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Beyond Happiness: Building a Science of Discrete Positive Emotions

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While trait positive emotionality and state positive-valence affect have long been the subject of intense study, the importance of differentiating among several "discrete" positive emotions has only recently begun to receive serious attention. In this article, we synthesize existing literature on positive emotion differentiation, proposing that the positive emotions are best described as branches of a "family tree" emerging from a common ancestor mediating adaptive management of fitness-critical resources (e.g., food). Examples are presented of research indicating the importance of differentiating several positive emotion constructs. We then offer a new theoretical framework, built upon a foundation of phylogenetic, neuroscience, and behavioral evidence, that accounts for core features as well as mechanisms for differentiation. We propose several directions for future research suggested by this framework and develop implications for the application of positive emotion research to translational issues in clinical psychology and the science of behavior change.

Keywords: positive emotion, discrete emotions, evolution, dopamine, reward

The positive emotions were once on the periphery of affective science. Despite being a common subject of philosophical analysis (Nussbaum, 1996; Solomon, 1977), a focus of Darwin's (1872/1965) early work on emotional expression, and experienced far more frequently than negative emotions across the life span (Carstensen, Pasupathi, Mayr, & Nesselroade, 2000), positive emotions were represented in psychologists' early taxonomies of emotion by just a single construct ("happiness" or "enjoyment," e.g., Ekman, 1992; Izard, 1977; Oatley & Johnson-Laird, 1987; Tomkins, 1984). Later influential taxonomies included other positive emotions, such as love and pride, but were still dominated by negative emotions (e.g., Fehr & Russell, 1984; Lazarus, 1991; Roseman, Spindel, & Jose, 1990; Smith & Ellsworth, 1985). This imbalance had profound implications for empirical research, as groundbreaking cross-cultural studies of facial expression recognition (Ekman et al., 1987), emotion-antecedent appraisals (Scherer, 1997), and autonomic specificity (Ekman, Levenson, & Friesen, 1983; Levenson, Ekman, Heider, & Friesen, 1992) included just one positive emotion among several negatives. Most subsequent studies have followed suit, and it is still unusual for a single study to include more than one or two positive emotions.

This is not to say that researchers have entirely neglected the positive side of our emotional lives. At some levels of analysis (Rosenberg, 1998), a great deal of work has been done. At the level of personality/individual differences, for example, traits such as happiness/well-being (e.g., Myers & Diener, 1995; Diener, Lucas, & Scollon, 2006; Ryff, 1989; Ryff & Keyes, 1995), dispositional positive affect (Watson, Clark, & Tellegen, 1988), and approach motivation (e.g., Elliot & Thrash, 2002) have received intensive study. Researchers have noted the robust link between positive emotionality and extraversion (e.g., Costa & McCrae, 1980; Larsen & Ketelaar, 1991; Lyubomirsky, King, & Diener, 2005) and proposed a common neural basis of these two traits (Depue & Collins, 1999). Life trajectories linked to high positive emotionality have been documented (e.g.,

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Harker & Keltner, 2001), as have health outcomes of positive emotionality (e.g., Pressman & Cohen, 2005).

Research at another level of analysis, emphasizing positive valence in experienced affect, has also yielded rich insights about properties of positive emotion. Scholars have linked positive affect with heuristic-driven yet creative cognition (e.g., Bodenhausen, Kramer, & Süsser, 1994; Forgas, 2008; Isen, Daubman, & Nowicki, 1987; Mackie & Worth, 1989; Schwarz & Bless, 1991) as well as behavioral approach motivation (e.g., Carver & White, 1994; Harmon-Jones, 2003). An important advance at this level of analysis has been Fredrickson's (1998) broaden-and-build theory, which proposes that positive emotions help us acquire long-term informational, social, and material resources that are important for survival. The broaden-and-build approach has inspired dozens of studies relating positive emotions to desirable effects, ranging from more global attentional scope in visual processing (Fredrickson & Branigan, 2005) to reduction in signs of the outgroup homogeneity effect (Johnson & Fredrickson, 2005), as well as documenting upward spirals of positive emotional experience, prosocial engagement, and aspects of health and well-being (e.g., Fredrickson, 2001; Fredrickson & Losada, 2005; Fredrickson, Tugade, Waugh, & Larkin, 2003; Garland et al., 2010).

When compared to the study of negative emotions, however, a lacuna remains at a third level of analysis—the level emphasizing differentiation among "discrete" positive emotions. Here, emotions are defined as brief, multicomponent, largely automatic psychological mechanisms that coordinate a variety of cognitive, physiological, and motor processes, facilitating an adaptive response to particular kinds of fitness-relevant opportunities or threats (e.g., Ekman, 1992; Frijda, 1986; Levenson, 1999; Plutchik, 1980; Tooby & Cosmides, 2008). Subjective feeling is deemphasized in this definition, which instead highlights biological systems and cognitive mechanisms that support motivation and behavior. The extent to which emotional responding can be characterized in terms of evolved, universal, discrete categories remains controversial (e.g., Barrett, 2006b; Ortony & Turner, 1990), with ongoing debates about how to collect and interpret meaningful evidence on facial and vocal expressions of emotion (e.g., Ekman, 1994; Gendron, Roberson, van der Vyver, & Barrett, 2014; Jack, Caldara, & Schyns, 2012; Russell, 1994; Scherer, 1992), and neural activation patterns (e.g., Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Vytal & Hamann, 2010), in particular. Even among those who endorse a discrete emotion perspective, there is considerable debate about what discrete emotions really are (e.g., Ekman, 1992; Nesse & Ellsworth, 2009; Roseman, Wiest, & Swartz, 1994; Shaver, Schwartz, Kirson, & O'Connor, 1987; Tooby & Cosmides, 2008). Nonetheless, analyses of discrete negative emotions' specific adaptive functions (e.g., disgust as a response to pathogen threat; Oaten, Stevenson, & Case, 2009) have long guided discovery in affective science, producing a rich and fine-grained body of research (Keltner & Lerner, 2010).

Throughout the 20th century, comparable analyses of specific positive emotions were rare. Now, the tides are shifting. Psychologists are actively studying emotions such as pride (Tracy & Robins, 2007; Tracy, Shariff, Zhao, & Henrich, 2013; Williams & DeSteno, 2008), gratitude (Algoe, 2012; Bartlett & DeSteno, 2006; DeSteno, Li, Dickens, & Lerner, 2014; Gordon, Impett, Kogan, Oveis, & Keltner, 2012; Jia, Li, & Tong, 2015; McCullough, Kilpatrick, Emmons, & Larson, 2001), amusement (Martin, 2010; Ruch, 1993), love and sexual desire (Diamond, 2003; Gonzaga, Turner, Keltner, Campos, & Altemus, 2006; Muise, Impett, & Desmarais, 2013), and awe (Piff, Dietze, Feinberg, Stancato, & Keltner, 2015; Shiota, Keltner, & Mossman, 2007). Empirical studies have also begun to compare several positive emotions at once with respect to appraisals, expression, physiological responding, relation to personality traits, and/or implications for cognition (e.g., Algoe & Haidt, 2009; Campos, Shiota, Keltner, Gonzaga, & Goetz, 2013; Griskevicius, Shiota, & Neufeld, 2010; Güsewell & Ruch, 2012; Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006; Mortillaro, Mehu, & Scherer, 2011; Roseman, 1996; Sauter & Scott, 2007; Shiota, Neufeld, Yeung, Moser, & Perea, 2011). For the most part, however, programs of research on various positive emotions have developed independently. These emerging areas of inquiry highlight the need to develop an overarching theoretical framework that integrates the evidence to date, and can guide future research.

In the present article, we offer a new framework for conceptualizing and studying the positive emotions. We begin by considering examples of evidence for positive

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emotion differentiation across several aspects of emotional responding. Building upon a foundation of phylogenetic, neuroscience, and behavioral evidence, we then propose a novel theoretical framework for the positive emotions as functionally discrete entities. This framework recognizes a common positive emotion core, yet describes a mechanism by which this core might have developed "branches" in response to new categories of fitness-relevant resources emerging over our evolutionary history—an analysis that yields a taxonomy of specific constructs. We next address gaps in the current evidence for this framework, each translating into a direction for future research. Finally, we discuss implications of a discrete positive emotion approach for translational issues in clinical psychology and the science of behavior change—two areas in which a nuanced application of positive emotion science may have powerful impact.

Current Evidence for Positive Emotion Differentiation

Empirical research on positive emotion has burgeoned in the 21st century. This development traces in important ways to Fredrickson's (1998) proposal that, beyond being pleasant, positive emotions serve valuable adaptive functions—broadening our attention and guiding behavior in ways that help us build crucial resources. Most early studies explicitly or implicitly addressed positive emotions as a class, emphasizing how they differ from negative emotions and neutral-affect states. More recently, studies have sought to compare several positive emotions at once, asking whether there is important differentiation within the positive emotion domain. This work highlights the hazard of assuming that all positive emotion is alike.

Expression in the Face, Posture, Touch, and Voice

The social functions of emotion, in which emotions support the interdependent bonds on which humans rely for survival and reproductive success, may be especially important for understanding positive emotions (Niedenthal & Brauer, 2012; Shiota, Campos, Keltner, & Hertenstein, 2004). If so, the ability to clearly express positive emotions to conspecifics is crucial, and new evidence is revealing the diversity of ways in which positive emotions are communicated nonverbally (e.g., Cordaro, Keltner, Tshering, Wangchuk, & Flynn, 2016; Keltner & Cordaro, 2015; Sauter, Eisner, Ekman, & Scott, 2010; Tracy & Robins, 2008). These studies have gone beyond facial expressions to examine posture, touch, and tone of voice (for a review, see Keltner, Sauter, Tracy, McNeil, & Cordaro, 2016).

