As noted previously, and as is evident here, this framework has been

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applied mostly to pathogenic elements of health: vulnerability, disease, psychosis, pain, and other unpleasant symptoms. A goal of this paper is to argue that this same type of analyses can be applied to generate salutogenic inquiries: why has natural selection shaped the human body and mind to be nourished and satisfied by certain experiences?

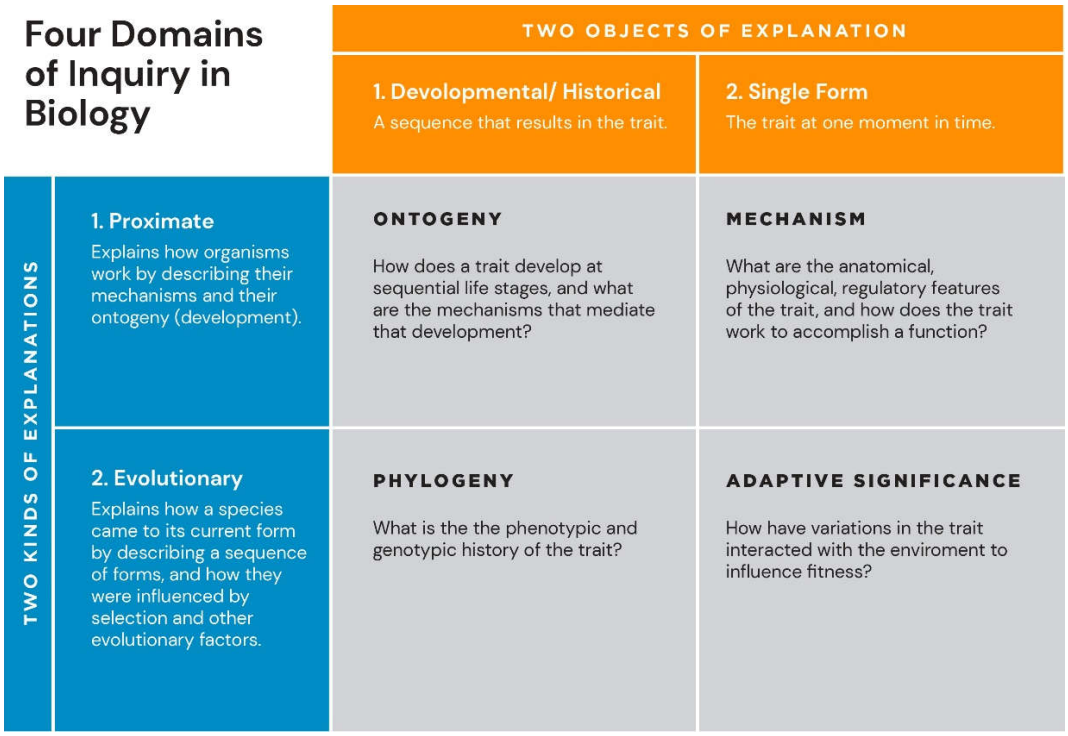

Figure 1. Nesse's organization of Tinbergen's four questions [3]. These domains of inquiry are not alternatives, rather necessary complements for understanding biological phenomena.

The founders of evolutionary medicine identified three primary evolutionary explanations of human vulnerability [8]. First is the inability of slow-moving human selection to cope with fast-evolving pathogens and novel environments. Second are the constraints of natural selection and downsides of trade-offs. Third are the consequences of a selective process that favors reproduction over well-being. These three primary pathways are expanded into eight categories of greater specificity [9]. A list of these eight evolutionary explanations for body/mind vulnerability is provided in figure 2.

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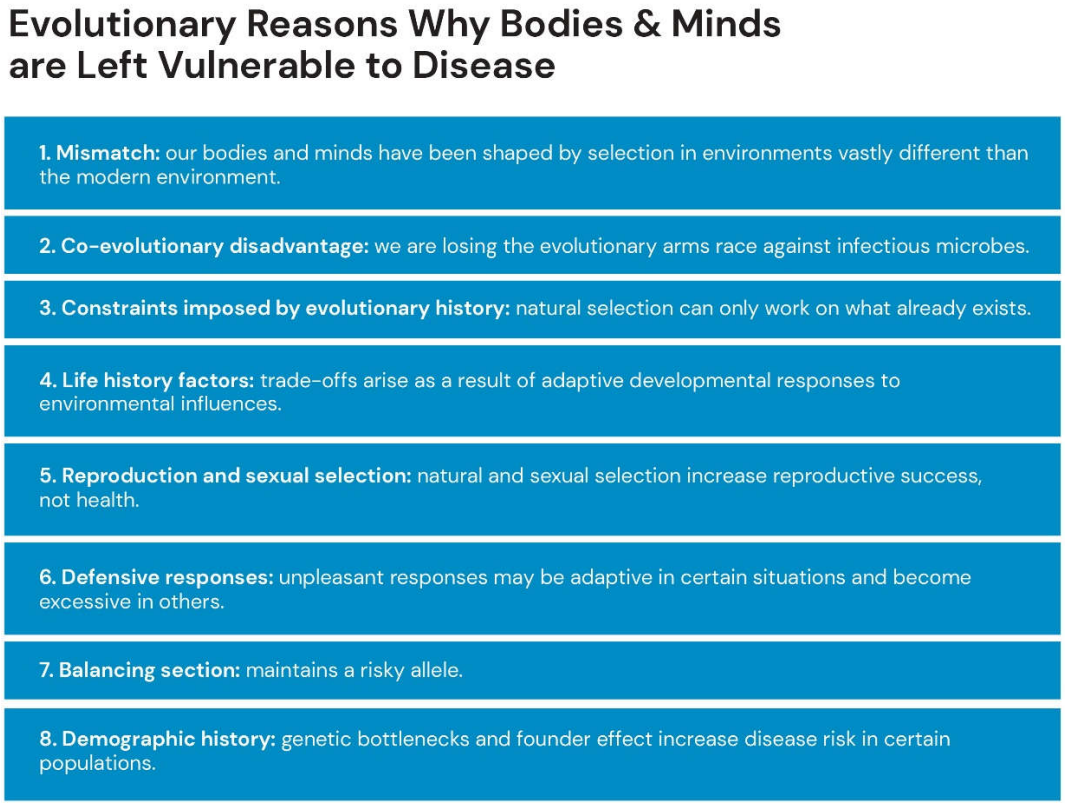

Figure 2. A list of eight pathways of evolutionary influence on disease vulnerability. I created this by combining similar lists in works published by influential evolutionary medicine scholars Randolph Nesse [7] and Peter Gluckman [8]. The final two pathways (#7 and #8) are unique to Gluckman's list and incorporate population genetic effects.

