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Trends in Cognitive Sciences

Opinion

Semantic Space Theory: A Computational Approach to Emotion

Alan S. Cowen[1,*] and Dacher Keltner[1]

Within affective science, the central line of inquiry, animated by basic emotion theory and constructivist accounts, has been the search for one-to-one mappings between six emotions and their subjective experiences, prototypical expressions, and underlying brain states. We offer an alternative perspective: semantic space theory. This computational approach uses wide-ranging naturalistic stimuli and open-ended statistical techniques to capture systematic variation in emotion-related behaviors. Upwards of 25 distinct varieties of emotional experience have distinct profiles of associated antecedents and expressions. These emotions are high-dimensional, categorical, and often blended. This approach also reveals that specific emotions, more than valence, organize emotional experience, expression, and neural processing. Overall, moving beyond traditional models to study broader semantic spaces of emotion can enrich our understanding of human experience.

Highlights

In the past decade, scientists have systematically moved beyond the six traditionally studied emotions to document a broader array of emotion-related experiences and expressive behaviors.

Semantic space approaches to emotion organize the study of emotion-related behavior by establishing the number of distinct patterned responses that occur systematically within an emotion-related modality, how these behaviors are most precisely conceptualized, and whether these behaviors are discrete or exist along a continuum.

Computational methods reveal emotional behavior to be high dimensional, involving upwards of 25 distinct kinds of emotion. Specific categories of emotion, more so than valence and arousal, drive the representation of emotion in experience, expression, and neural processing. Much of emotional response is found to be systematically blended rather than discrete.

Reexamining the Nature of Emotion

For 2500 years, scholars have mapped our mental and social lives in terms of emotions that animate thought and action. In the scientific literature that finds provenance in this theorizing, four central questions have emerged. What interpretive processes give rise to emotional experience? How do people recognize emotional expression in others? How does the brain represent these processes? What behaviors are universal across cultures and species?

Two contrasting perspectives have fueled scientific attempts to answer these questions: basic emotion theory (BET) and constructivism (with appraisal theories typically falling in between; Table 1). Although these perspectives diverge on what emotions are, they converge in assuming that emotions solve a biological dilemma: that our brains are adapted for survival and reproduction, but our daily decisions are often many steps removed from these goals. This makes the evolutionary calculus of daily life – risk-taking, courtship, and tribal politics – immensely complex. The cognitive priors that enable our brains to approximate this calculus are, in most any theory of emotion, at the root of emotional behavior.

Where these theories diverge is in the extent to which emotions are biologically prepared, how they should be conceptualized, and how they organize behavior (Table 1). Within BET, it is assumed that there are only a few emotions, that they are separated by clear boundaries, and that categories such as anger or awe capture universals in emotional experience, recognition, and brain representation. Constructivist accounts, by contrast, posit that core affect, or valence and arousal, are primary in emotional experience, and that people place different interpretations upon core affect, giving rise to significant individual and cultural variation in experience and the meaning of expressive behavior.

Efforts to adjudicate between these theories have centered upon tests for one-to-one mappings between six kinds of emotion – anger, disgust, fear, happiness, sadness, and surprise – and

[1]Department of Psychology, University of California, Berkeley, 2121 Berkeley Way, Berkeley, CA 94704, USA

*Correspondence:
alan.cowen@berkeley.edu (A.S. Cowen).

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Table 1. Past Theoretical Claims Regarding the Biologically Preparedness, Conceptualization, and Structure of Emotional Behavior

	Basic emotion theory	Appraisal theories	Constructivism	Refs
Claims regarding biological preparedness	Emotional feelings associated with specific cognitive appraisals and behaviors are biologically prepared and modified by experience. Emotional states intervene between appraisal and response.	Certain appraisals (e.g., certainty, pleasantness or goal conduciveness) are biologically prepared and modified by experience. Patterns in emotion-related response can be explained by mappings from appraisal to behavior.	Certain valence/arousal responses are biologically prepared. Specific emotions involve valence and arousal but are artifacts of language (i.e., infants and nonhuman animals do not have emotions).	[12,13,119]
Claims regarding how emotions should be conceptualized	Patterns in emotion-related behavior are best conceptualized in terms of specific emotions such as awe and fear.	Emotion-related behaviors are best explained in terms of particular cognitive appraisals (e.g., certainty), not specific emotions.	Emotions are best conceptualized in terms of valence, arousal and language-based conceptual knowledge.	[12,33,120]
Claims regarding the structure of emotion-related behaviors	Traditional BET reduces emotions to six or seven discrete clusters of states. Revised BET admits of complex (>25 kinds), blended emotions.	Emotions reduce to a specific set of appraisal dimensions, usually <10 (in a few cases, many more) and may or may not fall into discrete clusters.	Emotion-related behaviors are fundamentally low-dimensional and lack any inherent categorical structure.	[2,11,12,33,60,120,121]

subjective experience, prototypical expression, and underlying body and brain states [1–7]. In BET, evidence confirming these one-to-one mappings reveals the nature of emotion [8]; in constructivist accounts, evidence disconfirming these one-to-one mappings reveals that emotions are not natural kinds [6,7,9]. This narrow empirical focus limits the inferences to be drawn regarding the broader structure of emotion [10,11]. As a result, entrenched disagreements persist over the nature of emotion based on summaries of the same data (Table 1) [6,11–16].