Positive emotions in the face and posture. While various negative emotions have long been associated with distinctive patterns of facial muscle contraction, only one display had been linked to positive emotion—the Duchenne smile (Ekman, 1992). This smile involves activity of the *zygomatic major* muscle, which pulls the lip corners up, and the *orbicularis oculi* muscle, which surrounds the eyes, and is recognizable worldwide as a display of positive feelings (Frank, Ekman, & Friesen, 1993). However, facial muscles are not the only ones humans use to convey emotion, and in fact they have signaling limitations. Unlike many facial muscle movements, head movements and postural changes are more easily detected at a distance (Ekman, 2004). People may have difficulty distinguishing intense positive from intense negative emotions based on spontaneous facial expressions (e.g., identifying those who had just won vs. lost a point in a tennis match), but can do so reliably based on body posture (Aviezer, Trope, & Todorov, 2012). Tracy and Robins (2008) found that postural expansion and an upward head tilt—a high-status pose—is reliably decoded as pride in different cultures. Amusement is associated with a distinctive bouncing, tilting head movement, as well as the drop-jaw open mouth Duchenne smile of laughter and play (Campos et al., 2013; Keltner & Bonanno, 1997; Sarra & Otta, 2001). Self-reports of love are associated with open-arm gestures that convey the intent of affectionate touch (Gonzaga, Keltner, Londahl, & Smith, 2001).

In one study, Campos and colleagues (2013) asked 94 participants to relive recent experiences of several positive emotions, and then to pose "how you would express that emotion to another nonverbally" (p. 45). These poses were analyzed using Facial Action Coding System (FACS) coding for facial muscle and head movements (Ekman & Friesen, 1978), supplemented by a comprehensive set of pos-

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tural movements. Prototypical poses of amusement, contentment, joy, love, and pride each included a Duchenne smile. However, several of these poses also included a distinctive head or postural movement. As noted above, amusement poses commonly included a bouncing and/or tilted head along with a widely dropped jaw (even without outright laughter). Contentment poses commonly included a still body and a small but sharp head nod. Love poses often included a head tilt to the side, as well as a "self-hug" in lieu of another person to touch. Pride poses included the postural expansion and head lift previously reported by Tracy and Robins (2007). Awe and interest poses did not include smiles at all, but were characterized by distinctive patterns of eyebrow lifts, mouth movements, and forward movement of the head and/or torso.

A social functional perspective predicts emotion-specific expressions such as those described above will show continuity with primate behaviors that communicate qualities of relationships between conspecifics (e.g., reproductive interest, dominance/submissiveness, play; Eibl-Eibesfeldt, 1989). In research guided by ethological studies of species-characteristic affiliative and sexual behavior, Gonzaga and colleagues examined the expressive behaviors associated with romantic love and sexual desire (see Table 1). In one study of romantic partners, self-reports and partner attributions of love were associated with 1–5 second nonverbal displays of smiling, mutual gaze, affiliative hand gestures, open posture, and forward leans. In contrast, reports and attributions of sexual desire were predicted by mouth movements such as lip licks, lip wipes, and tongue protrusions (Gonzaga et al., 2001). In a follow-up study of women recounting a positive close relationship experience, the affiliative nonverbal display of love—but not the lip-licks of sexual desire—predicted the peripheral release of oxytocin (Gonzaga et al., 2006). Thus, even the closely related states of love and sexual desire showed differences in expression that tracked theoretically relevant physiological response.

Positive emotions in touch. Touch is central to mammalian patterns of greeting, flirtation, play, soothing, food sharing, and proximity maintenance (Eibl-Eibesfeldt, 1989; Hertenstein, 2002; Hertenstein, 2011; Hertenstein, Verkamp, Kerestes, & Holmes, 2006). In humans, touch rewards: Gentle, affiliative touch is detected by specialized mechanoreceptors in the skin (Löken, Wessberg, Morrison, McGlone, & Olausson, 2009), and triggers activation in the orbitofrontal cortex, a region included in the reward circuit (Rolls, 2000). Touch bonds: Affectionate touch is considered a key mechanism for parent-infant bonding (Bai, Repetti, & Sperling, 2016; Feldman, Weller, Zagoory-Sharon, & Levine, 2007). Touch soothes: Married women anticipating an electric shock showed decreased threat-related activity in key brain areas when holding the hand of a spouse, but not that of a stranger (Coan, Schaefer, & Davidson, 2006).

Guided by these findings, Hertenstein, Keltner, App, Bulleit, and Jaskolka (2006) investigated how positive emotions are signaled with touch between humans. In multiple studies an encoder (the toucher) and decoder (the touchee) sat at a table separated by a black curtain, which prevented all communication between the two participants other than touch. The decoder's arm extended to the encoder's side of the curtain; the encoder attempted to convey different emotions from a list of terms by touching the decoder's arm; and the decoder selected which emotion had been communicated from the list of words presented to the encoder. People in the United States and Spain reliably communicated love and gratitude with this brief tactile contact, and each of these emotions was communicated via a distinct set

Table 1
Distinct Correlates of Love and Desire Displays

Study	Love display	Desire display
Study 1: College romantic partners		
Experienced love		
Self-report	.28*	−.19
Partner attribution	.21*	−.17
Experienced desire		
Self-report	−.11	.34*
Partner attribution	.05	.34*
Experienced happiness		
Self-report	.04	−.23†
Partner attribution	.00	−.07
Study 2: Adult women		
Oxytocin release	.50*	.11

Note. Adapted from "Romantic Love and Sexual Desire in Close Relationships," by G. C. Gonzaga, R. A. Turner, D. Keltner, B. Campos, & M. Altemus, 2006, *Emotion*, *6*, 163–179. Copyright, 2006 by American Psychological Association.
$^\dagger p < .10$. $^* p < .05$.

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of behaviors (see Table 2). In a follow-up study, in which encoders were allowed to touch any part of the decoders' bodies, love (68%), gratitude (74%), and happiness (60% accuracy) were all decoded at above-chance levels, although pride was not (Hertenstein, Holmes, McCullough, & Keltner, 2009). These findings suggest that touch is more than a generic signal of hedonic tone, or amplifier of positive affect expression as signaled by the face. Rather, the distinct communicative functions of touch appear especially important for those positive emotions involving relational closeness or interdependence.

Positive emotions in the voice. With emerging bipedalism, the hominid vocal apparatus evolved dramatically—the vocal tract elongated, the area behind the mouth expanded, and the tongue developed greater dexterity—morphological changes that allow for precise and diverse vocal communication (Ehrlich, 2000). Recent studies have examined emotion-specific vocal bursts, brief, nonword utterances that arise between speech incidents or nonsemantic vocalizations (Banse & Scherer, 1996). These new studies reveal the voice to be rich with information about positive emotion (Juslin & Laukka, 2003; Laukka et al., 2013). One vocal burst study reported an overall accuracy rate of 81.1% in recognizing several displays, including those of admiration and elation (Schroder, 2003). Another reported 70.1% accuracy for five positive emotions—achievement, amusement, contentment, and pleasure—in two different cultural groups (Sauter & Scott, 2007). Simon-Thomas, Keltner, Sauter, Sinicropi-Yao, and Abramson, (2009) asked participants to read short descriptions of 13 positive emotions and produce vocal bursts to communicate each emotion. Vocal bursts were then presented to a second set of participants, who chose the emotion term that best matched the tone of the burst from a list, which included a "none of the above" option. Participants identified amusement (81%), interest (66%), enthusiasm (42%), pleasure (35%), awe (30%), and triumph (29%) at levels of accuracy significantly above chance (see Figure 1). Accuracy rates rose further when trials were limited to prototypical vocal bursts rather than using the complete set—in the case of awe, more than doubling accuracy rates.

Other positive emotions were less reliably identified in vocal bursts, including compassion, gratitude, love, contentment, desire, and pride. These findings have since replicated in a study of 10 cultures and one remote village in Bhutan (Cordaro et al., 2016). Thus, the emotions involved in close relationships—love, desire, and gratitude, for example—appear not to be as easily identified solely through vocal cues. Rather, positive emotions identified easily in the voice are elicited by objects or events in the broader environment. Combined with the data on communication via touch, these findings support Ekman's (1992) proposal that the expressive signals of various emotions are far from random, but selectively involve those modalities most consistent with the function of the emotion itself and the context in which the emotion is most likely to occur.

We do not claim that the "mapping" of nonverbal expressions to emotion states is completely understood, in terms of either the extent or the precise mechanisms of specificity. Nor do we claim that humans universally express a given emotion with an identical set of wholly evolved nonverbal cues. Taken as a whole, the available data suggest that nonverbal expressions and their interpretation are shaped by a combination of evolved, universal signal features and learned, culturally idiosyncratic components, as well as

Table 2
Touch Elements Used to Communicate Four Positive Emotions and Percent Accuracies in Decoding Target Emotion From Touch, United States and Spain

Emotion	Touch element frequencies	Percent recognition	
		United States	Spain
Gratitude	Shaking 67% Lifting 9% Squeezing 6%	55%	66%
Love	Stroking 40% Finger Locking 13% Rubbing 12%	51%	62%
Happiness	Swinging 55% Shaking 15% Lifting 7%	30%	21%
Pride	Shaking 39% Lifting 16% Squeezing 15%	18%	n/a

Note. n/a = not applicable. Adapted from "Touch Communicates Distinct Emotions," by M. J. Hertenstein, D. Keltner, B. App, B. A. Bulleit, & A. R. Jaskolka, 2006, *Emotion, 6*, 528–533. Copyright, 2006 by American Psychological Association.

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display rules guiding modulation of expression in particular contexts, in complex ways that are far from clear at this time (Elfenbein, Beaupré, Lévesque, & Hess, 2007; Matsumoto, Yoo, & Fontaine, 2008; Russell, 1994). We do suggest that the nonverbal expression of positive emotions is likely to be as diverse and sophisticated as that of negative emotions, and that similar work is needed to investigate the processes by which they are communicated without words.