Nesse [7] identifies mistakes in medicine and psychiatry that a foundation in evolutionary biology can help avoid. First, common in medicine, and endemic to psychiatry, is viewing symptoms as diseases. In medical practice, drugs may be used to relieve symptoms of pain, vomiting, cough, fever, neonatal jaundice, irritable bowels, weight gain/loss, sleep disturbance, and inflammation without consideration of cause. This practice can be deleterious in that it misses important clues to underlying pathogenic conditions, and worse may attenuate a naturally protective bodily defense [10]. While much of medicine has advanced to avoid viewing symptoms as diseases, Nesse posits that the fallacy is deeply rooted in psychiatry, which characterizes, diagnoses, and treats low mood, anxiety, and attention deficit as disorders, irrespective of their situational causes. The intangibility of cause in psychological disorders makes this mistake more challenging to overcome in psychiatric practice than in the other domains of medicine.

Evolutionary medicine makes a related, but contrastive mistake. Nesse [7] states that viewing diseases as adaptations is the most common pitfall of evolutionary medicine. This error comes from misunderstanding diseases as naturally selected. To overcome this error, evolutionary medicine must shift from looking for adaptive explanations of disease to describing traits that leave us vulnerable to disease. Proposals about the utility of diseases themselves, including psychosocial pathologies, are wrong from the start. Rather, the existence and persistence of these human plights should be described using combinations of the eight evolutionary explanations of vulnerable traits in figure 2. Explanations of anorexia from evolutionary psychology (the topic of the next section) show how this error of viewing diseases as adaptations manifests. It has been suggested that restricted food intake and excessive exercise characteristic of anorexia are psychological strategies shaped by natural selection to buffer food shortages and flee areas of famine. This attempts to explain the utility of anorexic pathology without evidence of evolutionary reproductive logic. Instead of advancing this "just-so" explanation, evolutionary psychiatry

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considers a combination of factors, including environmental mismatch and social learning. The error of viewing diseases, and in some cases all aspects of human experience as adaptive traits, has been a scab in evolutionary thinking that has led to debate, division, and for some even disregard of evolutionary explanations in health and well-being. Overcoming this issue is crucial for advancing sound evolutionary medicine, psychiatry, and psychology. Besides this, Nesse suggests two other ways in which evolutionary thinking about the psyche and mind must catch up to the rest of medicine. First, is attending to dysregulation of control systems, rather than searching for specific underlying causes or pathologies. Second is an understanding of normal useful functions that neuropsychological mechanisms provide. In this latter suggestion, Nesse is invoking salutogenic realms of health and well-being, aligning with the driving force of the positive psychology movement: knowing what works and why is as important, or more important, than knowing what does not work.

2.1.1. Pain and Pleasure in Perspective

The principles of evolutionary medicine offer a simple but profound view of the foundational experiential dichotomy of pain and pleasure. Experiences of pain and pleasure are central to learning and development, as will be discussed more later in this paper. This dichotomic framework is mirrored in other structurings of human physiology and psychology. The motivational system is organized into approach-avoid reactions to appetitive or aversive stimuli [11-13]. This approach-avoid framework also articulates with the neuropsychology of wanting and fearing, which are dissociable from pleasure and pain. The distinction here lies in the expectancy and temporality of the stimulus: pleasure and pain are responses to a stimulus while wanting and fearing are prospective states in anticipation to a stimulus that has not yet been somatically integrated. Said another way, the stimulus may be present in states of wanting and fearing, but remains "outside" of the person, and not yet productive of a responsive pleasure or pain. Wanting and fearing are states of incentive (i.e., motivational states), while pain and pleasure are responses that influence learning and produce subsequent states of wanting and fearing via memory (figure 3). Another related experiential/motivational dichotomy is neophilia-neophobia, which describes cognitive appraisals of approachability and avoidability in novel ecological contexts. Two distinct neuropsychological systems interact to produce variable individual dispositions towards novel items in context, ranging from appetitive/approachable to aversive/avoidant [14]. Studying these experiential/motivational systems follows Neese's suggestion to focus on evolved regulatory systems rather than seeking single adaptationist causes of specific human emotions/behaviors.

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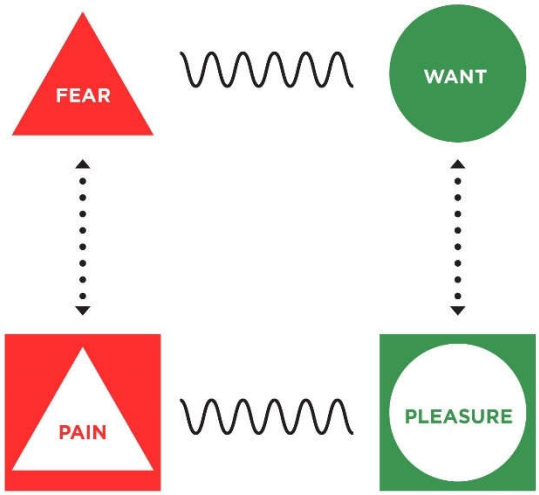

Figure 3. An original schematic to depict relationships between components of the basic experiential dichotomy (pain-pleasure) and the basic motivational dichotomy (fearing-wanting). Pain and pleasure are regulated by distinct neurological systems, as are fearing and wanting. While pain and pleasure are in partial opposition, they are not perfectly contrastive, and the same for fearing and wanting [15] (represented by the wavy connector line). The relational form of these two semi-dichotomies exists in parallel (represented by parallel wavy lines), creating analogous spatial/temporal connections between the parallel components (represented by parallel dotted lines): fearing is to pain as wanting is to pleasure. Fearing and wanting elicit behaviors that alter experiences of pain and pleasure, while pain and pleasure elicit learning that produces states of fearing and wanting in the future (represented by bidirectionality of dotted lines).

Applying Nesse's organization of Tinbergen's evolutionary questions to address the utility of (or least the vulnerability to) pain and pleasure advances our understanding of these foundational animalian experiences, and possibly guides us on how to relate to them. We can pursue ontological questions to explore the development of pain-pleasure/avoid-approach neurobiological mechanisms across the lifecourse. Ontological questions consider the degree to which these systems are innate and genetically determined, and how developmental trajectories result in variable sensitivities of these systems. We can pursue phylogenetic questions of these mechanisms to explore the degree to which pain-pleasure/avoid-approach systems are ancestral or derived, and how modern species relate in their form and utility. We can ask mechanical questions about the neurological structures and pathways that are responsible for experiences of pain and pleasure, and how these structures interact systemically in ecological context to produce motivated behavior. And we can ask questions of adaptive significance to understand how pain-pleasure systems influenced reproductive success in ancestral environments, and why they have persisted in current environments.