Here we offer a different approach – semantic space theory. Our approach formalizes the study of emotion in the investigation of representational state spaces capturing systematic variation in emotion-related response (including experience and expression, as well as associated physiology, cognition, and motivation). We integrate computational studies of emotional experience, facial–bodily expression, and vocalization to visualize what one might think of as an emerging taxonomy of emotion. Next, we discuss how the brain represents these experiences in distinct configurations of activity across the default mode network and subcortical areas. Building upon these advances, we synthesize literatures on nonhuman emotion-like behavior and nervous system response, highlighting emerging evidence that emotional behaviors differentiated within a fine-grained taxonomy have animal homologies and evolved neural mechanisms. The implication of these developments is clear: moving beyond traditional models to a broad taxonomy of emotion (Figure 1) will provide for a richer, more comprehensive science of emotion [17].

Semantic Spaces of Emotion

Central to advances of the past 50 years is the question William James posed 140 years ago: What is an emotion [18]? A consensus exists that emotions involve appraisals, experiences, expressive behavior, physiological response, influences upon ensuing thought and action, and language-based representations of these unfolding processes [19,20].

Answers to this first question are shaped by knowledge related to a second: what are the emotions? Out of the rich array of emotions we experience, how many are distinct? Out of the thousands of facial–bodily and vocal signals that people are anatomically capable of producing [21–24], how many have distinct meanings? To answer these questions is to map the meanings of emotional experiences and expressions within a semantic space [25–28].

Semantic spaces of emotion are defined by three properties (Figure 1A). The first is their dimensionality: how many different kinds of emotion are distinguished within the space? The second is the

