

A Cross-Species Comparative Approach to Positive Emotion Disturbance

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Abstract

Recent discoveries stress the importance of studying positive emotion disturbances (PED) yet there remains little empirical work or integrative conceptual framework in this domain. We suggest that an ideally suited opportunity to advance the study of PED is to consider a cross-species evolutionary framework. We apply this framework—drawing from principles of stabilizing selection—to recent empirical findings in humans and nonhumans suggesting how positive emotion and associated play behaviors may lead to detrimental outcomes. This cross-species approach suggests a potential paradigm shift in the way psychologists and evolutionary biologists approach positive emotion functioning, opening the possibility for new conceptual opportunities and interdisciplinary dialogues and research.

Keywords

comparative, cross-species, emotion, evolution, happiness, positivity

Feeling good, or experiencing positive emotions, is a basic building block of human nature. Positive emotions motivate us to pursue important goals, allow us to savor important experiences, and reinforce adaptive behavior patterns (e.g., Fredrickson, 1998), and has been linked to lower stress reactivity, higher social functioning, and attainment of important life goals (e.g., Fredrickson, 1998; Lyubomirsky, King and Diener, 2005). Positive emotions are clearly a vital ingredient of our well-being and ability to flourish (Lyubomirsky, King, & Diener, 2005; Seligman & Csikszentmihalyi, 2000). At the same time, a burgeoning wave of research also suggests that positive emotion disturbances (hereby referred to as PED) are related to poor health outcomes and clinical syndromes both cross-sectionally and longitudinally, particularly when the magnitude and duration are inappropriate to the context (Gruber, Mauss, & Tamir, 2011; Gruber & Moskowitz, 2014). Recent empirical findings also associate PED with problematic drug and alcohol use, risky sexual behavior, and increased mortality, thus placing it as a high priority in recent mental health initiatives (e.g., Cuthbert & Insel, 2013; Cuthbert & Kozak, 2013; Insel et al., 2010; Sanislow et al., 2010). The field of PED is thus gaining increasing momentum and

importance in both illuminating the basic role of positive emotion for our survival and optimal well-being, as well as offering insight into identifying and ameliorating public health burden associated with costly and chronic psychiatric illnesses associated with PED (e.g., du Pont, Welker, Gilbert, & Gruber, in press).

Despite these advances, puzzles remain. To date, it has proved difficult to generate a conceptual framework that can account for two parallel but seemingly irreconcilable set of findings in the literature on positive emotions; namely, that positive emotions both promote behaviors that are adaptive or positively valued, such as helping behavior, creativity, and goal pursuit; as well as behaviors that are maladaptive or negatively valued and behaviors that are adaptive or positively valued, such as risk-taking, stereotyping, stealing, and shallow information processing (e.g., Gruber & Moskowitz, 2014). Thus, there remains a need for a mechanistic framework to situate the broad range of harmful physical, social, and health outcomes associated with positive emotions (e.g., Oishi, Diener, & Lucas, 2007; Watson & Naragon-Gainey, 2010). Can we locate a unified framework that can help account for PED, and in doing so thus account for the broad range of effects observed?

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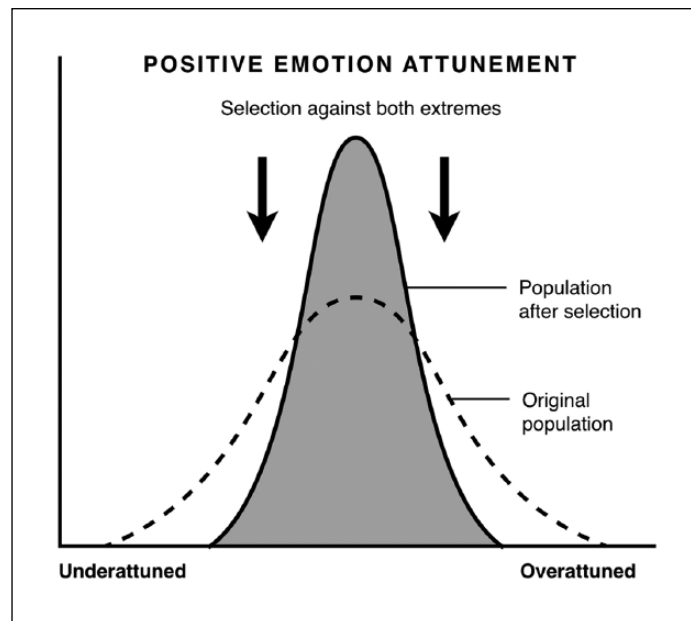


Figure 1. Stabilizing selection of positive emotion attunement.