While caution is warranted when searching for adaptive functions for human disease [7], pain and pleasure are not diseases or disorders in themselves, they are signals that guide learning and motivation. The regulatory mechanisms that control pain and pleasure can become disordered, and this type of disordered pathology is likely out of the scope of adaptationist explanations. However, the ability to experience pain and pleasure is certainly a trait, and possibly the foundational trait, that has been shaped by natural selection, because it is the mechanism by which individuals psychologically adapt to various environments (i.e., learn).

A basic insight of evolutionary medicine is that most pain is a symptom rather than a disease. And the same can be said for pleasure. Few doctors need an evolutionary medicine course to comprehend this. A patient complaining of pain is rarely provided with pain-killers and sent away without a work up. Rather, the cause of the pain is sought out. Unfortunately, as Nesse [7] points out, this basic distinction between symptom and cause is often missed in psychiatry when dealing with complaints of psychological pain. In these

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cases, the psychological pain itself is diagnosed as the disorder, rather than a symptom. The issue becomes more complicated for both physiological and psychological manifestations when we realize that the regulatory systems of pain-pleasure can become disordered in ways that are the underlying cause of debilitation (i.e. a disease). Neuropathy and substance addiction are examples of pathological dysregulation. These insights are important for everyone because merely thinking about pain and pleasure from an alternative perspective has the power to alter experiences of them. Cognitive and sociolinguistic conceptualizations of pain and pleasure [16] and modes of somatic/bodily attention [17] can influence evaluations and experiences of pain and pleasure.

2.2. Evolutionary Psychology: Sense and Nonsense

The theory of evolution has always been scandalous. It is simultaneously complex and simple, liberating and confining, awesome and materialist. Some people are enamored by its explanatory power, others fear it as a tribal religion. It has caused division in families, churches, governments, and universities. Even within anthropology departments, the discipline most responsible for the study of human evolution, staunch differences exist in attitudes about what and how much variation in human experience can be explained by evolution. For those of us who are compelled by evolutionary thinking, there can be a natural tendency to carve experience into categories defined by function and view most everything as an adaptation [7]. This "adaptationist" perspective is erroneous as the expanded version of viewing diseases as adaptations (discussed previously). Ranging from extreme adaptationist views to moderate perspectives, various schools of thought have emerged that take different angles on evolutionary explanations of human experience [18]. From the middle to the other, anti-adaptationist extreme, social scientists have expressed skepticism, and even hostility, regarding explanations of traits' adaptive utility, pointing instead to culture and learning. A thesis of this current paper is that learning serves as the crux of reconciliation between the extremities of viewpoints. As discussed previously, dichotomous neuroregulatory systems of pleasure-pain, wanting-fearing, and neophilia-neophobia are neuropsychological traits that have been shaped by natural selection. Interestingly these traits, with clear evolutionary bases, are the mechanistic pathways through which culture and learning have their influence on thought and behavior.

Kevin Laland and Gillian Brown have written a book called *Sense & Nonsense* [18] to overview debates across evolutionary perspectives on human behavior. Their review includes human sociobiology, human behavioral ecology, evolutionary psychology, memetics, and culture-gene coevolution as distinct but integratable analytics for explaining human conditions of suffering and well-being. These approaches differ mostly in methodological and conceptual habit, leading some to see them as providing competing views of human behavior. However, *Sense & Nonsense* demonstrates and concludes that these analytics are complementary, consistent, and most powerful when integrated. Elements of each "church" of thought have been rightly critiqued and shown fallible. Inflammatory declarations, careless popularizations, and adaptationist storytelling have provoked hostile disapprobation from sociocultural theorists. Despite these challenges, contemporary versions of each approach in this still-young field have been updated with rigorous theorizing and empirical testing to provide sound evolutionary insights.

Of the various forms of evolutionary analysis of human behavior, evolutionary psychology has emerged as the most popular [18]. Its success likely relates to the ease in which it translates theory into scientific research, which in turn becomes visible, adopted, and popularized by the media. Evolutionary psychology is characterized by targeting human universals, which is less threatening than evolutionary explanations of human differences to critics who associate evolutionary explanations with reductionistic racism. Central to evolutionary psychology are hypotheses about evolved psychological mechanisms as adaptations that underpin human mental and behavioral universals. Researchers and theorists in this tradition focus on the mismatch between contemporary environments and psychological mechanisms selected in the environment of evolutionary adaptedness.

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They emphasize domain-specific mental organs/modules as adaptations to problems in ancestral environments (conceived of as the Pleistocene environment inhabited by stone-age hunter gatherers). The neuropsychological mechanisms of pain-pleasure and fearing-wanting (discussed above, see figure 3) are examples of domain-specific, naturally selected mental modules. However, these foundational mechanisms extend much deeper into the ancestral past than Pleistocene hunter-gatherers. The approach-avoid motivational framework is shared by most multicellular organisms, and even single cell organisms [19]. Evolutionary psychologists generally theorize and study more derived, complex psychological mechanisms that evolved to become human universals like speech and language, certain emotions and corresponding facial expressions, phobias, aggression and cooperation, and preferences in partners [20]. For example, much evolutionary psychology work on sexuality and emotions, like the adaptiveness of jealousy, has been popularized. In this example, theory can be empirically tested by measuring jealousy in participants placed in varied sexual contexts [21].

2.2.1. Cruelty and Kindness in Perspective

While evolutionary psychology has been marred by weak but popular studies that contrive a "just-so" evolutionary story based on Pleistocene stereotypes, it has also contributed sophisticated evolutionary thinking to elucidate the human mind, particularly proximate mechanisms [18]. The field has brought into evolutionary focus crucial human universals that influence health and well-being. In a society where physical interpersonal violence remains a leading cause of debilitating injury [22], half of marriage unions dissolve [23], and emotional distress and deaths of despair continue to rise [24], applying evolutionary logics to disturbing behaviors and psychological mechanisms seems urgent. While remaining diligent to avoid condoning an overly gendered, brutish psyche, the quest to illuminate innate psychological mechanisms can help to explain, normalize, and thereby relieve confusion and shame of shared mental tendencies. More positively, the work of evolutionary psychology can integrate a salutogenic approach to identify the most effective ways to satisfy innate psychological mechanisms, maximize cooperation, and guide individual and societal efforts on best practices to support well-being. In short, by studying psychological mechanisms, evolutionary psychology can identify both mismatches and matches to remediate the former and promote the latter. Some scholars have already gone to work on this task [25, 26]. Having reviewed the leading disciplines that apply evolutionary analytics to the study of human health and well-being, let us now turn to the progress they have made in understanding human emotion and motivation, the foundation of subjective well-being.