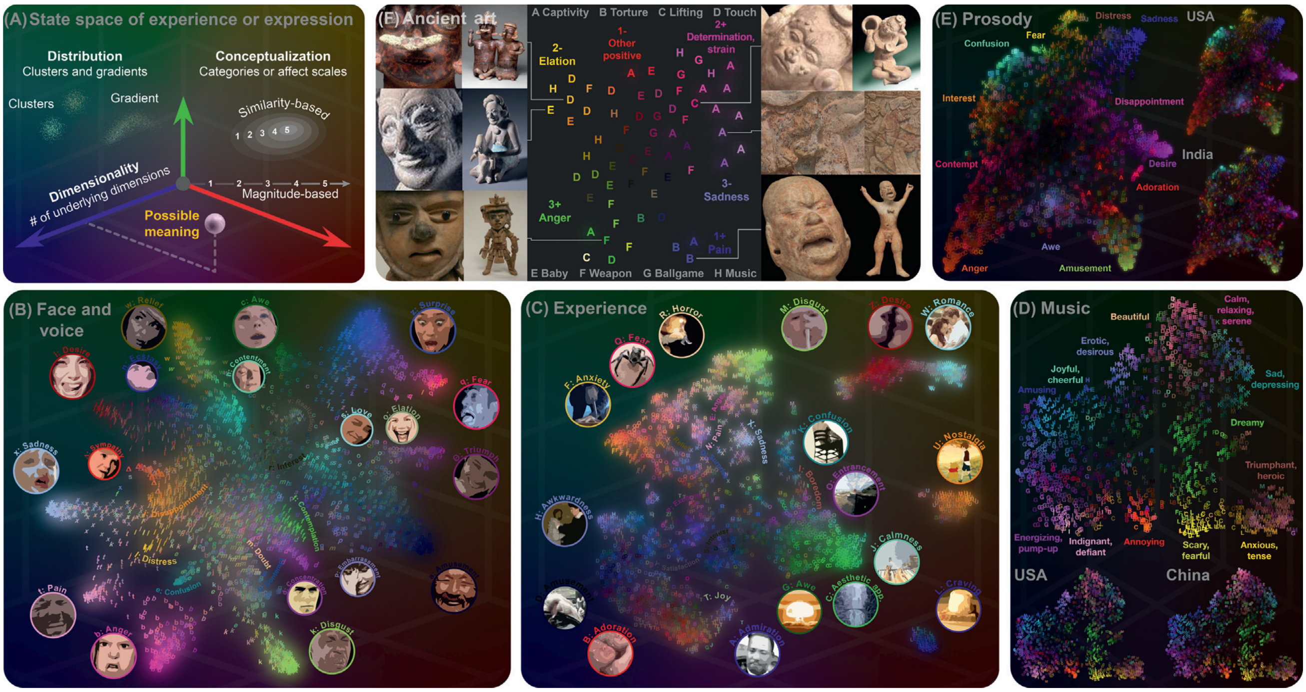

Figure 1. Semantic Spaces of Experience and Expression. (A) The semantic space framework. A semantic space is described by (i) its dimensionality, or the number of distinct meanings of experiences or expressions within the space; (ii) the conceptualization of these meanings in terms of mental states, intentions, or appraisals; and (iii) the distribution of experiences or expressions within the space, capturing clusters or blends of states. (B) Semantic space of facial–bodily and vocal expression. A total of 3523 expressions are lettered, positioned, and colored according to 28 distinct emotions that people reliably attribute to them (28 in facial expression [42] and 24 in vocal expression [25]). Within the space are gradients in expression between emotions traditionally thought of as discrete, such as fear and surprise. To explore these expressions, see the interactive maps (face: https://s3-us-west-1.amazonaws.com/face28/map.html, voice: https://s3-us-west-1.amazonaws.com/vocs/map.html). (C) Semantic space of emotion evoked by 2185 brief videos. At least 27 distinct affective states are reliably captured in reports of emotional experience evoked by video, best conceptualized in terms of emotion concepts such as fear [26]. Again, gradients bridge emotion concepts traditionally thought of as discrete, such as fear and surprise. Interactive map: https://s3-us-west-1.amazonaws.com/emogifs/map.html. (D) Semantic space of emotional experience evoked by 1841 music samples in multiple cultures [36]. Music samples are positioned and colored according to 13 emotions with which they are reliably associated in both the USA and China. Within the space, we find gradients among these states. The similarities in affective response across cultures were most reliably revealed in the use of specific emotion concepts (e.g., desire and fear). Interactive map: https://s3.amazonaws.com/musicemo/map.html. (E) Semantic space of emotion conveyed by prosody in 2519 lexically identical speech samples. Across the USA and India, at least 12 kinds of emotion are preserved in the recognition of mental states from speech prosody, most reliably revealed in the use of emotion concepts [28]. Interactive map: https://s3-us-west-1.amazonaws.com/venec/map.html. (F) Emotional expression in Ancient American art [58]. Ancient American sculpture was found to portray at least five distinct kinds of facial expression that accord, in terms of the emotions they communicate to westerners, with western expectations for the emotions that might unfold in the eight contexts portrayed. Colors of individual faces (letters) are weighted averages of colors assigned to each kind of perceived facial expression. Eight example sculptures are shown. (To explore all 63 sculptures, see online map: https://s3.amazonaws.com/precolumbian/map.html.) Credit, from top left down: (i) Metropolitan Museum of Art 2005.91.12, gift of the Andrall and Joanne Pearson Collection, 2005; (ii) Princeton University Art Museum 2003-26, gift of G. G. Griffin; (iii) Metropolitan Museum of Art 1979.206.578, Michael C. Rockefeller Memorial Collection, Bequest of Nelson A. Rockefeller, 1979; (iv) Kerr Portfolio 342, Jaina Figure, photo by J. Kerr; (v) Kimbell Art Museum, Fort Worth, Texas, AP 1971.07, Presentation of Captives to a Maya Ruler (detail); and (vi) Photograph: Museum of Fine Arts, Boston 1983.288, gift of L.T. Clay.

distribution of states within the space: are there discrete boundaries between emotion categories, or is there overlap [26,29]? The third is the conceptualization of emotion: what concepts most precisely capture people's implicit or explicit differentiation of subjective experiences and expressive behaviors [30,31]? Do experiences and expressions correspond to specific emotions (e.g., interest, sadness, and amusement) or broader affect and appraisal evaluations such as valence and arousal [2,29,32] or certainty [33], as posited in appraisal and constructivist theories?

Capturing semantic spaces of emotional response requires new kinds of data and statistical approaches. The prevalent focus on a limited number of emotions and prototypical stimuli [4,6] captures, as we detail in the following text, approximately 30% of the information conveyed in self-report and expressive behavior [34]. Characterizing the meaning of self-report and expression requires vast arrays of evocative stimuli and expressions [11] and participants' responses in terms of widely varying emotion terms and questions that capture appraisal processes [27] or nonverbal behaviors [35]. It requires moving beyond univariate measures [8], recognition accuracy [4], and factor analysis [2,33], approaches that presuppose universal one-to-one mappings between emotion-related behaviors and discrete labels (e.g., anger) or position along a few broad dimensions of response (for limitations of factor analysis, see Video S1 in supplemental information online).

Semantic spaces embody a broader goal: to separate signal from noise. To carry signal about emotion, all instances of a particular behavior (e.g., a smile) need not map to an identical emotional state, as long as they carry informational value regarding emotional experience. Indeed, we have identified facial expressions used in everyday life in multiple ways, such as sentimental expressions of musical performers that resemble expressions of pain [35].