Positive Emotions and the Autonomic Nervous System

In 1884, William James suggested the possibility that "no shade of emotion, however slight, should be without a bodily reverberation as unique, when taken in its totality, as is the mental mood itself" (James, 1884, p. 192). This autonomic specificity hypothesis (ASH) has been a particular focus of emotion researchers. From the earliest carefully controlled studies of the ASH (e.g., Ekman et al., 1983), through meta-analyses of the available evidence (Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000), the overwhelming emphasis has been on anger, fear, sadness, disgust, and a single positive state—happiness. The conclusion for positive emotion researchers has been grim, with "happiness" evoking far milder physiological responding than seen in negative emotions (Cacioppo et al., 2000). From a strict Jamesian perspective, this might even imply that the positive emotions are not really emotions at all.

As with expression, however, a more nuanced approach and novel measures lead to a different story, one in which physiological distinctions among different positive emotions are increasingly clear. Few ASH-inspired studies prior to 2000 had clearly stated what they meant by "happiness," or explicitly compared different positive emotions. Also, most research on the ASH had used measures of autonomic responding, such as heart rate and blood pressure, that confound multiple neural mechanisms. Recent advances in our understanding and measurement of autonomic physiology have changed this dramatically. Although Walter Cannon (1929) originally thought that the "fight–flight" re-

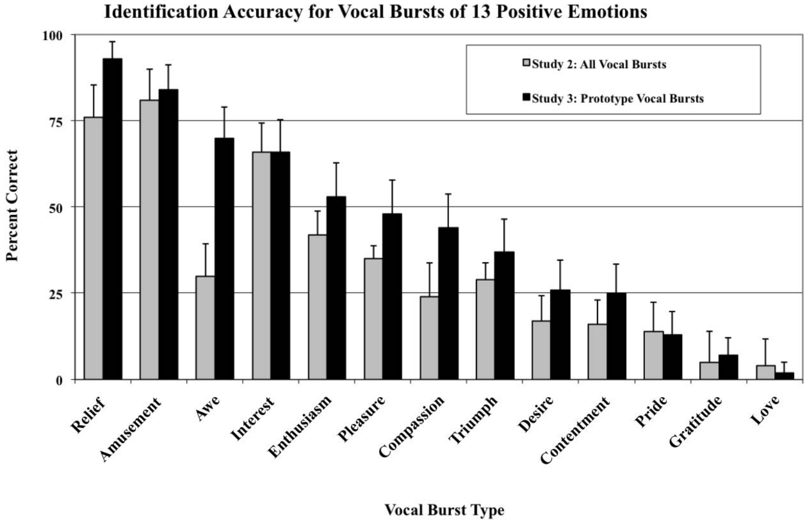

Figure 1. Percent accuracy in decoding vocal bursts of thirteen positive emotions. Reprinted from "The Voice Conveys Specific Emotions: Evidence From Vocal Burst Displays," by E. Simon-Thomas, D. J. Keltner, D. Sauter, L. Sinicropi-Yao, & A. Abramson, 2009, *Emotion, 9,* 838–846. Copyright, 2009 by American Psychological Association.

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sponse occurred only in a fully coordinated, all or none manner, it is now clear that the sympathetic branch of the ANS mediating this response involves multiple neurotransmitter mechanisms and receptor subtypes that may be activated selectively, that receptor activation may be modulated by neuropeptides that differ across various visceral organs, and that neural and hormonal mechanisms of activation can operate independently of each other (e.g., Folkow, 2000; Jänig & Häbler, 2000; Kreibig, 2010). New measurement technologies can now tease apart some of these mechanisms, and new statistical techniques can discern profiles across multiple physiological variables (Kragel & LaBar, 2013; Stemmler, Grossman, Schmid, & Foerster, 1991). These developments offer far more opportunity to investigate James's "shades of emotion" proposition than previously thought possible.

As one illustration of this invigorated inquiry, Shiota and colleagues (2011) examined participants' physiological reactivity while viewing slide sets that elicited five different positive emotions as well as a neutral state. Emotion-specific slide sets evoked significantly different profiles of physiological reactivity across several measures (see Figure 2). For example, during anticipation of a monetary reward ("enthusiasm," evoked by a series of lottery-like slides in which participants won an increasing amount of money) participants showed a broad increase in sympathetically mediated activation across cardiac, vascular, and electrodermal systems. The "attachment love" slides depicting childhood fictional icons, such as Big Bird, evoked heightened cardiac activity without signs of vascular constriction, akin to a "challenge" profile documented in agentic appraisals of difficult tasks (Tomaka, Blascovich, Kibler, & Ernst, 1997). In contrast, responding to awe slides strongly suggested withdrawal of sympathetic influence on the heart, consistent with preparation for stillness rather than physical movement. Recent studies suggest that awe may also be accompanied by a "chills" response, likely involving piloerection (Maruskin, Thrash, & Elliot, 2012). A recent, comprehensive review of the literature on the autonomic properties of emotion also provides support for important differences among anticipatory pleasure, contentment, amusement, and affection that are not easily described in terms of general levels of "arousal" (Kreibig, 2010).

Effects on Cognition and Judgment

Positive subjective affect, broadly speaking, has profound implications for how we process information: feeling good can facilitate creativity, broadening of attentional scope, and/or increased reliance on heuristics (e.g., Bodenhausen et al., 1994; Clore & Huntsinger, 2007; Forgas, 2008; Fredrickson & Branigan, 2005; Isen et al., 1987; Johnson & Fredrickson, 2005; Mackie & Worth, 1989). However, the question of whether different positive emotions have different implications for cognition has also begun to receive serious attention. For example, Gable and Harmon-Jones (2008) found that high-approach, appetitive emotions tended to narrow attentional focus whereas low-approach emotions broadened it. Oveis, Horberg, and Keltner (2010) reported differing effects of compassion and pride on patterns of perceived self-other similarity: compassion, thought to direct attention toward vulnerable or suffering others, increased perception of self-other similarity for weak others; pride, a high-status-signaling emotion, increased perception of self-other similarity for strong others, and reduced self-other similarity to weak others.

Studies conducted by Griskevicius et al. (2010) found that two positive emotions bucked a trend reported in prior research, in which positive emotion promotes increased reliance on peripheral, heuristic-driven routes to persuasion at the expense of critical evaluation of the message (e.g., Mackie & Worth, 1989). Awe, thought to promote accommodative cognition when processing new information (Shiota et al., 2007), and nurturant love, which should promote vigilant attention to the environment (Hrdy, 2006) both increased the effect of argument quality on peoples' endorsement of a persuasive message, relative to a neutral-affect condition. Anticipatory enthusiasm, contentment, attachment love, and amusement all reduced this effect, with participants relying on a simple "number of arguments" heuristic to endorse the message regardless of argument quality, as seen in earlier research (see Figure 3). Importantly, the overall pattern of effects could not be accounted for by any single dimension of appraisal (e.g., certainty) or subjective experience (e.g., pleasantness).

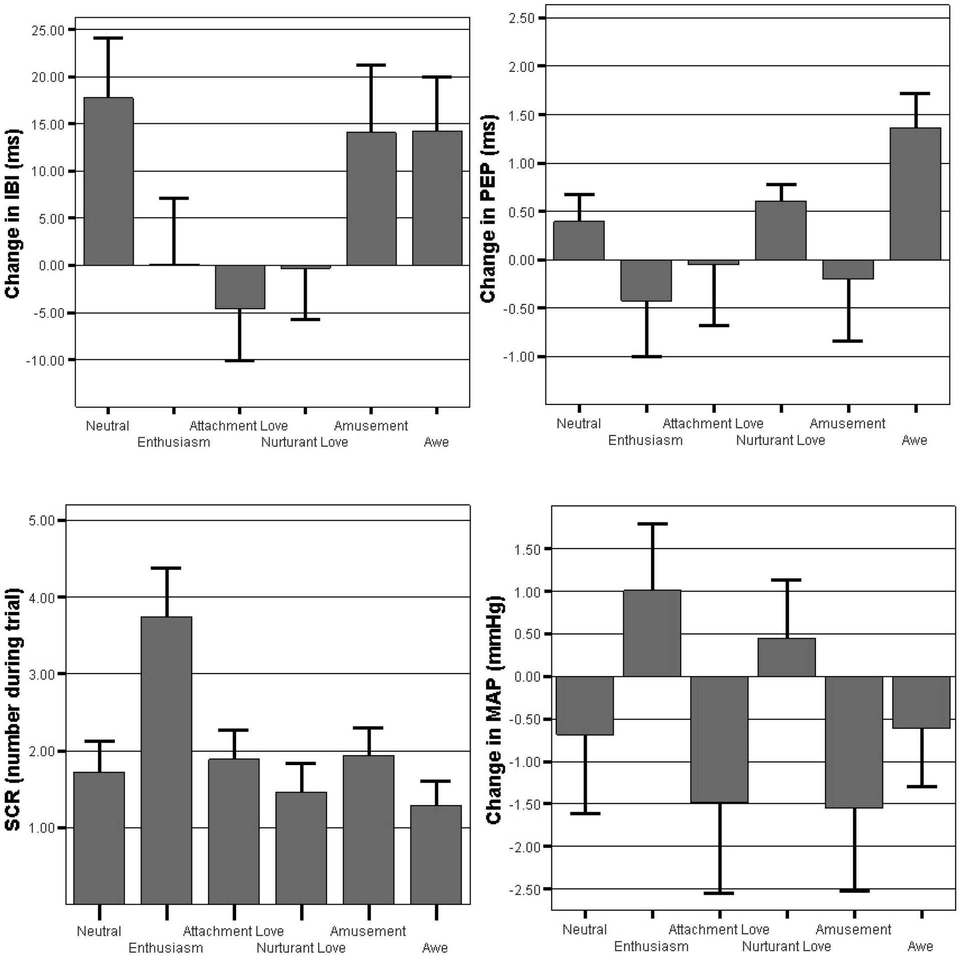

Figure 2. Baseline-to-trial changes in cardiac interbeat interval, preejection period, number of skin conductance responses, and mean arterial pressure during five positive emotions. Adapted from "Feeling Good: Autonomic Nervous System Responding in Five Positive Emotions," by M. N. Shiota, S. L. Neufeld, W. H. Yeung, S. E. Moser, & E. F. Perea, 2011, *Emotion, 11*, 1368–1378. Copyright, 2011 by American Psychological Association.