3. The Evolution of Emotion

The terminologies and concepts regarding emotions, as with those regarding health and well-being in general, are characterized by inconsistency and ambiguity within and across disciplines. The basic definition of what emotions are, how many emotions there are, and what is normal and abnormal emotionality remains controversial. Nesse [7] suggests that common misunderstandings and oversights must be addressed if the controversies are to be resolved. First, is the failure to recognize emotions as useful, for our genetic reproduction that is (see figure 2, #5 & #6). Second, is failing to explain emotions beyond proximal mechanisms (see figure 1). Third, is conceptualizing emotions as part of a designed system in which each emotion has a different function. In Nesse's evolutionary view, single emotions are multi-functional, and single functions may be served by various emotions, depending on the situation. This section of the paper provides a general overview of emotions from an evolutionary perspective that attempts to integrate Nesse's suggestions for a more accurate and complete conceptualization.

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3.1. Theories of Emotion

Nesse [7] defines emotions in explicitly evolutionary terms, as modes of operation (or specialized states) that increase the ability to cope with certain situations (i.e., meet adaptive challenges to maximize reproductive success). When working toward a useful definition of emotion it is important to consider other related terms. Psychologists typically differentiate the terms emotion, mood, and feeling [27]. Emotion (sometimes called affect) comprises an immediate specific response to environmental stimuli or internal thoughts. Emotions have three interactive components: physiological changes, behavioral reactions, and a feeling based on cognitive appraisal of the other two components in an environmental context. So, a feeling is the subjective experience of the emotion. Alternatively, moods are diffuse, lasting, and less-specific emotional states without a clear identifiable trigger. Despite these distinctions, researchers and practitioners using the DSM, which is the taxonomic and diagnostic tool published by the American Psychiatric Association, have historically used "mood disorders" as the broad taxonomic category under which various "emotional disorders" are grouped [28]. This taxonomic ordering likely relates to the temporal dimensions of diagnosis with the DSM, which specifies criteria for minimum duration of disordered emotionality.

Theories that guide categorization of emotions have been abundant, and a few incorporate Nesse's organization of Tinbergen's four questions for evolutionary explanation. As has been typical of most medically oriented enterprises, proximal mechanisms have been the primary focus of explanation. The circumplex map of emotion [29, 30] describes the proximal mechanism in a way that is open to Tinbergen's other domains of evolutionary inquiry. In this model, emotions vary according to degree of valence (ranging from positive/pleasure to negative/pain) and physiological arousal (ranging from low activation to high activation). Crossing these two dimensions and plotting emotions circularly around them creates a "circumplex" map of emotional categorization (figure 4). This model allows for the definition of emotion as a universal psychological mechanism (a goal of evolutionary psychology), with an open-ended generativity for individual learning and cultural variation. However, this model has been critiqued for viewing positive and negative experiences as existing on opposite, contrastive ends of a continuum. I addressed this misconceptualization of pain-pleasure as perfectly contrasting previously in this paper (see figure 3). Indeed, neurological studies have shown that mixed emotional states exist that include both negative and positive valence [31].

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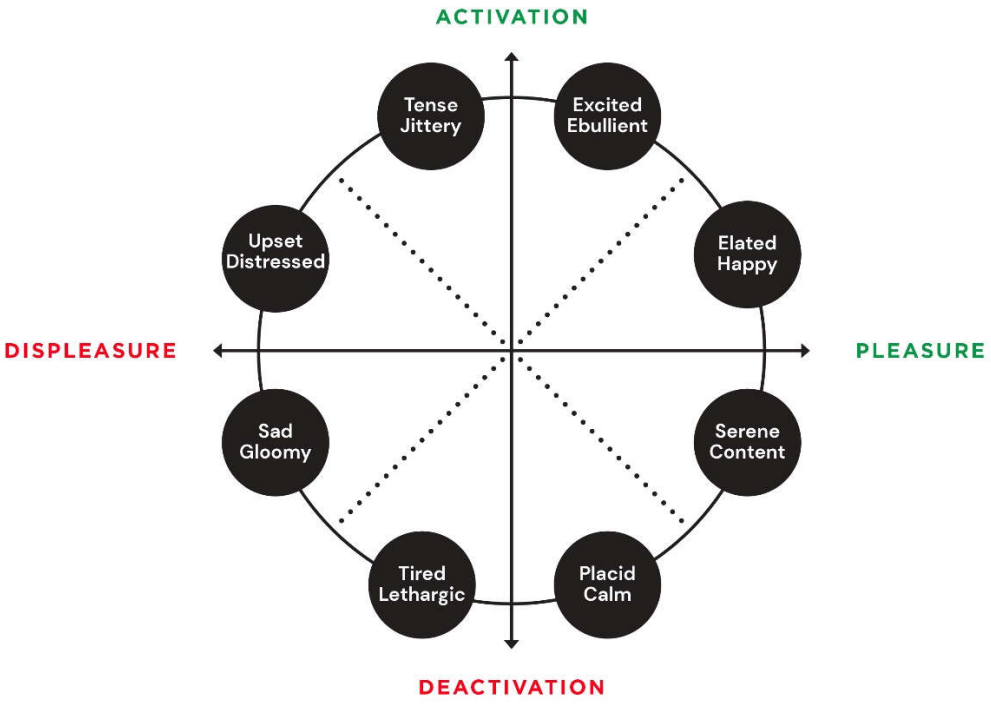

Figure 4. A circumplex map of emotions along the dimensions of valence (pleasure-displeasure) and arousal (activation-deactivation), based on the work James Russell [30]. This style of categorization requires the evolution of only two basic emotional "ingredients", which when combined with cognitive-linguistic ability and experience is generative of unlimited formulations of specific emotions. This model is consistent with research that finds a few basic human universal emotions (e.g., sad, happy, fear, anger), and abundant individual and cultural variation [32]. .