To represent such meanings precisely is to project them onto dimensions that capture the systematic variance in emotion-related behavior. Identifying these dimensions, whether they are few and broad or numerous and nuanced, requires multidimensional reliability analysis approaches – such as principal preserved components analysis – which satisfy the mathematical objective of finding preserved dimensions across individuals or groups [28,36,37]. In contrast to recognition accuracy and factor analysis, such approaches neither assume one-to-one mappings between experiences and expressions, nor ignore dimensions of meaning that are nuanced yet reliable.

Semantic spaces are further characterized by the distribution of states along their dimensions. How sharp are the boundaries between different categories of emotion? What is lost by sorting emotions into discrete classes? Answers to this question inform whether emotions should be understood as discrete affect programs [38] or continuous processes [39], where experiences are blended, and transition readily from one to another.

Finally, how should we talk about, or conceptualize, the dimensions of a semantic space? Answers to this question are central to emotion theory, but formal answers require statistical modeling [40]. Analogously, the dimensions of perceived color can be conceptualized as red, green, and blue spectral channels [41]. As we will see, emotion has more dimensions than color, calling for more complex statistical models and larger-scale data. However, as with color, if the dimensions of a semantic space that explains emotion-related behavior are best conceptualized using specific categories (blue and awe), it is apt to refer to these dimensions as emotions.

Emotional Experience and Expression Is High Dimensional, Categorical, and Often Blended

Recent studies have applied these computational approaches to the study of facial–bodily expression [42], nonverbal vocalization [25], speech prosody [28], and the feelings evoked by music [36] and video [26], within and across cultures [28,36]. Three themes with theoretical relevance have emerged in replicable findings across studies.

First, emotion inhabits a high-dimensional space. People reliably distinguish at least 27 distinct subjective experiences associated with video [26], 24 distinct emotions in nonverbal vocalizations [25,28], and 28 distinct emotions in the face and body (Figure 1B,C) [42]. These findings were observed using both traditional rating methods and open-ended free response. The specific numbers here matter less than the more general point that emotion is at least four times more complex than that represented in studies of six emotions. This finding, replicated across response systems of emotion, is not anticipated by BET, and stands in contrast to assumptions of low dimensionality – that emotion is largely reducible to valence and arousal – found in constructivist accounts [12].

Which are more primary in emotional experience and recognition of emotion in the face and voice: specific emotions, as predicted by BET, or valence and arousal, as predicted by constructivism? Crosscultural studies reveal that specific emotions are more primary [25,26,28,36,42], in several ways. First, attributions of feelings such as amusement or embarrassment to oneself or another person are better preserved across cultures than valence and arousal attributions [28,36]. Second, valence and arousal attributions can be explained as culture-specific valuations of specific emotions. For instance, across the USA and India, people align more closely in evaluations of anger in vocal expressions than in evaluations of their valence. Yet, we can predict valence evaluations in one culture from emotion judgments in the other by taking into account how vocalizations perceived (in both cultures) as angry are considered more negative in the USA than in India [28] (a slight oversimplification; the predictions involve multivariate patterns of judgments). Similar findings emerge in the study of subjective experiences evoked by music across the USA and China [36]. The processes underlying subjective experience and emotion recognition seem to be grounded in the states we designate with specific emotion categories (sympathy and awe) in the same sense that color perception is grounded in three color channels. From these specific states, people infer valence, arousal, and eliciting appraisals in a more culture-specific manner [28,36] (just as we deem colors warm or cold [43]).

Finally, categories of emotion that have been treated as discrete [4] (e.g., anger and disgust) are bridged by gradients of blended experiences and expressions (Figure 1B–E) [25,26,28,36,42]. For instance, pure expressions of fear, surprise, and awe are bridged by gradients of composite facial–bodily and vocal displays that reliably transmit intermediate meanings [25,42]. Although there may be modal emotion-related responses [44], much of human emotional life is more complex.

Is there convergence across these studies of experience and expression? Might certain emotions – a taxonomy of states – emerge as crossmodal response patterns? In Figure 1B–E, we map the distinct mental states conveyed by upwards of 6000 distinct facial–bodily and vocal expressions (Figure 1B,E) and evoked by music and video (Figure 1C,D). This synthesis finds upwards of 18 emotions that can both be reliably be distinguished in facial–bodily and vocal expression (Figure 1B) and evoked by distinct videos (Figure 1C) or music samples (Figure 1D): amusement, anger, anxiety, awe, confusion, contentment, desire, disgust, elation, embarrassment, fear, interest, love, pain, relief, sadness, surprise, and triumph. Another 12 emotional states have documented associations with distinct antecedents and expressions only in certain modalities – for instance, shame in facial–bodily expression [42] and the dreamy sensation conveyed by some music [36] – either because other signals await discovery, or because the different modalities are nonredundant.