Similarly, studies by Griskevicius, Shiota, and Nowlis (2010) add important nuance to a proposed link between positive emotion and judgment and decision-making—the "rose-colored glasses" phenomenon. Extensive research shows that when people are in a pleasant mood they evaluate a variety of targets more positively, including political candidates, advertisements, and consumer products (e.g., Forgas, 1995; Gorn, Goldberg, & Basu, 1993; Isbell & Wyer, 1999; Murry & Dacin, 1996; Pham, 2007). Griskevicius and colleagues (2010) asked whether this effect was indifferent to the emotion and target in question, or whether particular positive emotions would tend to increase attractiveness of particular categories of motivationally relevant targets. They found that pride selectively increased the desirability of consumer products intended for public display, such as expensive watches and shoes, but not comparably priced products that would enhance comfort at home, such as a new sofa or bed; the reverse was true for contentment. These effects were even seen when holding product category constant (e.g., clothing), and were mediated by self-reported motivation to "have others notice you" versus "being in a comfortable place." These studies suggest that many current generalizations about the effects of positive emotion on cognition, judgment and decision-making may prove to be moderated by distinctions among specific positive emotions.

Proposed Theoretical Framework: The Positive Emotion Family Tree

The empirical studies described above converge on a critical point: it is no longer tenable to assume that all positive emotions have identical response profiles or effects upon motivation and cognition. The field has now moved

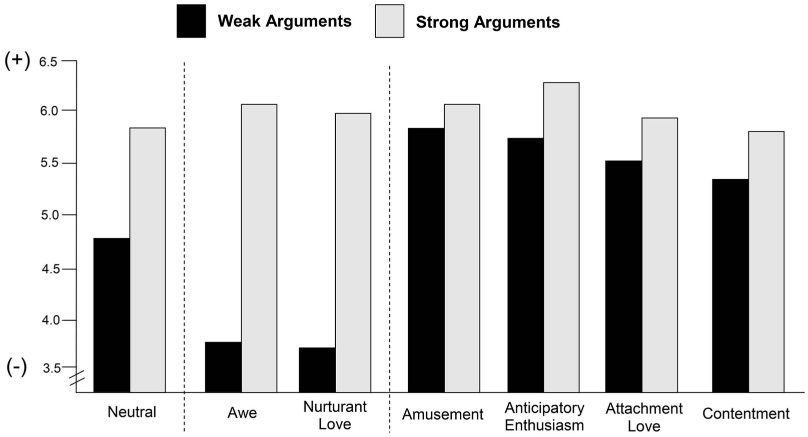

Figure 3. Impact of six positive emotions on persuasion by strong versus weak arguments. Reprinted from "Influence of Different Positive Emotions on Persuasion Processing: A Functional Evolutionary Approach," by V. Griskevicius, M. N. Shiota, & S. L. Neufeld, 2010, *Emotion*, *10*, 190–206. Copyright, 2010 by American Psychological Association.

well beyond this assumption, but is scattered. Researchers have tended to offer theories of individual positive emotions without explicitly addressing how different positive emotions might be related (e.g., McCullough et al., 2001; Ruch, 1993; Shiota et al., 2007; Tracy & Robins, 2007; for an exception, see Gable & Harmon-Jones, 2008). Nor is there great clarity on the structure of positive emotion space, that is, how different varieties of positive emotion might relate to one another. Here, we attempt to fill that gap, proposing an overarching theoretical perspective that includes a tentative phylogeny of positive emotions—a "family tree" (Nesse & Ellsworth, 2009). We posit that a number of distinct positive emotions exapted from a primordial state promoting the acquisition of food (see Figure 4). Importantly, our framework recognizes that evolution has a way of conserving old solutions to problems, and "tinkering" with them when new problems come along (Jacob, 1977; Lewin & Foley, 2004).

We define "positive" emotions in terms of a common aspect of adaptive function: to facilitate effective management of and response to opportunities, presented by the current environment, to acquire material, social, and/or informational resources that are crucial for promoting fitness. We assume this function is shared across positive emotions, but has been elaborated into more distinct functions over the course of our ancestors' evolution as new, qualitatively distinct kinds of resources were introduced. Our approach emphasizes similarities among the adaptive problems addressed by positive emotions as a class, rather than defining positive emotions in terms of subjective pleasantness or approach motivation.

Earlier, we differentiated emotion, as we use the term, from subjective feeling: emotions are evolved psychological mechanisms that coordinate observable cognitive, physiological, and motor processes to produce adaptive responses to particular kinds of eliciting situations (Ekman, 1992; Frijda, 1986; Levenson, 1999; Plutchik, 1980; Tooby & Cosmides, 2008); whereas feelings are subjective, internal

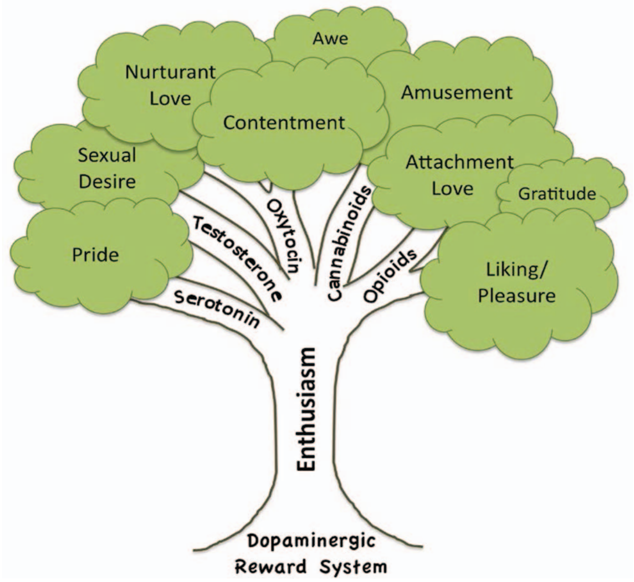

Figure 4. A proposed positive emotion "family tree." The trunk represents the ancient neural reward system giving rise to the positive emotions. Neurotransmitters shown at the base of new branches indicate the key, reward system-modulating roles they might have played at the beginning of each new positive emotion. Clusters of leaves represent proposed "discrete" emotions experienced by modern humans; at this level, each emotion is expected to involve complex profiles of activation across multiple neurotransmitter systems throughout the brain, and interactions with uniquely human cognitive capacities, as well as central roles of dopamine and the neurotransmitter associated with that branch. See the online article for the color version of this figure.

experiences that may include conscious awareness of these responses but interpret them and their meaning through socially and psychologically constructed concepts (Barrett, 2006b; Russell, 2003). Consistent with this distinction, the feeling of pleasantness is influenced by cultural and psychological factors (e.g., Kitayama, Karasawa, & Mesquita, 2004), and "negative" emotions such as sadness, anger, and fear can be experienced as pleasant under the right conditions (Rozin, Guillot, Fincher, Rozin, & Tsukayama, 2013; Wilson-Mendenhall, Barrett, & Barsalou, 2013). While the mechanisms that produce subjective pleasantness are of great interest, our focus here is on positive emotions as defined above.

Behavioral approach motivation is another candidate for the defining feature of positive emotion. This would have striking implications for the boundaries of this category. A rich body of neurological and behavioral evidence indicates that high approach motivation is characteristic of anger, as well as many emotions commonly considered positive (Carver & Harmon-Jones, 2009; Harmon-Jones & Allen, 1998). By any other criterion, anger is somewhat difficult to categorize cleanly as either positive or negative. While usually experienced as unpleasant, it can also be quite enjoyable under some circumstances (Apter, 2015; Averill, 1980). If anger is defined as an emotional response to the thwarting of one's progress toward desired goals (Carver & Harmon-Jones, 2009), it can be seen as a response to the combination of reward *and* threat in the environment. While making it easier to classify anger, defining positive emotions as those involving high approach motivation would leave out some states that clearly reflect adaptive management of resources and, moreover, are experienced as enjoyable (e.g., contentment; Gable & Harmon-Jones, 2008). We do not include anger in the analysis below, but acknowledge that future research may prompt revisiting this decision. We consider approach motivation to be an important aspect of emotional responding that may be involved, to varying degrees, in both positive and negative emotion. As we shall see, however, emotions facilitating long-term resource acquisition do not always involve immediate approach behavior.

With these considerations in mind, we now turn to our functional analysis of the positive emotions, reaching deep into our evolutionary history to consider primordial animal mechanisms for acquiring a fundamental resource needed for survival—food.

The Trunk: The Neural Reward System

Organisms throughout the animal kingdom have evolved neural systems for avoiding threats and acquiring resources. Like other scholars, we propose that the latter system forms the foundation or "trunk" of positive emotional responding, as defined above (Berridge & Kringelbach, 2013; Carver & White, 1994; Davidson, 2004; Nesse & Ellsworth, 2009; Sutton & Davidson, 1997). Neuroscientific evidence strongly indicates that acquisition and management of fitness-relevant resources is supported by a highly conserved circuit of neural structures, often referred to as the "reward system." In mammals, the mesolimbic pathway linking the ventral tegmental area and nucleus accumbens is a key component of this system; the system also includes the uncinate fasciculus, ventral pallidum, and areas of the frontal cortex (Der-Avakian & Markou, 2012; Haber & Knutson, 2010; O'Doherty, 2004; Rolls, 2000).