Another set of emotional theories that articulate with evolutionary thinking differentiate between primary emotions and secondary emotions. From this perspective, primary emotions are innate, evolutionary adaptive, and universal. Secondary emotions are blends and variants of primary emotions based on social learning and cultural context [33]. Comparing the ontogeny and mechanisms of emotion and language demonstrates how genetically based, universally shared neurocognitive modules can generate superficial variations via learning and development. Humans are born with a universal capacity for language, structured according to the basic unit of phonemes (sounds), their organization into morphemes (minimal sound clusters with meaning), rules of syntactic grammar (ordering and combining morphemes), and rules of pragmatics (social rules). This structural framework of speech-language communication is genetically based and neuropsychologically innate. However, the manifestation of language is entirely dependent on the social and linguistic input a developing human receives. Without input, the underlying neurocognitive mechanisms of language learning and structure (i.e., the "language faculty") seems to dissipate after a critical period of time has elapsed [34]. The ability to distinguish between phonemes is lost for phonemes not present in the developmental linguistic environment [35]. Variation in morphology, syntax, and pragmatics seem to be nearly unrestricted and develop in accord with the sociolinguistic developmental environment.

I am arguing here, perhaps newly, that the circumplex and primary-secondary models of emotion posit a mechanism of development analogous to that of language. Humans are born with the basic capacity to experience and subjectively feel emotions as combinations of valence and arousal. The four poles of the circumplex model provide physiologically straightforward, universally experienced emotional states. How these basic emotions are labeled, valued, and attended to are driven by sociolinguistic learning and cultural environment, even more so for emotions characterized by physiologically ambiguous or complex combinations. For example, naming and evaluating the bittersweet feeling of nostalgia takes sociolinguistic input. It is interesting to consider if a critical period of

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sensitivity may also exist in emotional development, as it does for language. Are the salient elements of emotion in a given culture only available for developmental integration during a critical period of necessary exposure?

Expanding the explanatory lens from proximal mechanisms to Tinbergen's other questions, Jablonka and colleagues [36] have taken an "evolutionary-developmental" perspective to argue that emotion and language co-evolved through shared pathways of culture-driven adaptation. They emphasize the structural "evo-devo" similarities of emotion and language, and the interdependence of their current forms. Indeed, viewing emotions as adaptive and evolved is important for understanding them. While viewing emotional disorders as adaptations is a critical error, viewing emotions in general as adaptative is a crucial insight. The capacity for emotions and the ability to learn from them provided an adaptive benefit in ancestral environments, and this benefit continues in some situations today. By motivating behaviors in response to situations, emotions can guide solutions to problems of survival and reproduction. Most work on the evolutionary function of specific emotions has been applied to negative emotions [37], while others have focused on the function of positive emotions to broaden thought-behavior repertoires and build personal resources [38].

Nesse [7] posits that trying to match each emotion to a single function misrepresents emotions as part of a designed machine. As stated previously in this section, he proposes that an evolutionary science of emotion must realize that certain emotions serve multiple functions, and certain functions may be served by various emotions. It is not one-to-one, but rather an interactive web of environmental stimuli, physiological reactions, cognitive appraisals, behavioral modifications of the environment, and so on. In this vein, some researchers have identified generalized cognitive and social functions of emotions [39, 40]: signaling the importance of stimuli to personal goals, preparing actions aimed at achieving those goals, social communication, and strengthening interpersonal relations. Nesse develops a theory of emotion in his book, *Good Reasons for Bad Feelings*, that articulates with the approach-avoid framework of motivation and the circumplex model of emotion (these models were discussed previously, see figures 3 and 4). In this formulation, the positive emotions motivate organisms to seek out and stay in situations that offer good fitness opportunities, while negative emotions motivate avoidance and escape from situations of threat and loss of fitness. This shows how the dimension of valence (ranging from positive to negative) in the circumplex map of emotion evolved by providing a selective advantage. Nesse does not directly address the circumplex model's other dimension, arousal, which is where his theory diverges. Instead of a full circle, Nesse conceptualizes a half-circle shape rooted in arousal because only arousing situations with threats or opportunities influence fitness (figure 5).

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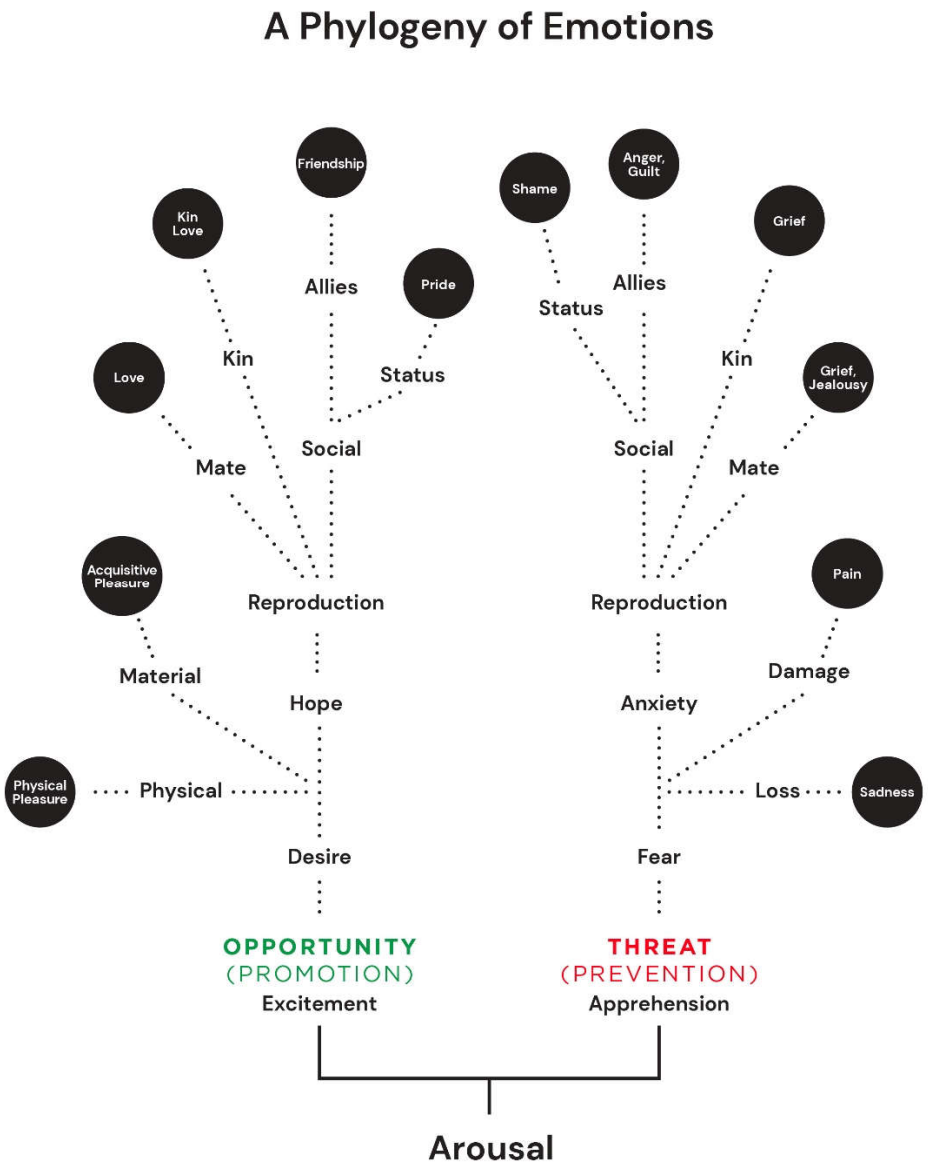