A caveat to the findings shown in Figure 1B,C is that they are based on behavioral responses by American English speakers. However, other studies are finding that people in different cultures attribute similar mental states to a wide range of expressions [4,28,36,45–55], while culture-specific accents and display rules account for a consequential, but typically smaller, amount of systematic variance in emotion attribution (25–30%) [35,50,53,55–57]. For example, responses to Western and Chinese music in the USA and China (Figure 1D) occupy 13 preserved dimensions, or kinds of emotional experience [36]. Likewise, speech prosody recognition in the USA and India (Figure 1E) occupies 12 shared dimensions of emotion [28]. With statistical modeling, broad arrays of stimuli, and fine-grained behavioral measures, we uncover a wider range of crosscultural parallels in emotional behavior than previously documented.

There are lingering questions regarding the recognition of emotion in cultures with limited western contact, given the methodological complexities of studying such cultures [6,15,34]. By turning to a broader array of emotions, new kinds of stimuli, and open-ended methods of emotion labeling, a recent study introduced a new approach to examining emotional behavior in cultures isolated from the west. This study, a computational analysis of facial expressions portrayed in Ancient American sculpture, rules out western contact and circumvents biases and nonequivalences across languages in survey-based methods [58]. Facial expressions in 63 sculptures from the Ancient Americas were found to accord with contemporary western expectations in terms of their portrayal in specific social contexts. Ancient American sculptures tend to portray at least five facial expressions in contexts predicted by westerners, including pain in torture, determination/strain in heavy lifting, anger in combat, elation in social touch, and sadness in defeat (Figure 1F) – supporting the universality of these facial expressions.

The insights revealed in Figure 1 bring into focus how much information is captured by traditional models of emotion – the Basic 6 and valence and arousal – and how much is overlooked. With predictive (crossvalidated) models, the Basic 6 and valence and arousal are each found to capture around 30% of the systematic variance in judgments of a wide range of emotion categories (an upper bound, given that an even broader range of stimuli and responses may expose other dimensions of variance). Thus, studies relying on these traditional models capture only about 30% of the systematic variance in any response modality, and likely underestimate the diagnostic value of self-report and expression in terms of how they map onto patterns of physiological and neural response, predict subsequent behaviors, and influence the behavior of others (Figure 2) [4,6,7,34,59].

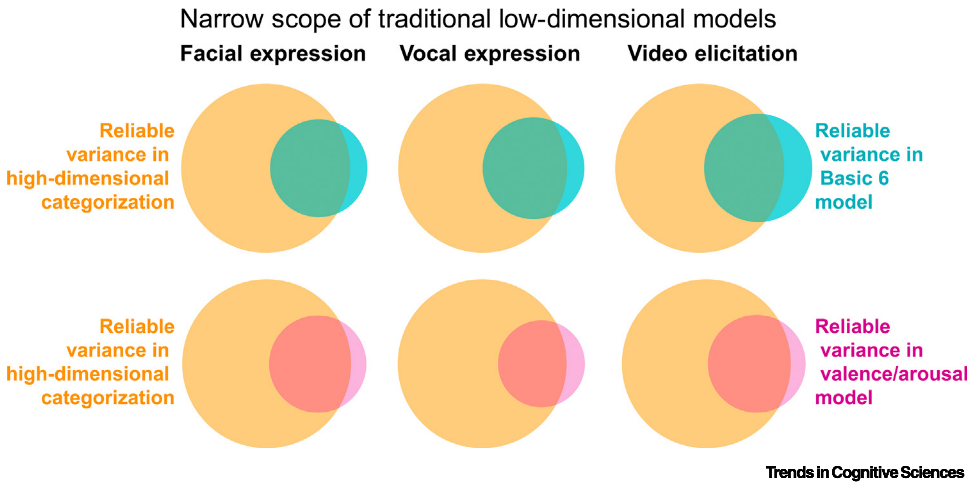

Figure 2. What Traditional Models Capture. Venn diagrams represent the proportion of the reliable variance in emotional behavior captured by the Basic 6 and valence/arousal. By mapping reported emotional experiences and facial expressions into a high-dimensional space, we can largely predict how they are recognized in terms of the Basic 6 and valence/arousal. However, the Basic 6 capture only a fraction of the information reliably conveyed by facial expression, vocal expression, and self-reports of emotional experience in response to video – 28%, 30.8%, and 30.2%, respectively. Valence/arousal capture only 28.5%, 21.3%, and 29.1%, respectively. Altogether, traditional models based on the Basic 6 and valence and arousal largely fail to capture the rich and variegated space of the meanings that emotional expressions convey and that emerge in subjective responses to evocative stimuli.

Extensions of an Emergent Taxonomy: Patterns of Brain Response and Mammalian Behavior

The search for the neural responses that accompany emotional experience and expression, and their parallels in mammalian neurophysiology and signaling behavior, have been central areas of inquiry. Such evidence is germane to evolutionary arguments about the biological preparedness of emotions and the functions they serve (Table 1). Past efforts in these areas of inquiry have focused on the Basic 6, but are significantly advanced by considering the broader taxonomy of states we have observed across studies.