The mesolimbic pathway and its structures are functionally heterogeneous; recent research has uncovered distinct microcircuits supporting a variety of processes, including appetitive motivation, subjective hedonic pleasure or "liking," attention, and prediction and reinforcement learning mechanisms for both positive and negative outcomes (Beier et al., 2015; Berridge & Kringelbach, 2013; Cox et al., 2015; Lammel, Lim, & Malenka, 2014). After some years of debate over which process these structures *really* mediate, new evidence indicates the presence of multiple, specialized mesolimbic microcircuits dedicated to reward-seeking behavior (e.g., rostral nucleus accumbens shell; Berridge & Kringelbach, 2013; Richard & Berridge, 2011; see also du Hoffmann & Nicola, 2014) and hedonic pleasure (e.g., rostrodorsal quadrant of the medial nucleus accumbens shell and posterior ventral pallidum; Berridge & Kringelbach, 2013; Peciña & Berridge, 2005; Smith & Berridge, 2007); as well as reinforcement learning. Working together, these microcircuits constitute a sophisticated, flexible system for predicting and managing opportunities for reward in all its forms (Der-Avakian & Markou, 2012).

In humans, activation along the mesolimbic pathway has been linked to appetitive motivation and pleasurable anticipation across a wide range of rewarding stimuli, including desirable foods, monetary rewards, addictive substances and cues predicting their availability, video games, sexually attractive people, babies, humor, and peak moments in one's favorite music (e.g., Bartels & Zeki, 2004; Blood & Zatorre, 2001; Glocker et al., 2009; Kampe, Frith, Dolan, & Frith, 2001; Knutson, Adams, Fong, & Hommer, 2001; Koepp et al., 1998; Mobbs, Greicius, Abdel-Azim, Menon, & Reiss, 2003; O'Doherty, 2004; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001; for a recent review, see Berridge & Kringelbach, 2013). Such stimuli share the property of "incentive salience" (e.g., Berridge & Robinson, 1998), eliciting an emotional state of anticipatory "wanting" that promotes appetitive behavior (e.g., Berridge & Robinson, 1995). Abnormal function of structures along the mesolimbic pathway has been linked to symptoms of depression, particularly anhedonia and lack of appetitive motivation (e.g., Der-Avakian & Markou, 2012; Nestler & Carlezon, 2006).

The neurotransmitter dopamine plays a major role in activity within the mesolimbic reward pathway (Berridge, 1996; Robinson, Sandstrom, Denenberg, & Palmiter, 2005). Dopamine is by no means limited to reward-related function; this neurotransmitter is also crucial in brain regions that support motor control and "executive" cognition (e.g., focusing or switching attention), among others (Arnsten & Li, 2005; Braver, Barch, & Cohen, 1999; Volkow et al., 1998). Even within the mesolimbic pathway, some dopamine neurons respond primarily to rewards, others primarily to aversive stimuli, and yet others to both of these (e.g., Matsumoto & Hikosaka, 2009). However, resource-acquisition motivated behavior has consistently been linked to dopaminergic activity within this system (Berridge & Kringelbach, 2013; Berridge & Robinson, 1998; Floresco, 2015; Richard & Berridge, 2011). Even among worms dopaminergic activity mediates approaching high-nutrient areas (Sawin, Ranganathan, & Horvitz, 2000), indicating that the origins of its involvement in resource acquisition are ancient.

In humans, administration of L-DOPA (or levodopa, a drug that enhances dopaminergic function) has been found to enhance reward prediction learning (Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006), increase anticipation of pleasure (Sharot, Shiner, Brown, Fan, & Dolan, 2009), and increase risk-taking and subjective outcome-related pleasure when gains, but not losses, are at stake (Rutledge, Skandali, Dayan, & Dolan, 2015). Linking the trait and state levels of analysis, dopamine receptor allele variation has been found to link trait extraversion with the magnitude of neural responses to rewarding stimuli (Cohen, Young, Baek, Kessler, & Ranganath, 2005). Importantly, however, dopamine does not act alone in the mesolimbic reward pathway; other neurotransmitters including serotonin, opioids, and neuropeptides are highly active here as well, modulating dopaminergic activity and contributing to distinct behavioral and experiential phenomena (e.g., Alex & Pehek, 2007; Bartels & Zeki, 2004; Berridge & Kringelbach, 2013; Lammel et al., 2014; Seymour, Daw, Roiser, Dayan, & Dolan, 2012; Smith, Berridge, & Aldridge, 2011; Striepens et al., 2014).

Facilitating attention and behavioral response toward cues of imminent material resource acquisition, such as appetizing food or, for humans, money, is one major function of this circuit (Alcaro, Huber, & Panksepp, 2007; Floresco, 2015; Haber & Knutson, 2010; du Hoffmann & Nicola, 2014). In humans, the emotion state that most closely corresponds to this function has been called appetitive or anticipatory *enthusiasm* (Driver & Gottman, 2004; Griskevicius et al., 2010; Gruber & Johnson, 2009; Harmon-Jones, Gable, & Peterson, 2010; Reis & Wheeler, 1991; Shiota et al., 2011). Research in humans links experimentally elicited enthusiasm to globally heightened "fight-flight" sympathetic nervous system activation (Kreibig, 2010; Shiota et al., 2011), to narrowing of attentional focus (Gable & Harmon-Jones, 2008), to enhanced memory for centrally rather than peripherally presented visual information (Gable & Harmon-Jones, 2010), and to increased reliance on cognitive heuristics (Griskevicius et al., 2010). Each of these is consistent with a general function of supporting fast, active pursuit of tangible resources—including prey that can run away, and even fight back.

The Branches: Modulation of the Reward System

Branches emerge from tree trunks without leaving them behind. In this case, "branches" of the positive emotion tree consist of specialized responses to new kinds of resources, still mediated by the ancient reward system, but modulating the effects of that system and/or the conditions in which it is activated. In many cases these new opportunities are social in nature, reflecting increasing complexity of relations with conspecifics across major phases of human evolution (Wilson, 2015). What follows is necessarily speculative, given the early state of what is known about the human and mammalian central nervous systems and the complex, multifaceted nature of emotion. However, evidence is strong and growing that a variety of neurotransmitters and peptides modulate dopaminergic activity within the mesolimbic pathway as well as the structures to which it projects. These neurotransmitters have widespread independent effects (Alldredge, 2010; Bartels & Zeki, 2004), track the emergence of new selection pressures throughout our evolutionary history, and can be associated with meaningful human positive emotion constructs.

Serotonin. Serotonin also plays an important role in supporting reward-related behavior. In worms, serotonin activity impacts dopamine-mediated movement toward nutrient-rich areas based upon degree of food deprivation versus satiety (Sawin et al., 2000). In mammals (e.g., mice, rhesus monkeys) some serotonergic cells originating in the dorsal raphe nuclei are selectively activated while anticipating rewards or performing tasks earning a reward (Bromberg-Martin, Hikosaka, & Nakamura, 2010; Cohen, Amoroso, & Uchida, 2015). This activity tends to increase activation of mesolimbic dopamine neurons (Alex & Pehek, 2007; Doherty & Pickel, 2000). Consistent with this, tryptophan depletion (which reduces serotonergic activity) has been shown to reduce people's neural (e.g., nucleus accumbens) and behavioral sensitivity to reward contingencies in a gambling task (Seymour et al., 2012).

Serotonergic systems throughout the brain support a wide range of functions, including sleep cycle regulation (Portas, Bjorvatn, & Ursin, 2000), memory (Buhot, Martin, & Segu, 2000), and executive cognition (Chamberlain et al., 2006). In the socioemotional domain, studies of the serotonin transporter gene provide growing evidence that serotonergic activity supports modulation of behavior in response to the social environment (Homberg & Lesch, 2011). In particular, serotonin appears to play an important role in detecting and responding to cues of social status (Chiao, 2010; Edwards & Kravitz, 1997). Although the status hierarchies of group-living mammals are particularly sophisticated, even invertebrates such as crayfish and lobsters compete for and benefit from dominant positions within hierarchies, obtaining preferential access to food, territory, and mating opportunities (Gherardi & Daniels, 2003; Kravitz & Huber, 2003). From lobsters to humans, serotonin levels are correlated with behavioral dominance, although the direction of this association differs across species (Edwards & Kravitz, 1997). Among rhesus macaques, individuals with "short" serotonin transporter alleles (which extend the duration of serotonergic activity) are more reactive to status and hierarchy, showing more submissive behavior and greater physiological stress when in a submissive social position (e.g., Jarrell et al., 2008; Watson, Ghodasra, & Platt, 2009). Moreover, population frequency of the short allele is higher in both macaque species and human cultures with more hierarchical social structures (Chiao, 2010).

Humans with a serotonin receptor gene variant resulting in enhanced serotonergic activation enjoy greater social popularity and esteem (Burt, 2008). Experimental enhancement of serotonin activity has also been shown to produce more assertive, confident behavior (Wai & Bond, 2002). Consistent with the finding that serotonin enhances dopaminergic mesolimbic pathway activity, social dominance has pronounced implications for reward-seeking behavior. Rats previously ranked as socially dominant, for example, self-administer cocaine at higher rates when exposed to this drug, take more risks, and are more aggressive in pursuing food rewards (Davis, Krause, Melhorn, Sakai, & Benoit, 2009; Jupp et al., 2015). These effects are mediated in part by dopamine receptor binding in the nucleus accumbens shell, and are limited to socially housed animals, suggesting that they are elicited by the experience of social dominance rather than reflecting preexisting individual differences (Jupp et al., 2015). In humans, power leads to increased behavioral activation across a broad range of actions (Galinsky, Gruenfeld, & Magee, 2003). A serotonergic mechanism for modulating reward-seeking behavior based on one's level of dominance may have provided an ancient neurobiological foundation for human *pride*—an emotional response to the opportunity of high social status (Tracy & Robins, 2007; Tracy, Robins, & Tangney, 2007). Notably, the human pride display is highly similar to the dominance display of primates and other mammals (e.g., postural expansion; Tracy & Robins, 2008), and is recognized cross-culturally as an indicator of high social status (Tracy et al., 2013).