In this essay, we suggest that an ideally suited opportunity to advance the study of PED is to consider a cross-species evolutionary framework. The application of evolutionary frameworks to the study of emotion in humans is not a new idea (e.g., Ekman, 1992; Fredrickson, 1998; Goetz, Keltner, & Simon-Thomas, 2010; Griskevicius, Shiota, & Neufeld, 2010; Keltner, Haidt, & Shiota, 2006; Nesse, 1990, 2004; Nesse & Ellsworth, 2009). Indeed, critical insights into the function of emotions in identifying and pursuing important individual goals, avoiding threats or harm to the self, as well as coordinating complex social interactions have been provided by functionalist accounts of emotion grounded in evolutionary theory. However, one critical gap in this literature is accounting for PED (e.g., Nesse, 2004). This is not surprising given attention has only been recently devoted to the emerging area of PED (e.g., Gruber & Moskowitz, 2014). We suggest that a cross-species evolutionary account of PED is particularly well suited to fill this gap in the literature for a few reasons. First, an evolutionary account of PED can account for both desirable and undesirable effects of positive emotion, which can provide more general insights about human nature and generate fruitful research questions across human and nonhuman species. Second, such an account of PED is well positioned to account for the “two sides” of positive emotion (e.g., Gruber & Moskowitz, 2014); namely, how they are both essential to our survival (as well as peril) as well as how the experience of positivity reflects fundamental aspects of very own human nature. Third, we think such a perspective on what PED is (i.e., a descriptive account of the phenomena) as well as how it arises (i.e., underlying mechanisms) is essential to fostering inter-disciplinary dialogues between psychologists and evolutionary biologists.

Toward this end, we begin by drawing upon an evolutionary model known as *stabilizing selection* that provides a unique and importantly unifying mechanism by which positive emotion may be disturbed across species. We discuss how stabilizing selection may help account for, and shed new insights, into the extant research done on PED across species. Next, we provide a brief synthesis on current work in PED in both humans and nonhumans, which largely includes initial but promising empirical findings (in humans) and suggestive ethological observations (in nonhumans), both of which underscore the need for additional work in this area using a cross-species comparative approach. Finally, given the possibilities raised by this novel evolutionary account, we suggest several future avenues for research in both human and nonhuman species.

Stabilizing Selection: Evolutionary Account of Disturbances in Positivity

We begin with a question: can experiencing positive emotion too intensely incur significant and long-lasting costs across species? This question leads to more general questions of whether evolutionary principles of natural selection—defined as the processes by which organisms adapt to different environments to enhance survival and reproductive success—may also serve to place upper limits on states of positive emotion and their functional value. To answer this question, we invoke a well-accepted evolutionary principle called *stabilizing selection*. Stabilizing selection is one type of natural selection by which decreases in genetic diversity are associated with stabilization of a population on a particular trait value (e.g., Charlesworth, Lande, & Slatkin, 1982; Sober, 1993). Stabilizing selection,

by selecting against extreme values of a trait while favoring intermediate values, establishes boundary conditions upon which a phenomenon is most adaptive in moderation, but when experienced both at the lower (i.e., low levels or relative deficits) or upper limits (i.e., high levels or relative excess) of a given phenotypic expression of an observable trait or behavioral characteristic, that is in relative deficit or excess, it no longer confers its adaptive value and would no longer be evolutionarily advantageous or selected for. In the literature that is concerned with nonhuman animals, we know that across species there seem to be constraints on body size, number of offspring, and adornments such as antler size, and coloration, so asking about behavioral phenotypes is a natural extension of this type of natural selection (see Figure 1). For example, if birds lay too many eggs there are too many offspring to feed and the possibility of malnourished chicks, and if they lay too few they may lose them due to predation. Another common example of stabilizing selection would be cryptic coloration so that animals blend in with the environments in which they live.