The Primacy of Specific Emotions in Neural Response Patterning

The use of broad ranging stimuli, open-ended behavioral measurements, and model comparison methods can be readily extended to the study of the neural basis of emotion. Such an approach moves beyond the longstanding search for one-to-one mappings between six kinds of emotion and coarse brain regions toward data-driven models of emotion-related neural response [7,9]; a direction several functional magnetic resonance imaging (fMRI) studies have begun to take. However, investigations have still largely relied on relatively small numbers of stimuli or conditions [60–62] and been unable to adequately differentiate representations of emotion from representations of sensory and semantic features, which are encoded throughout cortex [60,63,64]. The richer space of emotion we have documented also highlights interpretive problems from these more narrowly focused brain studies [6,7]. Most notably, studies have treated states such as disgust and empathic pain as equivalent [7,8,65], although we now know that they involve distinct experiences and expressions [26,65,66] and in some cases have been showed to involve distinct neurophysiological systems (e.g., disgust involves the insula and gastric/immune systems while empathic pain involves the anterior cingulate cortex and autonomic nervous system [65–72]). Thus, it should come as no surprise that results have varied across studies [7,8,16,72].

A more recent study [66] has overcome these limitations by collecting whole-brain fMRI responses to over 2000 diverse emotionally evocative videos and using well-validated statistical modeling approaches [63,73–76] to differentiate neural representations of a wide range of emotions, broad affective features such as valence and arousal, and semantic and visual features. Dozens of emotions evoked by video could accurately be differentiated from patterns of brain activity. Such differentiation was not observed in simple one-to-one mappings between particular emotions and brain regions (e.g., fear and amygdala) [9] but in complex configurations across multiple brain networks (Figure 3) that are consistent across subjects (suggesting that they are not representations of learned concepts, which would recruit arbitrary and variable patterns of activity [77]). Emotion-related representations were distributed across transmodal brain regions near the hubs of the default mode network (DMN), such as the prefrontal cortex and angular gyrus. These findings build on well-replicated observations that the DMN is differentially active during experiences of emotion [78,79], zeroing in on what organizes these patterns of DMN activity. Namely, activity across the DMN corresponded to self-reported experiences such as anxiety, disgust and entrancement rather than broad dimensions such as valence and arousal (or the semantic contents of stimuli, such as animals or landscapes) [63]. Indeed, specific emotions explained greater variability in brain activity than affective dimensions in every cortical and subcortical region of the brain, even the amygdala and brainstem (using crossvalidated predictive models). This study suggests that specific emotions are primary in the representation of emotion throughout the brain [25,26,28,36,42,58].

Experiences of specific emotions, then, are found to involve multiple interacting systems – situated near DMN and subcortical regions – that enter distinct states in response to perceived threats and opportunities [9,62,80–82]. Given that these systems encode emotional experience