Opioid peptides. In the vertebrates we begin to see roles for the opioid peptides in analgesia (Sneddon, 2004), and regulation of temperature (Adler, Geller, Rosow, & Cochin, 1988), but also in signaling sensory enjoyment or pleasure (Berridge & Kringelbach, 2013). Opioid activity within the reward system is distinct from the activity linked to "wanting," and is observed primarily during the consumption of rewards rather than their anticipation. The capacity for hedonic pleasure likely evolved from early mechanisms for differentiating sweet from bitter tastes, present among early vertebrates and important for expanding food supply while avoiding toxins (Dong, Jones, & Zhang, 2009). Opioids modulate activity of distinct "hedonic hotspots" within the reward system (Berridge & Kringelbach, 2013), facilitating enjoyment of eating (e.g., Fields, 2007; Peciña & Berridge, 2005; Smith et al., 2011) and physical warmth (Rolls, Grabenhorst, & Parris, 2008). In both rodents and humans, this influence is accentuated for sweet, fatty, and other high-calorie foods (Baldo et al., 2013; Kelley et al., 2002). In particular, opioid activity in a microcircuit linking the rostrodorsal quadrant of the medial nucleus accumbens shell and the posterior ventral pallidum is associated with facial expressions indicating perception of sweet taste in apes, monkeys, rats, and mice (Berridge & Kringelbach, 2013). Extensive evidence now links activation in this microcircuit to the a state variously referred to as *liking,* "consummatory pleasure," and "hedonic pleasure" (Berridge & Kringelbach, 2013; Berridge & Robinson, 1995). Although subjective feeling of pleasure is a central feature of this response, we include it as a positive "emotion" because of its distinct function in distinguishing foods with high caloric value from potential toxins (Dong et al., 2009).

In vertebrates, opioid peptides also began to play important roles in the coordinated social behavior of group-living species, such as schooling in fish (Kavaliers, 1981). In humans as well as rats, mu-opioid activity in the cingulate cortex helps alleviate distress responses to separation from an attachment figure, rejection, and other social pain (e.g., Eisenberger et al., 2011; Panksepp, 2003; Panksepp, Siviy, & Normansell, 1985). However, opioid activity in the nucleus accumbens shell also appears to facilitate pleasure associated with affiliative contact (Inoue, Burkett, & Young, 2013; Moles, Kieffer, & D'Amato, 2004). Although the role of oxytocin in pair bonding is well-known (and will be discussed below), mu-opioid receptors in the dorsomedial nucleus accumbens have also been found to selectively mediate pair bonding among prairie voles, with blockage of these receptors inhibiting pair bonding (Resendez et al., 2013). Naltrexone, an opioid antagonist, reduces people's affiliative feelings toward partners in an economic trust game (Schweiger, Stemmler, Burgdorf, & Wacker, 2014). In one striking study, naltrexone was found to inhibit a previously observed effect in which physical warmth increased people's feelings of social connectedness (Inagaki, Irwin, & Eisenberger, 2015).

As a mechanism linking the pleasurable enjoyment of physical and social warmth, opioid activity within the mesolimbic pathway may provide a neurobiological foundation for mammalian *attachment love*—an emotional response to the opportunity of affiliation, interdependence, and intimacy. As noted earlier, love is one of the emotions most clearly communicated through touch, particularly skin-to-skin contact (Hertenstein et al., 2006, 2009); in the absence of a currently present partner, people will even hug themselves as part of the display (Campos et al., 2013). Notably, touch evokes an opioid response in many mammals including rodents, humans, and primates, providing a mechanism by which affiliative social contact might activate endogenous pleasure, as well as alleviate distress (Dunbar, 2010; Weller & Feldman, 2003). *Gratitude,* experienced when one unexpectedly benefits from another's altruistic act (McCullough et al., 2001), may be a distinct variant of attachment love in the context of relationships that are not currently communal and intimate, yet show strong potential for developing these qualities (Algoe, 2012).

Testosterone. In the tetrapods, the shared ancestors of reptiles, birds, marsupials and mammals, a diversity of gonadal steroid hormones and associated receptors evolved from ancestral estrogen (Thornton, 2001), as mate selection and sexual dimorphism became more important aspects of reproduction. The androgen testosterone, in addition to driving the development of masculine phenotype and peripheral sexual response (Bhasin et al., 2001; Penton-Voak & Chen, 2004), plays an important role in male and female *sexual desire*—an emotional response to the opportunity presented by a high-quality potential sex partner (Diamond, 2003; Wallen, 1995). Testosterone administration increases subjective feelings of sexual arousal in human men (Gray et al., 2005; O'Carroll & Bancroft, 1984) and women (Shifren et al., 2000; Tuiten et al., 2000), and experimentally induced testosterone deficiency sharply reduces sexual desire and functioning (Bagatell, Heiman, Rivier, & Bremner, 1994). Experiments with rats and hamsters suggest that the behavioral effects of testosterone are mediated, in part, by elevation of dopaminergic cell activity in the ventral tegmental area and nucleus accumbens (e.g., de Souza Silva, Mattern, Topic, Buddenberg, & Huston, 2009; DiMeo & Wood, 2006).

Cannabinoids and the basal ganglia. Tetrapods also had well-developed basal ganglia (a set of structures that includes the ventral tegmental area and nucleus accumbens as well as several others) thought to serve as a "switching mechanism" helping the organism select among a range of immediate behavioral options (Redgrave, Prescott, & Gurney, 1999; Stocco, Lebiere, & Anderson, 2010). Such a mechanism would be crucial for animals navigating increasingly complex interactions with the environment. The cognitive/behavioral flexibility supported by the basal ganglia plays a critical role in the play behavior of animals from reptiles to birds, rodents, and humans (Burghardt, 2005; Emery & Clayton, 2015). Whether play is physical, cognitive, social, or verbal (i.e., humor), it offers an opportunity to practice skills and test new strategies in a safe situation, where immediate fitness consequences are not on the line (Boyd, 2004; Pellegrini & Smith, 2005; Siviy, 2010; Wyer & Collins, 1992).

Basal ganglia activation is mediated by a wide range of neurotransmitters, including GABA, glutamate, norepinephrine, and an array of neuropeptides as well as dopamine (Graybiel, 1990). In rats, a moderate increase in dopaminergic activity within the basal ganglia promotes play, and dopamine antagonists reduce it, suggesting that dopamine may support play motivation (Graham & Burghardt, 2010; Siviy & Panksepp, 2011). Low doses of morphine (an opioid agonist) increase play, whereas naltrexone (an opioid antagonist) inhibits it, suggesting that opioid contribution to the mesolimbic reward pathway supports hedonic enjoyment of play, or "fun" (Trezza, Baarendse, & Vanderschuren, 2010). In addition, the basal ganglia is rich in receptors for cannabinoids, which work through retrograde signaling—a mechanism by which postsynaptic neurons can regulate neurotransmitter release by presynaptic neurons. Although direct cannabinoid agonists reduce play, agonists that inhibit cannabinoid degradation (prolonging effects of naturally occurring release) facilitate it, suggesting that this regulatory role of cannabinoid activity is important for play (Trezza, Baarendse, & Vanderschuren, 2010). Increasingly, *amusement* is recognized as a pleasurable emotional experience linked to opportunities for humor and play (e.g., Griskevicius et al., 2010).

Oxytocin. In the therapsids, the branch of the tetrapods that divided into marsupials and mammals, oxytocin and vasopressin split off from the neuropeptide vasotocin. Outside the brain, oxytocin receptors regulate contraction of smooth muscle tissues in the gastrointestinal tract, uterus, and mammary glands (Altura & Altura, 1977; Bolton, 1979; Qin et al., 2009). In the mammalian brain, hypothalamic oxytocin receptors help mediate satiety-related feelings and behaviors after food consumption (Mitra et al., 2010), given fullness cues from the gut as conveyed by cholecystokinin peptides and vagal afferents (Dockray & Burdyga, 2011). The mesolimbic reward pathway includes mechanisms for dopamine-oxytocin interaction (Romero-Fernandez, Borroto-Escuela, Agnati, & Fuxe, 2013). In rodents, central administration of oxytocin reduces food intake, especially of carbohydrates, in part by inhibiting dopaminergic reward circuit activity (Sabatier, Leng, & Menzies, 2013). In humans, intranasal oxytocin reduces snacking, especially on sweets, but not hunger-driven eating (Ott et al., 2013). This function of oxytocin may contribute to the human experience of *contentment*—the emotion associated with satiety after obtaining or consuming a resource. Contentment, which involves reduction in sympathetic nervous system activation as well as an increase in vagal parasympathetic activation (Kreibig, 2010), is thought to facilitate physical rest and digestion; studies with rats suggest it also promotes encoding of the memory for one's route to success (Foster & Wilson, 2006; consistent with a proposal by Fredrickson, 1998).

Behaviorally, therapsids moved in the direction of prolonged childhood dependence, requiring longer periods of parental investment for smaller numbers of offspring. This reproductive strategy requires extended commitment by parents to their young, and in some cases of the parents to each other, for the young to thrive. Ample evidence links oxytocin not only to childbirth and nursing, but also to the formation of bonds that facilitate this long-term commitment (e.g., Carter, DeVries, & Getz, 1995; Diamond, 2003; Gonzaga et al., 2006; Insel & Shapiro, 1992; Levine, Zagoory-Sharon, Feldman, & Weller, 2007). These effects appear to be mediated in part by activation of oxytocin receptors within the reward system (Bartels & Zeki, 2004; Skuse & Gallagher, 2009). Oxytocin receptors are dense in the nucleus accumbens of prairie voles, which show marked pair bonding, but not montane voles, which are polygamous (Insel & Shapiro, 1992). Indeed, injection of a dopamine agonist into the nucleus accumbens can promote prairie vole pair bonding even without mating, but this effect can be reversed with administration of an oxytocin antagonist, suggesting that the pair-bonding process involves oxytocin-dopamine interaction (Liu & Wang, 2003). In rats, injection of oxytocin into the ventral tegmental area leads to an increase in nucleus accumbens dopamine, and the magnitude of this effect predicts intensity of pup licking and grooming (Shahrokh, Zhang, Diorio, Gratton, & Meaney, 2010). Male oxytocin gene "knock-out" mice show failure to develop memory for familiar conspecifics, but no deficits in other aspects of memory, indicating effects specific to social stimuli (Ferguson et al., 2000).