Applied to the study of positivity, stabilizing selection suggests that there may be upper limits to the adaptive value of states of positive emotion for a given organism. Specifically, applying the principles of stabilizing selection to positive states, it would follow that there should be selection *for* happiness (a causal connection) meaning that happiness would confer a reproductive advantage to those individuals who experience it. For example, when playing, a dog would experience happiness and this would result in play being retained in her behavioral repertoire and as a result, she would benefit from engaging in play. In addition there should also be natural selection *of* attention and risk-taking (a by-product of direct selection for happiness) meaning that while individuals are playing they would have to remain aware of potential risks and danger, such as the presence of potential predators or objects into which they might run and injure themselves.

It is important to note that a stabilizing selection approach to PED does not imply a universal set point for either too much or too little positivity. Rather, stabilizing selection is a universal principle that applies across species and cultures which suggests upper and lower boundary limits of a given psychological phenomenon which also includes positive emotions. This is important given the majority of psychological and comparative literature to date has approached the experience of positive emotion and its related constructs (e.g., reward, incentive salience, hedonic capacity; Berridge & Robinson, 1998) are studied predominantly in adaptive terms without yet applying boundary conditions to when and how such states may portend dysfunction for a given individual in achieving his or her goals within a social group (cf. Grant & Schwartz, 2011; Gruber et al., 2011). Furthermore, the direct application of stabilizing selection models to PED is important given the dearth of empirical evidence exploring these issues and the need to motivate future work to carefully examine whether both humans *and* animals can ever experience too much positive emotion (i.e., ever be too happy) or engage in approach-related behaviors that are costly to the individual (i.e., ever have too much fun or play too much). In

sum, the application of stabilizing selection to the study of PED provides a window to gain a deeper understanding of how, when, and why positive emotions may both aid in, and at times impede, our survival.

We note that some of the principles of stabilizing selection which caution against extremes is echoed in the early philosophical writings of Aristotle. In his principles of moderation, Aristotle stipulated that emotions experienced in moderate degrees, in the right context and toward the right people, are functional with respect to the individual's well-being, but when taken to extremes, our emotions may become dysfunctional (e.g., Thomson, 1953). Moreover, ancient Buddhist texts emphasize the importance of attaining greater emotional stability, and experiencing emotions including positive ones, in moderation as part of well-being (e.g., "Niramisa Sutta," 2010). In addition, warnings against extreme manifestations of emotional states are consistent with recent mental health initiatives aimed at isolate more dimensional processes that reflect disturbances in positive emotional systems that are predictive of psychopathology (e.g., Cuthbert & Insel, 2013; Cuthbert & Kozak, 2013; Insel et al., 2010; Sanislow et al., 2010). We now turn to emerging work on PED in humans, which provides proof of concept demonstration of the importance of PED as well as how it may arise. The application of evolutionary principles to PED is thus timely from a clinical health perspective and of universal human interest and importance.

PED in Humans

Stabilizing selection suggests that there may be upper limits to the adaptive value of states of positive emotion when experienced in excess and beyond context appropriate amounts. Recent evidence in humans is consistent with this framework and reveals that disturbances in positivity—when positive emotions are experienced too intensely, in the wrong context, or when imbalanced with other emotions— can incur significant psychological and physical health risks for humans (e.g., Gruber et al., 2011; Gruber & Purcell, 2015).¹ These empirical findings provide insight into the nature of PED in humans, which we will highlight using recent key themes that encompass crucial positive emotion processes likely to be impacted by emotion disturbance. These themes include: *size* or magnitude of positive emotion response, *situation* or context in which positive emotions unfold, *specificity* of which positive emotions are experienced, and *spice* or the degree to which individuals experience a diversity of both positive and negative emotions.

Size: Overattunement of Positive Emotion Intensity?