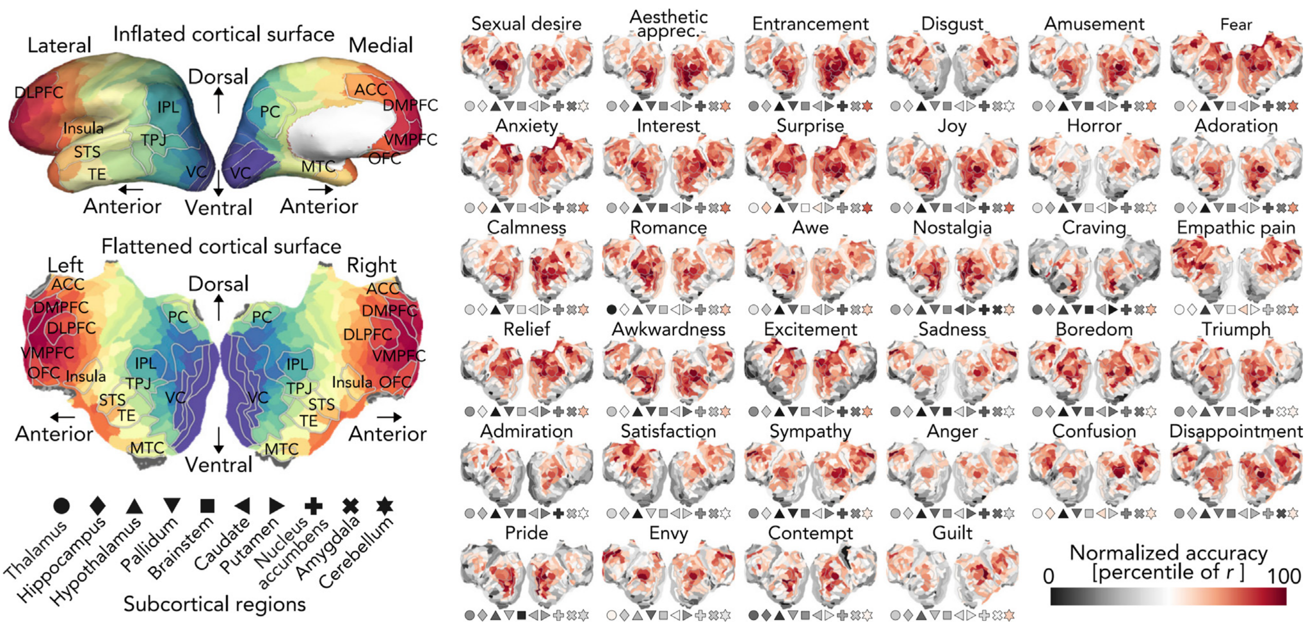

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Figure 3. Emerging Insights into the Brain Representation of Emotion. From Kamitani and colleagues (2020) [66]. Cortical surface maps of decoding accuracies for specific emotions (five subjects averaged) in 360 brain regions from the Human Connectome Project [154] and ten subcortical regions. Each subject was scanned by functional magnetic resonance imaging while passively viewing 2181 emotionally evocative videos over the course of seven or more sessions. Decoding models were trained to predict 34 emotion categories associated with each video. Abbreviations: ACC, anterior cingulate cortex; DLPFC/DMPFC/VMPFC, dorsolateral/dorsomedial/ventromedial prefrontal cortex; IPL, inferior parietal lobule; MTC, medial temporal cortex; OFC, orbitofrontal cortex; PC, precuneus; STS, superior temporal sulcus; TE, temporal area; TPJ, temporoparietal junction; VC, visual cortex.

(or affordances) during passive viewing of videos, these findings support the view that specific emotions proactively recruit psychological faculties likely to support adaptive behavioral responses, regardless of our intentions and beyond our immediate control [83,84]. Note also that the distribution of emotion-related brain activity reflected the blends we previously observed in the experiences of emotions such as anxiety and fear, suggesting that such blended states are actually represented in intermediate patterns of brain activity. The neural underpinnings of emotion inhabit a high-dimensional, complex semantic space. The complexity of this space is a lower bound: future studies using active and personal elicitors, for example, gaming, social interaction, will likely uncover further brain representations of emotion and appraisal.

High-Dimensional Parallels in Mammalian Behavior

Within evolutionary accounts, it is assumed that primates and other mammals demonstrate display behavior that in form, contextual occurrence, and function (e.g., effect upon nearby individuals), have parallels with human emotional expression [85]. These homologies have long resisted easy classification into categories of anger, disgust, fear, happiness, sadness, and surprise. Consider, for example, parallels in consolation behavior in other mammals (perhaps homologous to human sympathy) [85–89], the open-mouth smile and laughter-like utterances during play (amusement) [90–93], and displacement behaviors (anxiety) [94–98].

Our emergent taxonomy of states points to more precise comparisons between human emotion and mammalian behavior. In Table 2, we synthesize observations of mammalian behavior and neurophysiology with parallels to 12 emotions that have emerged as distinct in subjective experience, expression, and human brain activity. For example, that people link amusement to both open-mouth smiles and laughter [25,42,86,99–103] informs hypotheses regarding the

Table 2. Organizing Evidence for Dissociable Evolutionary and Physiological Underpinnings of Emotion-Related Behaviors within a Nuanced Semantic Space

System	Examples	Refs
Amusement, play	Play face in nonhuman mammals, laughter and play in mammals, brain stimulation and mirthful laughter	[86,90–92,99,103,105]
Anger, aggression	Growling/snarl homologies in mammals, hypothalamic aggression mechanisms	[122–126]
Anxiety, tension	Nonhuman displacement behaviors such as self-grooming and their relief via consolation in chimps and reduction by antianxiety drugs in macaques	[95–98]
Disgust, aversion	Sour/bitter facial response in primates, facial expression and neural correlates in mice, insula in disgust recognition/experience, gastric/immune system disgust response	[65,69–72,127–130]
Ecstasy, pleasure	Hedonic response in newborns/primates, facial expression and neural correlates in mice	[127–129]
Fear, alarm	Alarm calls in nonhuman animals, amygdala response to scream-like sounds, amygdala response to alarm faces, primate amygdala and alarm signals, facial expression and neural correlates in mice, joint brain mechanisms of fleeing/freezing in mouse brain stem	[81,129,131–135]
Love, bonding	Filial touch in animals, oxytocin in human bonding, oxytocin in rat/vole/tamarin bonding, oxytocin-moderated pupil dilation and affiliation	[108–114,136,137]
Pain, (physical/empathic)	Pain grimace in nonhuman animals, ACC and pain recognition/experience, facial expression and neural correlates in mice, dissociable psychophysiological response	[65,67,68,129,138–140]
Pride, status	Erect ape posture and bipedal swagger	[85,141,142]
Sadness, loss	Cry face and whimper in chimpanzees, midbrain responses to infant cries	[143–145]
Shame, submission	Submission displays of postural constriction and shrinkage in mammals and even nonmammals	[85,146–149]
Sympathy, consolation	Animal consolation behaviors, animal care response to distress cries, ACC oxytocin role in consolation behaviors, ACC/empathy network response and altruism	[87–89,150–153]