Figure 5. Nesse's conceptualization of emotions as a phylogenetic tree [7]. This model necessitates arousal as a basis for emotion, which contrasts with the circumplex model in figure 4 that includes low arousal (i.e., deactivation) as half of the emotional spectrum.

Nesse's model of emotion as arousal split into oppositional motivational states (labeled promotion and prevention in figure 5) connects with the work of Hans Eysenk and Jeffery Gray. Eysenk [41] develops a theory of optimal arousal, in which individuals prefer to operate, and operate best, at some optimal level of arousal. Some people have a resting level that is below their optimal level, while others have a resting level higher than their optimal level. Deviations from one's optimal level cause emotional states of boredom (when lower than optimal) and anxiety (when higher than optimal). These emotional states prepare behaviors that modify the environment in ways that increase or reduce stimulation to better achieve the optimal level of arousal. Jeffery Gray [42] expands on approach-avoid motivation and learning to propose three neuropsychological systems that help organisms respond adaptively to reinforcement and punishment. The behavioral approach system (BAS) is oriented to pleasure and the pursuit of rewards (combining the mechanisms of wanting and liking in my model, figure 3). The behavioral inhibition system (BIS) is oriented to punishment, is linked with anxiety, and cautiously slows pursuits when perceiving signs of threats. The flight-fight-freeze system (FFFS) correlates with the

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sympathetic nervous system, which activates fear and behaviors of immediate self-preservation.

All of these theories, while differing in some ways, revolve around the premise that the systems and structures of emotion, motivation, and learning are evolved products of natural selection and interact in developmentally plastic ways to produce situational-specific experiences of health and well-being. Looking across the spectrums of valence and arousal, advantage does not go to those who are continuously anxious, fearful, peaceful, or joyful, but rather to those who experience and act on emotions in accord with environmental conditions. For humans, environmental conditions comprise a complex mix of natural, social, and cultural stimuli. This complexity necessitates a great deal of plasticity, learning, and development in a multi-layered sociocultural context to respond in ways that are emotionally consonant [43], and therefore adaptive. As I have suggested throughout this paper, a review of evolutionary perspectives on well-being would be incomplete without a dedicated look at learning and its components, most of which have been discussed already.

3.2. Cognition, Language, and the Centrality of Learning

The mechanisms of learning are multitudinous, and many are shared across organisms. Psychology has produced the most scholarship on associative learning, in which the brain, either consciously or unconsciously, associates stimuli or events. The mechanisms of associative learning can be viewed as an ancestral trait with deep evolutionary roots [19, 44]. Operant conditioning is a powerful form of associative learning which increases behaviors resultant in pleasant outcomes and decreases behaviors resultant in unpleasant outcomes. Much organismic behavior can be attributed to, and even reliability predicted by, associative learning [45]. While the basic emotional dimension of pain-pleasure and the basic motivational/behavioral dimension of avoid-approach are biologically ancestral and widely shared, they are also foundational to more sophisticated learning processes. The mechanisms of learning, which have genetic and molecular bases [46], are acted on by natural selection, producing variation in learning across species. These variations in learning can be viewed as forms of descent with modification and specialized adaptations. Humans are equipped with effective sociolinguistic mechanisms of learning, to which anthropology has most closely attended [47, 48], including social observation/modeling, enculturation, and socialization. These types of learning take a fascinating holonic form [49] with emotion and language, in which the whole is simultaneously a part, and vice versa. By this I mean that humans *learn* emotion, language, and culture, and also learn *from* emotion, language, and culture. These specialized learning mechanisms both reflect the underlying innate neurobiology and produce the undetermined cultural and psychological variation in human experiences. This point is clarified with a popular phrase in education, "at a certain point children switch from learning to talk/read to talking/reading to learn" [50]. Learning itself takes an evolutionary-developmental form, making it a compelling subject of explanation using Nesse's organization of Tinbergen's four questions.

The evolutionary theorists of psychology and behavior perceive the mechanisms of learning as molded by natural selection. From this shared perspective, various evolutionary schools of thought have theorized on the role of learning and culture in human health and well-being [18]. These theories differentially emphasize cognitive, linguistic, and social practices that conspire to produce limited human universals and ample human variation. Theorists of human behavioral ecology view humans as predisposed to learn and socially transmit behaviors that maximize inclusive fitness in their specific ecological context. In this view, learning how to satisfy personal goals in an environmental context is broad and flexible. From this flexible learning, cultural variation springs as part of humans' general mechanism of behavioral adaptation. For human behavioral ecologists, variation by context is the target of study. Contrastingly, evolutionary psychologists target human universals and the underlying psychological mechanisms these human universals imply. Learning, from this perspective, occurs through cognitive mechanisms of

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information processing that evolved (i.e., were reproductively beneficial) in the environment of evolutionary adaptedness. Compared to the human behavioral ecologists who emphasize the flexibility of learning to match behavior to environments, evolutionary psychologists ascribe less flexibility to human cognition, which explains their emphasis on pathogenic conditions and contemporary environmental mismatches. This distinction can be understood by contrasting Steven Pinker's theory of the "language instinct" [51] with Elinor Ochs and Bambi Schieffelin's theory of "language socialization" [52]. Pinker's theory emphasizes the innate universality of language as an information processing mechanism, while Ochs and Schieffelin emphasize the way that language produces cognitive and experiential variation and then socially transmits that variation. I perceive no conflict, only complement, between these perspectives.