Aristotelian definitions of emotional health argue that positive emotions are beneficial up to a moderate degree, but can incur costs when experienced too intensely. Several empirical examples illustrate that a heightened positivity may be associated with negative psychological health outcomes. For instance, people with extremely high positive emotion levels are inclined to

engage in riskier behaviors, such as alcohol consumption, binge eating, and drug use. They may also neglect important dangers or threats in their environment that, in extreme forms, is associated with a greater mortality risk (Gruber et al., 2011). The position that a greater degree of positive emotion can constitute a source of psychological disturbance also finds support in the clinical domain and may serve as a marker of psychopathology, such as bipolar disorder (Bentall, 1992; Gruber, 2011). Heightened and persistent positive emotions in bipolar disorder undermine the ability to experience negative emotions in threatening or risky contexts and predict a more severe illness course, and greater relapse rates (Johnson, 2005). These studies, along with prior conceptual work (Grant & Schwartz, 2011), suggest that a greater magnitude of positive emotion is not always better, and may be associated with undesirable and unintended outcomes when it exceeds a certain threshold (for a more comprehensive review, see Gruber et al., 2011). From a stabilizing selection framework, high positive emotion intensity would be conceptualized as a overattunement, an example of PED on the upper end of the population distribution and would thus be selected against in order to maximize the individual's survival and reproductive success.

Situation: Underattunement or Overattunement of Context Appropriateness

As humans, we are built with the amazing capacity to experience a range of emotions to help us readily adapt to new circumstances, challenges, and opportunities. Anger mobilizes us to overcome obstacles; fear alerts us to threats and engages our fight-or-flight preparation system; and sadness signals loss of an important object, person, or place. The functions of these emotions are suited to help us meet particular needs in specific contexts. Just as we would not want every situation to make us feel angry or sad, we should not want to indiscriminately experience positive emotion in every situation. One example of positive emotion misappropriation in an incongruent context suggests that people induced into a happy mood performed worse than people in an angry mood when engaging in a competitive computer game task (e.g., Tamir, Mitchell, & Gross, 2008). A clinical example suggests that individuals who experience positive feelings in inappropriate contexts—such as watching sad films, listening to a distressed partner—were at greater risk for developing mania (Dutra et al., 2014a; Gruber, Johnson, Oveis, & Keltner, 2008) or prospectively predicted greater clinical symptom severity in bipolar patients (e.g., Gruber, 2011). In sum, positive emotion has a proper contextual timing, and is not always suited for every situation. From a stabilizing selection framework, when positive emotions are experienced either too infrequently in the appropriate contexts signaling positive emotion underattunement (i.e., signaling opportunities or in response to rewards) or too frequently in inappropriate contexts signaling positive emotion overattunement (i.e., during times of loss, suffering, or threat) would both be examples of PED and thus selected against.

Spice: Overattunement of Positivity Imbalanced With Negativity

We have thus far considered the magnitude of positive emotions as well as the frequency in which they are experienced in inappropriate contexts as indicators of PED. It is also critical to focus on the diversity and variety of emotions that people experience, as an independent and integral component of survival. Recent work suggests that positive emotions cannot be studied in isolation, and must be situated or balanced within an individual's broader emotional ecosystem. Much like biodiversity is critical to the healthy survival of a biological ecosystem by fostering resistance to pathogens and invasive species, emotional diversity (i.e., "emodiversity"; Quoidbach et al., 2014) is an arguably equally important component for the human internal emotional ecosystem. Specifically, emodiversity refers to the variety and relative abundance of the emotions they experience (Quoidbach et al., 2014), which is constituted by both the richness or number of specific emotions an individual experiences as well as the evenness or extent to which positive and negative emotions are experienced in the same proportion. Data from a large cross-sectional sample of over 37,000 adult respondents have revealed that greater diversity of emotions—that is, experiencing a variety of positive *and* negative emotions—is an independent predictor of increased mental health as well as decreased medical health issues. Thus, it is critical to experience a diverse landscape of both positive and negative emotions, rather than positive emotions in isolation. From a stabilizing selection framework, this work reveals that when one's emotional experiences are imbalanced, either too few positive emotions and too many negative emotions (i.e., signaling underattunement of emodiversity) or too many positive emotions and too few negative emotions (i.e., signaling overattunement of emodiversity) would reflect PED and thus selected against.