Abbreviations: ACC, anterior cingulate cortex.

role of animal homologies of the play face [86,90,91,100] and laugh-like utterances [92,93,99], organizing social functional accounts that aim to explain why these expressions often occur concurrently [86,104] and why their neural correlates overlap with those of play behaviors in humans and animals [92,103,105]. Similarly, that love is linked to both tactile and vocal signals [106–113] informs hypotheses regarding the animal homologies of filial touch [108,110,111,113,114] and nurturant prosody [109,112,115,116], and helps explain their overlapping endocrinological underpinnings, such as why both of these behaviors covary with the release of oxytocin [109,111,112]. Such findings support the role of evolutionary pressures in organizing the neurophysiological underpinnings of emotion-related behavior within a high-dimensional semantic space.

Concluding Remarks

Guided by a semantic space approach to subjective life, and new computational and open-ended methods, this integration of studies across methods of emotion elicitation and response modalities yields three important conclusions for the future study of emotion. We find that emotion is high dimensional, involving upwards of 25 distinct kinds of emotions, each with their own patterned profile of associated responses. We reveal how specific categories of emotion more so than valence and arousal organize the representation of emotion in experience, expression,

Outstanding Questions

How is emotional behavior universal, and how is it shaped by culture? Emotion recognition studies, constrained by language and the focus on the Basic 6, have led to divergent positions regarding the degree of cultural specificity or universality of emotion-related behavior. Studies of actual behavior are scant. However, newly available methods now enable broader observational studies of how people behave across cultures and naturalistic contexts, particular with machine learning. By documenting the real-life situations in which people in different cultures produce the wide range of emotional behaviors revealed in the study of semantic spaces of emotion, can we determine what aspects of emotional behavior are universal and which are shaped by cultural processes?

What does nonverbal expression really indicate about emotional experience? Suppose a film arouses laughs, cries, screams, or grimaces. What, if anything, can we infer about how it makes people feel? Answers to this question are supplied by everyday intuition, but remain elusive to science. Owing to the narrow focus on the Basic 6 and the face, there is a widely recognized need for broader evidence that can capture the more complex ways in which people actually move their faces, bodies and voices when they feel emotions. What will broader studies guided by semantic space approaches reveal about how people express subjective feeling in patterns of behavior?

What is the nature of the neurocomputational processes that generate richly varying emotional responses? Recent studies establish that the brain represents a wide range of specific emotional experiences (Figure 3). However, questions remain about the processing stages that give rise to these representations. How are perceptual inputs converted into high-level system wide representations of emotion? Which brain regions contribute to the conversion of sensory input into emotion-related appraisals and emotional experience, and which guide subsequent behavior?

and neural processing. Other findings suggest that boundaries between emotion categories are not discrete, and that much of emotional response is systematically blended.

In more specific terms, across subjective experience, facial–bodily expression, vocal bursts, prosody, and brain patterning, we find convergent evidence to be a rich semantic space of emotion. These results point to at least eight distinct, more negatively valenced states found across all modalities (anger, anxiety, confusion, disgust, embarrassment, fear, pain, and sadness); nine distinct positively valenced states (amusement, awe, contentment, desire, elation, interest, love, relief, and triumph); and surprise. Further emotional experiences and expressions may be modality specific, including pride and shame in the face/body [42,45] and the distinctive feeling of dreaminess or reverie evoked by certain pieces of music [36].

Understanding the dimensionality, distribution, and conceptualization of emotional experience and expression is a roadmap for the future study of the causes, dynamics, and functions of emotion. For instance, semantic spaces of emotion guide the study of emotional behavior using machine learning methods. These methods in turn enable empirical observation at a scale sufficient to relate complex patterns in expression to multifaceted contextual appraisals. One new study based on these methods [35] has leveraged an artificial deep neural network trained to map facial expressions into the semantic space represented in Figure 1B. Examining facial expressions in millions of natural videos from 144 countries, the study found that each of 16 distinct patterns of facial expression had different associations with a set of contexts that were 70% preserved across 12 world regions. Expressions associated with amusement occurred more often in videos with practical jokes; awe with fireworks; concentration with martial arts; contentment with weddings; doubt with police; pain with weight training; and triumph with sports. These findings are in keeping with theories proposing that facial expressions occur in psychologically relevant contexts [45,117,118]. Machine-learning methods guided by semantic spaces of vocal emotion, music, language [37], and studies of the dynamics and social functions of these behaviors are poised to unlock further insights into the processes by which emotions influence our lives.

The field of affective science has long been anchored to the study of six emotions [11]. In opening up inquiry to a richer space of emotion, one gains purchase in answering old questions in the field, as suggested in our syntheses of findings related to emotion-related neural response and mammalian behavior (see Outstanding Questions). Such findings support the organization of emotion-related physiological responses within a high-dimensional semantic space.

Supplemental Information

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