In humans, intranasal oxytocin has been found to increase early attention to positive facial expressions (Domes et al., 2013), cooperation in a repeated prisoner's dilemma game (Rilling et al., 2012), and subjective feelings of trust (Van IJzendoorn & Bakermans-Kranenburg, 2012). Modulating effects of oxytocin on dopamine activity within the mesolimbic reward pathway may support interdependent relationships in general, and provide a neurobiological foundation for *nurturant love* in particular—an emotional response to the important adaptive opportunity presented by offspring and other vulnerable kin.

The Leaves, or Why People Are Not Lobsters

The analysis above could be interpreted as reductionist in two ways that do a disservice to the field of emotion. First, it might be taken as a statement that we equate the human experience of pride with a lobster's display of dominance, or human romantic love with a prairie vole's postcoital bonding. This is not at all our intent. We consider the neural system(s) described above, and the mechanisms by which they facilitate adaptive behavior, to be evolutionarily conserved physiological-motivational-behavioral foundations on which the richness and complexity of human emotional experience is built. Millions of years of primate and hominid evolution added dramatic new capacities to the human nervous system, and with them, many layers of complexity to our experience of emotion; for a short list, consider interoception (Craig, 2009), language (e.g., Foroni & Semin, 2009; Tsai, Simeonova, & Watanabe, 2004), controlled or "executive" cognition (Miyake et al., 2000), self-consciousness (Tracy & Robins, 2007), self-concept (e.g., Moran, Macrae, Heatherton, Wyland, & Kelley, 2006), and theory of mind (e.g., Völlm et al., 2006). These and other capacities profoundly influence emotion—especially its subjective experience—in humans (and perhaps the few other species that may share these capacities, e.g., chimpanzees, dolphins), receiving input from, recruiting, interacting with, and in some cases overriding these ancient systems in ways we are barely beginning to understand (Barrett, 2006a; Lindquist et al., 2012).

If one defines "discrete" emotions primarily in terms of the adaptive problem they address, as we do here, new cognitive capacities such as self-representation, causal attribution, metaphorical thought, and schema formation may even interact with the ancient emotion systems outlined above in the face of new selection pressures to produce uniquely human emotional experiences. This has been suggested for *awe*, an emotional response to the opportunity presented by a vast, information-rich stimulus that is not accounted for by one's current knowledge, thought to promote schema construction or accommodative cognition (Danvers & Shiota, 2016; Griskevicius et al., 2010; Keltner & Haidt, 2003; Shiota et al., 2007).

The analysis above could be construed as reductionistic in a second way. In positing the role a neurotransmitter might have played at the beginning of a new "branch" of the positive emotion tree, we do not mean to suggest one-to-one correspondence between neurotransmitters and positive emotions. On the contrary, there is considerable evidence of complex involvement in positive emotions across neurotransmitter systems. For example, oxytocin has been implicated in aspects of mammalian sexual arousal and attachment love as well as nurturant love and contentment (e.g., Carmichael et al., 1987; Carter et al., 1995; Diamond, 2003). Serotonin modulates the experience of satiety and contentment, in addition to its involvement in dominance (Burton-Freeman, Gietzen, & Schneeman, 1999). In several human studies, basal testosterone levels have been found to interact with basal cortisol levels in predicting dominance-related behaviors (Mehta & Prasad, 2015; Mehta, Welker, Zilioli, & Carré, 2015). Evolution's tinkering would not have stopped at the major branch points; later growth and division likely added a variety of other neural mechanisms and associated psychological features to each branch.

Taken as a whole, this approach suggests that positive emotion space has an implicit hierarchical structure (as do analyses of emotion language that include negative and positive states, e.g., Shaver et al., 1987). The "trunk" of the tree in Figure 4 defines a broad category of emotional responding, with mechanisms by which the positive emotions discussed above should share some overlapping properties. At the same time, the branches of the tree reflect distinguishable manifestations of this core, differentiated through interaction with other neurotransmitter and brain systems, profiles of peripheral effects, and the behaviors that they support in response to prototypical kinds of opportunities (see Table 3). This necessitates an important caveat regarding our use of the term "discrete" in the present article's title—our discrete positive emotions are functionally semidistinct, and can be differentiated from each other on several aspects of emotional responding, but also share common features reflecting their relationship to a primordial mechanism promoting acquisition of food.

In developing this taxonomy we have chosen to emphasize the intersection among functional analysis, neuroscience, and analysis of behavior because work with both humans and nonhuman animals in these areas has been especially rich and coherent over the last 20 years (Keltner & Lerner, 2010). However, that work is far from complete. This theoretical framework and taxonomy are intended as starting points to catalyze additional discussion and research, rather than definitive conclusions. In the next section we consider important gaps in the evidence relevant to our framework, and note where research is most strongly needed.

The Work to Be Done: A Research Agenda

In Table 3, we attempt to summarize the current state of the evidence regarding central nervous system mechanisms, nonverbal expressions, peripheral physiology, cognitive processes, motivational and behavioral profiles, and subjective experience associated with each of the positive emotion constructs in our taxonomy. Check marks indicate fairly well-established findings, keeping pace with comparable research on negative emotions; "IP" indicates work that is developing or in progress; and "W" indicates that work in this area is weak or absent. Domains in which the evidence is strong and growing are evident, as are notable gaps. Overall strengths include evidence linking neural mechanisms to overt behavior, which is quite strong for some emotions (e.g., Berridge & Kringelbach, 2013; Boloña et al., 2007; Chiao, 2010; Edwards & Kravitz, 1997; Jupp et al., 2015; Ott et al., 2013; Sabatier et al., 2013) and at least growing for others (e.g., Machin & Dunbar, 2011; Trezza et al., 2010). The least is known about awe in this regard—to our knowledge, no studies have directly examined the neural activity or overt behavior associated with this state, much less attempted to link these together.

For some emotions, evidence of corresponding neural activation directly addresses the state in question (e.g., enthusiasm, liking/pleasure, contentment, sexual desire, amusement/play; Berridge & Kringelbach, 2013; Boloña et al., 2007; Sabatier et al., 2013; Trezza et al., 2010). For others, however, more is known about a trait-level analog of the emotion than about the emotion state. This is especially true for positive emotions in relational contexts, where there may be extensive research on the neural correlates of relationship status (e.g., dominance, attachment, bonding; Chiao, 2010; Edwards & Kravitz, 1997; Jupp et al., 2015; Leng, Meddle, & Douglas, 2008; Mehta & Prasad, 2015; Mehta et al., 2015), but far less on the emotional states that promote relationship building and maintenance. Evidence regarding neural mechanisms of relationship status may help inform research on associated emotion states, but cannot replace it. Also, while new techniques for measuring and even manipulating neural activity in humans are increasingly available and used to study positive emotions

Table 3
A Proposed Positive Emotion Taxonomy, With Current State of Evidence in Several Aspects of Emotional Responding

		Current status of evidence					
Emotion	Prototypical opportunity	Neural mechanism	Nonverbal expression	Peripheral physiology	Cognitive aspects	Motivation, behavior	Subjective experience
Enthusiasm	Food	✓	W	✓	IP	✓	W
Liking/Pleasure	Sweet (vs. bitter) taste	✓	✓	W	W	✓	✓
Contentment	Digestion	✓	IP	✓	IP	✓	W
Pride	Dominant social status	IP	✓	W	W	✓	IP
Sexual desire	Reproductive partner	✓	✓	✓	IP	✓	W
Attachment love	Affiliation, alliance	IP	IP	IP	W	✓	IP
Nurturant love	Altricial offspring, kin	IP	W	IP	W	✓	W
Amusement	Play; skill development	IP	✓	✓	IP	✓	W
Awe	Novel, complex information	W	✓	IP	IP	W	IP

Note. ✓ = evidence strong; IP = evidence preliminary or in progress; W = evidence limited or absent.

(e.g., Domes et al., 2013; Pessiglione et al., 2006; Rutledge et al., 2015; Schweiger et al., 2014; Seymour et al., 2012), the bulk of research is still on nonhuman animals. Although it is reasonable to presume that neural mechanisms for positive emotion have been highly conserved throughout our ancestors' evolution, research with humans allows investigation of links between neural activity, subjective feelings, and more subtle aspects of motivation than can be studied in nonhuman animals—this is an important direction for ongoing research.

Evidence for distinct nonverbal expressions is mixed, with strong data on some positive emotions and limited data on others (Keltner & Cordaro, 2015). The facial/postural displays of pride, hedonic pleasure, and amusement are well-established (Berridge & Kringelbach, 2013; Campos et al., 2013; Keltner, 1995; Parr, Waller, & Fugate, 2005; Tracy et al., 2013), yet little is known about enthusiasm or nurturant love. Reliably decoded vocal signals have been identified for some positive emotions, but not others (e.g., Cordaro et al., 2016; Sauter et al., 2010; Simon-Thomas et al., 2009). Research on peripheral physiology is in a similar state. Quite a bit is known about the autonomic and hormonal effects of appetitive enthusiasm, satiety-related contentment, amusement, and sexual desire (Kragel & LaBar, 2013; Kreibig, 2010; Masters & Johnson, 1966). Research on the remaining states is available and growing (e.g., Shiota et al., 2011), but currently limited. A key aim of our taxonomy of eight positive emotions is to offer a useful, common conceptual framework to guide additional empirical study and synthesis.