Despite these promising hints at how a stabilizing selection perspective could account for such distinct types of PEDs, and across health and clinical populations, the empirical work in this area is new. As such, additional scientific work on the newly emerging area of PED needs to be done to further test and explore the applicability of the stabilizing selection framework.

PED in Nonhumans

All that preceded is related to the study of positive emotion and its disturbance in humans, yet what do we know about PED in nonhumans? From these observations in nonhumans, many questions about the evolution of emotions in humans and how we can apply evolutionary principles to humans as well arise. Let's consider the case for nonhuman animals. It is well documented that many animals can experience and suffer from negative emotions including exhibiting symptoms consistent with those observed in posttraumatic stress disorder, anxiety disorders, and depression (Bekoff, 2007; Bekoff & Pierce, 2009; Ferdowsian et al., 2011; Ferdowsian & Merskin, 2012), yet there is little work to date examining the possibilities of

PED and its associated consequences (e.g., Bliss-Moreau, Bauman, & Amaral, 2011). By studying PED in nonhuman animals we can learn much about the evolution of many different types of behavior and what sorts of selective pressures might apply across species (e.g., Bateson & Martin, 2013). Such studies will forward our knowledge of the etiology and importance of positive emotion in survival across species more generally. This is particularly important given that dearth of attention paid to positive emotional states in animals (e.g., Bekoff, 2013).

The majority of work to date on positive emotion and potential sources of PED in nonhuman animals is based on ethological observations of naturally occurring behavior published by well-established field workers (e.g., Bekoff, 2013; Berger, 1979). Specifically, this includes the rigorous behavioral observation and field studies of social *play* and related behaviors such as laughing across a wide range of species including golden marmots (e.g., Blumstein, 1998), Australian marsupials (e.g., Byers, 1999), bighorn sheep (e.g., Berger, 1979), fur seals (e.g., Harcourt, 1991), rodents (e.g., Panksepp, 2007; Panksepp & Burgdorf, 2003; Pellis & Pellis, 2010), and canids including domestic dogs, coyotes, and wolves (e.g., Bekoff, 1995, 2013). Social play behavior is of particular importance given it is a common form of social interaction in young mammals, and thought to be highly rewarding (e.g., Vanderschuren, Niesink, & van Pee, 1997) and critical for adaptive social and cognitive development (e.g., Bekoff, 2013; Burghardt, 2005; Fagen, 1981; van Kerkhof et al., 2013). In addition, specific play signals in nonhumans (e.g., the “bow”) are used to initiate social play as well as to punctuate and carefully negotiate ongoing and often frantic, vigorous, and highly contagious play interactions (e.g., Bekoff, 2014a; 2014b, 2015; Bekoff & Pierce, 2009). Nonetheless, young animals engage in vigorous social and locomotor self-play during which losing oneself in the activity can be detrimental. This proposition can be paralleled to research on positive emotion in humans and possible detrimental consequences arising from “too much good,” as laid out before. Play behavior thus provides a prime candidate for scientific inquiry on PED in nonhuman animals given it is robustly associated with positive emotionality and activity in reward-relevant brain circuitry as well as its naturalistically occurring and ecologically valid consequences for the organism. Emerging insights point to the promise of attending to, and measuring how, play behavior—a behavior as discussed which is typically associated with positive emotionality in animals—can result in negative consequences for the organism, and thus signal PED. For example, play behavior in golden marmots has been scientifically linked with increased risk of death via greater exposure time to predators (e.g., Blumstein, 1998). Specifically, Blumstein observed that during play golden marmots demonstrated a delayed (i.e., longer) response time to seek out safety and refuge from a potential predator in the environment, thus suggesting that increased play might inadvertently expose individuals to predation. Ethological observations of increased play behavior in bighorn sheep have been associated with physical harm including running shoulder-first into painful cacti while playing outside of a field site in the Palm Desert (e.g., Berger, 1979).