Some evolutionary thinkers have advanced a theory of memetics, proposing that the observational/imitative mechanisms of learning create cultural evolution that is separate from genetic evolution [53]. In this view, culture itself is a form of phenotypic plasticity that evolves separately from genes through the selective forces of social learning. Other approaches accommodate the interaction between genes and culture, proposing models of gene-culture coevolution (e.g., [54]). From this perspective, cultural information is transmitted via social learning, and social learning is structured according to evolved biological dimensions of emotion and motivation. All of these perspectives attempt to organize the same components of biology and culture and the same mechanisms of learning and social transmission. Where they differ is how these components and mechanisms relate to each other and their proportional influence on human behavior and well-being.

Social learning is central to culture, and for humans social learning occurs through two primary pathways: behavioral observation/imitation and language socialization [16, 52]. These pathways depend on the interaction of emotion and language, at the individual's cognitive level and at the sociolinguistic level. Theory and research on language socialization posits that language creates and transmits culture, and thereby creates and transmits experiences of agency and well-being. Variation in language results in different conceptualizations of emotion across cultures. Variation in the socialization of these conceptualizations results in different experiences of well-being [54, 55]. Nesse [7] states that the English word "emotion" lacks exact translation across many languages, and words to describe certain feelings exist in some cultures but not others. Wierzbicka, in a study of emotion and language across cultures, suggests humans share a "semantically primitive" concept of feeling, and that a few feelings like happy, sad, shame, and fear universally match with certain situations [32]. These studies indicate that the basic foundations of emotion are shaped by natural selection, which provides a template from which learning and developmental expansion of emotional experience occurs. Early in development, the basic emotion-motivation framework is the foundation of associative learning; later in development it becomes the object of language socialization practices leading to cultural variation. The basic neurophysiology of emotion is limited to a couple evolved dimensions, and it is only through the cognitive and social filters of developed language that emotions manifest in endless forms most beautiful [56-59].

4. Conclusions

Although complex and dynamic, the phylogenetic, developmental, mechanistic, and adaptive formulations of human emotions have taken shape through this paper. The capacity for emotion can be understood as an evolved psychological mechanism which forms the basis for learning. Uniquely human forms of sociolinguistic learning are influenced by ancestral mechanisms of emotion and motivation, but also build on and alter these ancestral mechanisms through developmental plasticity. Therefore, human well-being has few universal elements and many variants.

Evolutionary perspectives in medicine, psychiatry, and psychology have guided inquiries into human well-being that have advanced understanding beyond mechanical pathologies. By broadening the scope of research on human biopsychosocial well-being, a

more complete picture is starting to emerge. As with all scholarly perspectives, mistakes and fallacies have been highlighted by critics, and the evolutionary study of human behavior, emotion, learning, and well-being must continue to amend its assumptions to avoid dogmatic entrenchment. Through continuous self-reflection and openness to revision, evolutionary science becomes an avenue of great insight to the human condition. These insights have the potential to benefit individual and societal self-awareness of how and why we think, feel, and act in ways that detract and ways that promote well-being. Individual and societal self-awareness is a crucial first step in efforts to reduce suffering and advance well-being, which is the distilled motivation of most human enterprise.

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References

1. Engel, G. L. (1977). The need for a new medical model: a challenge for biomedicine. *Science*, 196(4286), 129-136.
2. Nesse, R. (2008) "The importance of evolution for medicine" in Trevathan WR, Smith OE, McKenna JJ. *Evolutionary medicine and health: New Perspectives*. Oxford University Press: Oxford, UK; pp. 416-31.
3. Nesse, R. M. (2013). Tinbergen's four questions, organized: a response to Bateson and Laland. *Trends in Ecology & Evolution*, *28*(12), 681-82.
4. Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für tierpsychologie*, *20*(4), 410-433.
5. Nesse RM, Stearns SC. (2008) The great opportunity: evolutionary applications to medicine and public health. *Evolutionary Applications,1*:28–48.
6. Nesse, R. M., & Williams, G. C. (1995). *Why we get sick: The new science of Darwinian medicine.* Vintage: New York, NY.
7. Nesse, R. M. (2019). *Good reasons for bad feelings: insights from the frontier of evolutionary psychiatry.* Penguin: New York, NY.
8. Gluckman, P. D., Low, F. M., Buklijas, T., Hanson, M. A., & Beedle, A. S. (2011). How evolutionary principles improve the understanding of human health and disease. *Evolutionary applications, 4*(2), 249–263.
9. Gluckman PD, Beedle AS, Hanson MA. (2009) *Principles of Evolutionary Medicine*. Oxford: Oxford University Press: Oxford, UK.
10. Brett J and Niermeyer S. (1999) "Is neonatal jaundice a disease or an adaptive process?" in Trevathan WR, Smith OE, McKenna JJ. *Evolutionary medicine and health: New Perspectives*, Oxford University Press, pp. 7-25.
11. Berridge, K. C., Robinson, T. E., & Aldridge, J. W. (2009). Dissecting components of reward: 'liking', 'wanting', and learning. *Current opinion in pharmacology, 9*(1), 65-73.
12. Corr, P. J. (2013). Approach and avoidance behaviour: Multiple systems and their interactions. *Emotion Review, 5*(3), 285-290.
13. McNaughton, N., & Gray, J. A. (2000). Anxiolytic action on the behavioural inhibition system implies multiple types of arousal contribute to anxiety. *Journal of affective disorders, 61*(3), 161-176.
14. Greggor, A. L., Thornton, A., & Clayton, N. S. (2015). Neophobia is not only avoidance: improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences, 6*, 82-89.
15. Watson, D., Wiese, D., Vaidya, J., & Tellegen, A. (1999). The two general activation systems of affect: Structural findings, evolutionary considerations, and psychobiological evidence. *Journal of personality and social psychology, 76*(5), 820.
16. Corwin, A. I. (2021). *Embracing age: How Catholic nuns became models of aging well.* Rutgers University Press: New Brunswick, NJ.
17. Csordas, T. J. (2002). "Somatic modes of attention." in *Body/Meaning/Healing* (pp. 241-259). Palgrave Macmillan: New York, NY.