Implications of emotion for cognitive processing are strongly emphasized in evolutionary psychology approaches to discrete emotions (Tooby & Cosmides, 2008). Theoretical perspectives emphasizing the valence of core affect have inspired extensive programs of research on pleasant mood and cognitive processing (Ashby, Isen, & Turken, 1999; Bless & Fiedler, 2006; Forgas, 2008), yet this aspect of emotional responding has traditionally received limited attention from discrete emotion researchers (Lerner, Li, Valdesolo, & Kassam, 2015). Reflecting this neglect, the "cognitive aspects" column of Table 3 has no checks, though work is in progress for several positive emotions. Research on cognitive effects may be most advanced for awe, the positive emotion whose theorized function most explicitly involves cognition (e.g., Griskevicius et al., 2010; Rudd, Vohs, & Aaker, 2012; Shiota et al., 2007; Valdesolo & Graham, 2014), and for sexual desire, which has been found to influence risk-related decision-making (e.g., Baker & Maner, 2008; Li, Kenrick, Griskevicius, & Neuberg, 2012). The extent to which cognitive effects of positive emotions can be differentiated is an area in need of future research.

As noted above, another substantial gap can be found in evidence linking neural activity and motivated behavior to subjective experience, or feeling. This reflects a number of methodological issues, not least of which is that neural activity and overt behavior are most easily studied in nonhuman animals, whereas reports of subjective feelings can only be obtained from human participants. In the last decade, however, more sophisticated techniques have become available for manipulating neurotransmitter systems noninvasively in humans through drugs, diet, and nasal sprays, as well as imaging neural activity at finer temporal scales. The literature reviewed in presenting our new theoretical framework included several examples of studies using these methods, and assessing subjective as well as behavioral response (e.g., Bagatell et al., 1994; Gray et al., 2005; Ott et al., 2013; Schweiger et al., 2014; Tuiten et al., 2000). However, strong research in this area will require development of more fine-grained measures of subjective experience as well, measures that differentiate various kinds of positive emotion. Commonly used self-report measures of overall positive affect, such as the Positive and Negative Affect Schedule (PANAS; Watson et al., 1988), will not capture differences among specific positive emotional states. Caution is also needed in assuming that research participants attach the same meaning to emotion terms that researchers do. Going beyond simple emotion labels to examine thought content, feeling and subjective motivation during an emotional experience will strongly enrich this approach.

Although much of the neuroscience and behavioral evidence comes from nonhuman animals, few studies have been conducted across multiple cultures. The exceptions are few, and limited to nonverbal communication of positive emotions, but valuable (e.g., Cordaro et al., 2016; Laukka et al., 2013; Sauter & Scott, 2007; Tracy & Robins, 2008; Tracy et al., 2013). Using functional analyses to hypothesize the effects of evolved emotion mechanisms is a legitimate approach in evolutionary psychology, especially where these effects would not be predicted by social or psychological construction models, but cross-cultural research is necessary to assess the extent of universality versus culture-specificity.

Finally, research seeking to advance our understanding of the positive emotions should include multiple constructs in the same study, as often as possible. While studies looking closely at a single emotion can offer valuable information, research on the relationships among these constructs is needed to move toward a careful mapping of the positive emotion terrain.

Lost in Translation: Positive Emotion Differentiation in Applied Research

To this point, we have emphasized the theoretical rationale for, and implications of, adopting a discrete emotion approach in research on positive emotion. Our framework also has important implications for applied psychology. Basic affective science guides practices in clinical psychology, marketing, education, public health, business, and a number of other practical domains (e.g., Ashkanasy & Humphrey, 2011; DeSteno, Gross, & Kubzansky, 2013; Griskevicius et al., 2009; Linnenbrink, 2006; Watson & Spence, 2007). The assumption that effects observed for one variety of positive emotion will hold true for all positive emotions could, if incorrect, have dire implications for translational work. In contrast, the understanding that different positive emotions can have quite different effects would facilitate interventions and practices that match emotion states to desired outcomes in precise, yet theory-driven ways.

As one example, take the implications of a discrete positive emotion approach for clinical psychology. Researchers have long proposed that dysregulation of reward responding and positive emotionality plays an important role in the mood disorders (e.g., Carver & Johnson, 2009; Henriques & Davidson, 2000; Nestler & Carlezon, 2006; Willner, Muscat, & Papp, 1992). Deficits in positive emotion have also been linked to social anxiety (e.g., Kashdan & Breen, 2008) and schizophrenia (Watson & Naragon-Gainey, 2010). However, the vast majority of research addressing these links has used either global self-report measures of positive affect, or a single induction of positive feelings (e.g., viewing photos of ice cream, or a humorous video). The few studies that have measured different positive emotions speak to the utility of this approach. For example, dispositional joy (a construct similar to enthusiasm in the present taxonomy) and amusement have been found to prospectively predict subsequent increases in mania symptom severity, whereas compassion (a construct similar to nurturant love) shows the opposite effect, and awe and contentment show no effect at all on mania symptom magnitude (Gruber & Johnson, 2009). Similarly, studies have linked depressive symptom severity specifically to deficits in dispositional and experimentally evoked pride (Gruber, Oveis, Keltner, & Johnson, 2011). In these and other disorders, distinguishing among positive emotions may prove important for the purposes of differential diagnosis and treatment development.

Careful consideration of the distinct functions, elicitors, and motivational/behavioral implications of specific positive emotions is an important part of this strategy. For example, although all would currently be classified as core symptoms of major depression, chronic deficits of appetitive enthusiasm, pride, sensory pleasure, and attachment love likely reflect differing neural and environmental etiologies, should cluster with differing sets of additional symptoms, and may be ameliorated by different treatment plans. Individual profiles of depression symptoms are remarkably heterogeneous, with nearly 1,500 unique potential combinations that would qualify for diagnosis (Ostergaard, Jensen, & Bech, 2011). Research already suggests that certain symptom clusters are associated with particular kinds of losses (i.e., of an important relationship partner vs. failure; Keller & Nesse, 2006). Functional analyses of the four positive emotions above could be used to develop hypotheses about distinct symptom clusters expected given disruption of emotional responding to the corresponding kinds of rewards.

Positive emotion differentiation may be crucial in the domain of behavior change research as well. Health behavior interventions such as antismoking, antidrug, and antiobesity campaigns routinely use fear appeals, which have well-recognized drawbacks; unless the threatening message is accompanied by content that succeeds in increasing self-efficacy, the message is simply tuned out (Hastings, Stead, & Webb, 2004; Peters, Ruiter, & Kok, 2013). Increasingly, health psychologists are calling for interventions that use positive rather than negative emotions to motivate change (e.g., Cameron & Chan, 2008; Peters et al., 2013).

The nuances of *which* positive emotion to employ may, however, prove crucial. Here, again, functional analyses of distinct positive emotions should facilitate their effective use in interventions, and help prevent backfires. For example, positive emotions involving strong appetitive motivation, such as enthusiasm and pride, are unlikely to help people resist temptation. Perhaps for this reason, some "positive affect" manipulations have been found to increase alcohol craving in alcohol-dependent participants (Mason, Light, Escher, & Drobes, 2008), and high-calorie snacking in obese participants (Udo et al., 2013). However, Tice and colleagues (2007) have found that the experience of amusement/humor may help restore self-regulatory capacity, making it easier to nudge behavior in desired directions. Different positive emotions may also have different implications for health message processing. As discussed earlier, many positive emotions promote shallow, peripheral processing of persuasive messages—hardly ideal for achieving lasting effects. However, nurturant love and awe were both found to have the opposite effect, promoting more systematic processing and, in awe, greater cognitive elaboration of the message as well (Griskevicius et al., 2010). A discrete positive emotion approach built on functional analyses may help those developing health behavior interventions to leverage positive emotions more effectively.

Conclusion: What We Gain From a Science of Discrete Positive Emotions

Advances in affective science depend critically on the constructs we use, and on our operational measures. The science of positive emotion has largely emphasized trait positive affect and global positive feeling or mood, rather than the functionally "discrete" states often studied in research on negative emotion. While a great deal has been learned from the former approaches, the study of more specific states is revealing rich diversity in the features and implications of different positive emotions across several emotion response systems. Our aim here has been to begin integrating the relevant literature and offer an overarching theoretical perspective that accounts for existing findings, and points the way to much-needed future research. As the gaps in currently available evidence are filled in, we anticipate that the model we have proposed will be adjusted in many important, empirically informed ways.

Is the discrete emotion approach "right" within affective science, broadly speaking? How "discrete" will the positive emotion constructs we have proposed prove to be? At the current stage of evidence, we consider these questions to be highly worth pursuing, rather than having clear answers. Questions regarding the psychological nature and mechanisms of emotion have been at the forefront of emotion theory and research for decades. Any attempt to answer them depends on data assessing links among various components of emotional responding—elicitors, appraisals, cognitive biases and processes, neural activity and peripheral physiological reactivity, expression, behaviors and action tendencies—at many clearly defined points in emotion space. Such data can be used to test whether variability in the positive emotion domain is best explained by the relatively categorical approach emphasized here, or, for example, in terms of the effects of a series of continuous, interacting appraisal dimensions (Scherer, 2009).

The theoretical framework we have described facilitates hypotheses and research designs that will produce these data, while acknowledging that the boundaries between emotion constructs may be fuzzy rather than sharp. We anticipate that data will ultimately point to a convergence of the discrete function, appraisal component, and dimensional theories of emotion, in which each understanding of "emotion" maps to a psychological mechanism that is real in the neural, behavioral, and phenomenological sense. To achieve this goal, however, researchers must seek as much knowledge about variety in the positive emotion domain as they have long done for the negative emotions. Beyond "happiness" lies a rich and underexplored realm, where clues to human functioning and happiness are sure to be found.

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