Moreover, in South American fur seals ethological observations by Harcourt (1991) provide suggestive evidence that play behavior can lead to decreased attentiveness to potential threats (i.e., ignoring predators) and thus signal a potential downside of “too much positivity” in seals. Specifically, southern fur seals are more likely to be killed by southern sea lions when playing in shallow sea water than at other times (i.e., 85% of fur seals observed were killed during these situations), perhaps because they are more conspicuous and less vigilant (e.g., Bateson & Martin, 2013). Finally, Caro (1995) noted that when young cheetahs play, they reduce the hunting success of mothers. Taken together, these observations suggest that one aspect of PED relevant to nonhuman animals would include prolonged or context-inappropriate engagement in rewarding play behaviors, which may result in decreased threat detection and vigilance or attention to predators, thus directly demonstrating links between engagement in play and mortality risk. Applying the principles of stabilizing selection to these observations, it may be that in addition to the increased magnitude of the unbounded exuberance evident during play, there is a risk associated with the *context or situation*, with the excessive *size* of positivity, in that they express themselves via play in the wrong time or in the wrong place. These questions recall the themes of PED in humans identified before.

Despite these rich ethological observations, the comparative database is surprisingly scant (Bekoff & Byers 1998; Burghardt, 2005; Fagen, 1981; Pellis & Pellis, 2010). Indeed the majority of the aforementioned work relies heavily on observational data used in common scientific practice to support scientific theories and generate further research questions and ideally experimental tests of these principles. Yet there is a critical dearth of work to date that has experimentally unpacked these ideas outside of the ethological literature, including testing key hypotheses posited in the human literature that heightened positivity may be associated with decreased attention to threats, increased risk-taking, and increased bodily harm and mortality rates. It is thus critical for further empirical work to test these potential hypotheses and more broadly illuminate the principles underlying stabilizing selection and how too much positivity (and associated behaviors, such as play) may portend maladaptive outcomes across human and nonhuman species. It is this lack of empirical work and conceptual models of PED that underscores the importance of this essay and what we hope will spur greater interdisciplinary dialogue and cross-field research.

A Cross-Species Approach to PED: Roadmap for Future Research

Given the possibilities raised by this evolutionary account, more comparative data are needed to determine if there is a general evolutionary explanation for having “too much of a good thing” in both human and nonhuman species. New research paradigms in this area, in particular both the design and implementation of novel (and noninvasive) laboratory and field studies for understanding animal cognition and happiness, are imperative. For

example, researchers may consider field experiments in which the introduction of model predators are presented following a naturalistically occurring positive mood induction (such as play between conspecifics) to test the hypothesis for how it affects threat detection, vigilance, and safety seeking behaviors which are required in that situation. Typically this should elicit the cessation of play related behavior and increased vigilance and safety seeking behaviors (e.g., withdrawal from play and retreat to safety situation such as den or tree—prairie dogs and marmots run into burrows). Such experiments would allow for testing the hypothesis that those individuals who demonstrate extreme positivity during play may show decreased reaction time (e.g., slow time to cease play behavior, slower time to reach safety related hiding spot) and decreased vigilance (i.e., decreased visual attention to threat). Furthermore, the use of archival data that have not been previously considered can also provide answers relating to the extremity and potential maladaptive consequences of positive states when reviewed from a new perspective. This field of research also requires more data on humans to know whether ideas from stabilizing selection can be translated into practical interventions aimed toward promoting well-being for humans.

This essay suggests a potential paradigm shift is on the horizon in the way both psychologists and evolutionary biologists think about positive emotion. In addition, it provides a broad model for understanding other psychological phenomena. This new focus paves the way for exciting conceptual opportunities and interdisciplinary dialogues that probe into the elusive, deep-rooted mechanisms concerning the evolution of positivity.

Declaration of Conflicting Interests

None declared.

Note

- 1 By positivity, we refer to a psychological state comprised of at least three components; namely, more positive affect, less negative affect, and life satisfaction, commonly referred to as happiness (e.g., Gruber, Mauss & Tamir, 2011).

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