18. Laland, K. N., Brown, G. R. (2011). *Sense and nonsense: Evolutionary perspectives on human behaviour*. Oxford University Press: Oxford, UK.
19. Lyon, P. (2015). The cognitive cell: bacterial behavior reconsidered. *Frontiers in microbiology, 6*, 264.
20. Brown, D. E. (2004). Human universals, human nature & human culture. *Daedalus, 133*(4), 47-54.
21. Buss, D. M. (1994). *The evolution of desire: Strategies of human mating*. Basic books: New York, NY.
22. Abelson-Mitchell, N. (2008). Epidemiology and prevention of head injuries: literature review. *Journal of clinical nursing, 17*(1), 46-57.
23. Raley, R. K., & Sweeney, M. M. (2020). Divorce, repartnering, and stepfamilies: A decade in review. *Journal of Marriage and Family, 82*(1), 81-99.
24. Case, A., & Deaton, A. (2021). The great divide: education, despair, and death. *Annual Review of Economics, 14*(1).
25. Geher, G., & Wedberg, N. (2019). *Positive evolutionary psychology: Darwin's guide to living a richer life*. Oxford University Press: Oxford, UK.
26. King, P. E., Barrett, J. L., Greenway, T. S., Schnitker, S. A., & Furrow, J. L. (2018). Mind the gap: Evolutionary psychological perspectives on human thriving. *The Journal of Positive Psychology, 13*(4), 336-345.
27. Godovykh, M., & Tasci, A. D. (2021). Emotions, feelings, and moods in tourism and hospitality research: Conceptual and methodological differences. *Tourism and Hospitality Research, 22*(2): 247-253.
28. Parker, G. F. (2014). DSM-5 and psychotic and mood disorders. *Journal of the American Academy of Psychiatry and the Law Online, 42*(2), 182-190.
29. Kuppens, P., Tuerlinckx, F., Russell, J. A., & Barrett, L. F. (2013). The relation between valence and arousal in subjective experience. *Psychological bulletin, 139*(4), 917.
30. Russell, J. A. (2003). Core affect and the psychological construction of emotion. *Psychological review, 110*(1), 145.
31. Hoemann, K., Gendron, M., & Barrett, L. F. (2017). Mixed emotions in the predictive brain. *Current Opinion in Behavioral Sciences, 15*, 51-57.
32. Wierzbicka, A. (1999). *Emotions across languages and cultures: Diversity and universals*. Cambridge University Press: Cambridge, UK.
33. Ekman, P., Friesen, W. V., O'sullivan, M., Chan, A., Diacoyanni-Tarlatzis, I., Heider, K., Krause, R., Pitcairn, T., LaCompte, W.A., Scherer, K., Tomita, M., Ricci-Bitte, P.E., & Tzavaras, A. (1987). Universals and cultural differences in the judgments of facial expressions of emotion. *Journal of personality and social psychology, 53*(4), 712.
34. Hurford, J. R. (1991). The evolution of the critical period for language acquisition. *Cognition, 40*(3), 159-201.
35. Friedmann, N., & Rusou, D. (2015). Critical period for first language: the crucial role of language input during the first year of life. *Current opinion in neurobiology, 35*, 27-34.
36. Jablonka, E., Ginsburg, S., & Dor, D. (2012). The co-evolution of language and emotions. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1599), 2152-2159.
37. Lench, H. C., Bench, S. W., Darbor, K. E., & Moore, M. (2015). A functionalist manifesto: Goal-related emotions from an evolutionary perspective. *Emotion Review, 7*(1), 90-98.
38. Fredrickson, B. L. (2004). The broaden–and–build theory of positive emotions. *Philosophical transactions of the royal society of London. Series B: Biological Sciences, 359*(1449), 1367-1377.
39. Moors, A., Ellsworth, P. C., Scherer, K. R., & Frijda, N. H. (2013). Appraisal theories of emotion: State of the art and future development. *Emotion Review, 5*(2), 119-124.
40. Tsai, J. L. (2017). Ideal affect in daily life: Implications for affective experience, health, and social behavior. *Current Opinion in Psychology, 17*, 118-128.
41. Eysenck, H. J. (1967). *The biological basis of personality* (Vol. 689). Transaction publishers.
42. Gray, J. A. (1990). Brain systems that mediate both emotion and cognition. *Cognition & emotion, 4*(3), 269-288.

43. Dressler, W. W. (2012). Cultural consonance: Linking culture, the individual and health. *Preventive Medicine, 55*(5), 390.
44. Waddell, S., and Quinn, W. G. (2001). Flies, genes, and learning. *Annual Review of Neuroscience 24*(1), 283-1,309.
45. Brembs, B. (2003). Operant conditioning in invertebrates. *Current opinion in neurobiology, 13*(6), 710-717.
46. Dunning, J., & During, M. J. (2003). Molecular mechanisms of learning and memory. *Expert reviews in molecular medicine, 5*(25), 1-11.
47. Blum, S. D. (2019). Why don't anthropologists care about learning (or education or school)? An immodest proposal for an integrative anthropology of learning whose time has finally come. *American anthropologist, 121*(3), 641-654.
48. Rasmussen, S. J. (2012). "Cultural anthropology." in *The Oxford handbook of culture and psychology*. Oxford University Press: Oxford, UK.
49. Koestler, Arthur (1967). *The Ghost in the Machine* (1990 reprint ed.). Penguin Group: New York, NY.
50. Kameenui, E. J. (1996). Learning to read/reading to learn: Helping children with learning disabilities to succeed. Information kit. *National Center to Improve the Tools of Educators*: Eugene, OR.
51. Pinker, S. (1994). *The Language Instinct: How the Mind Creates. Language*. Harper Collins: New York, NY.
52. Ochs, E., & Schieffelin, B. B. (2011). The theory of language socialization. *The handbook of language socialization*, 1-21.
53. Blute, M. (2008). Memetics and evolutionary social science. *A Memetics Compendium*, 223.
54. Kitayama, S. E., & Markus, H. R. E. (1994). Emotion and culture: Empirical studies of mutual influence (pp. xiii-385). *American Psychological Association*.
55. Kitayama, S., Markus, H. R., & Kurokawa, M. (2000). Culture, emotion, and well-being: Good feelings in Japan and the United States. *Cognition & Emotion, 14*(1), 93-124.
56. Barrett, L. F. (2013). Psychological construction: The Darwinian approach to the science of emotion. *Emotion review, 5*(4), 379-389.
57. Lindquist, K. A., & Gendron, M. (2013). What's in a word? Language constructs emotion perception. *Emotion Review, 5*(1), 66-71.
58. MacCormack, J. K., & Lindquist, K. A. (2017). Bodily contributions to emotion: Schachter's legacy for a psychological constructionist view on emotion. *Emotion Review, 9*(1), 36-45.
59. Schachter, S., & Singer, J. (1962). Cognitive, social, and physiological determinants of emotional state. *Psychological review, 69*(5), 379.