The cultural evolution of emotion

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Abstract | Scholarly debates about the nature of human emotion traditionally pit biological and cultural influences against one another. Although many existing theories acknowledge the role of culture, they mostly treat emotion categories such as 'anger' as biological products. In this Perspective, we summarize traditional assumptions about the roles of biology and culture in emotion alongside supporting and conflicting empirical evidence. Building on constructionist models of emotion, we introduce a cultural evolutionary perspective that moves beyond a strict biology-versus-culture dichotomy. This cultural evolutionary perspective uses dual inheritance models of cultural transmission to explain how variation in emotion can arise across groups, how affect-laden information can travel throughout populations, and why people in different cultures use both similar and different emotion concepts and non-verbal expressions. This cultural evolution framework allows for new hypotheses about the development of emotion categories and challenges longstanding claims about the universality of emotion.

People around the world appear to cry when sad, startle when afraid, and smile when joyous. Yet even a casual viewer of a foreign film or international news footage can recognize that there is also rich cultural variation in human emotions. Emotions therefore seem to be both universal and culturally variable[1–3], which makes it difficult to know whether the origins of emotional experiences, expressions and perceptions are a product of humans' shared biology, culturally dependent learning, or both. Whether emotions are universal or culturally relative has wide-ranging implications for science and society. An understanding of the roles of biology and culture in emotion could inform whether emotions are expected to have the same impact on physical health across cultural groups, whether mental health interventions are valid in different world regions, or whether artificial intelligence algorithms can predict emotional behaviour in people around the globe. Understanding the relative roles of biology and culture in emotion could also contribute to cross-cultural adaptations of speech, literature, film and art, and could facilitate efforts at cross-cultural diplomacy and commerce in a rapidly globalizing society.

Scholarly debates about the nature of emotion traditionally pit biological and cultural influences against one another[4]. One side of the debate emphasizes the role of genetics, neurophysiological anatomy, and mammalian biological evolution as causal mechanisms of universal human emotions[5,6]. Humans share 99.9% of their genome with one another, suggesting shared neurophysiological 'hardware' for producing emotions. Aspects of this neurophysiology are shared with non-human animals, suggesting a role of reproductive selection pressures on so-called 'emotional' mammalian behaviours such as freezing, fleeing, attack and maternal care (BOX 1). These biological factors have led some scholars to search for similarities in emotion across human cultural groups, which could be the product of shared biological adaptations. For instance, one study used machine learning to classify facial expressions that recurred in 6 million YouTube videos across 144 countries during emotional events (such as weddings, sports competitions and protests). The authors found global variation in the base rate of emotional situations and the facial muscle movements that occurred in these situations, but also found that an a priori set of 16 patterns of facial muscle movements appeared around the globe. When a given pattern occurred, it did so in similar situations (such as at a wedding) up to 70% of the time across the various cultural contexts[7]. These findings led the researchers to conclude that discrete emotions are products of biological natural selection[7].

The other side of the debate emphasizes the roles of local ecology and cultural learning in producing culturally relative emotions[8–10]. Groups of humans live in different ecologies, subscribe to different norms and values, and have experienced different levels of intergroup exposure across history[11–13]. These cultural facts have led some scholars to assume that diverse cultural backgrounds produce variation in how humans around the world experience, express and perceive emotions. For instance, there is observed cross-cultural variation in self-reported emotional experiences[14,15], in the neural correlates of emotion experiences and perceptions[16–18], in the production of facial muscle movements[7,19], and in the perception of emotion in others' faces[20–24] and voices[25] (see REF.[9]).

Analysing vocabularies across cultural groups can also demonstrate variation in emotion because people use language to categorize their experiences and perceptions. Linguistic ethnographies suggest that only 22% of languages have a word roughly equivalent to the English-language word 'fear', and only 13% have a word roughly equivalent to 'surprise'[26], indicating that these categories might not be universal. These percentages are probably underestimates because dictionaries of small-scale languages are incomplete. However, even emotion category words that do have translational equivalents show variability in meaning. For example, a study that quantified semantic similarity amongst 24 emotion categories such as 'fear', 'love' and 'anger' found that specific meanings of emotion categories varied substantially across the 2,474 languages studied[26]. However, category meanings were universally organized according to pleasure–displeasure and physiological arousal–quiescence. These findings suggest that beyond basic similarities, emotion categories might have different conceptualizations across cultural groups.

In this Perspective, we aim to reconcile the role of biologically evolved

Box 1 | **How survival pressures selected for mammalian affective behaviours**

It is well accepted that brains evolved through natural selection. What remains debated is which neural processes were selected for[184]. Most research on the biological evolution of emotion categories looks to non-human mammals[36,185–188] for answers to these questions. Yet the roots of adaptive mammalian behaviours such as feeding, freezing, flight and attack[36] are probably tied to very early developments in evolutionary history[189].

The earliest unicellular organisms (bacteria) evolved over 3.5 billion years ago and faced selection pressures not unlike those faced by contemporary animals: they needed to maintain efficient energy metabolism and the balance of fluids and electrolytes, to thermoregulate and to reproduce[189]. Even early bacteria developed mechanisms to regulate these needs adaptively (allostasis)[51]. The emergence of adaptive behaviours such as locomotion probably exerted additional selection pressures on the mechanisms of allostasis because locomotion is metabolically costly, but also affords opportunities that increase survival such as foraging, threat avoidance and social behaviour[51,189]. Thus, the neural roots of adaptive behaviours emerged long before the first mammal[189], and some scholars have argued that early nervous systems — and eventually brains — evolved expressly for the purpose of more effectively enacting allostasis and survival[51,75,189].

Allostasis predictively regulates an organism's survival needs before they occur because prediction is more metabolically efficient than reaction. To make situation-dependent predictions, allostasis relies on representations of both the internal and external milieu of an organism, as well as learning from prior experiences[51,75,190]. Allostatic predictions originate in the limbic cortex as visceromotor predictions that regulate the state of the body via subcortical and brainstem regions that activate the autonomic nervous system, neuroendocrine system, immune system and motor outputs[51,75,190]. Efferent copies of visceromotor predictions feed forward to the primary sensory cortices, primary motor cortex and primary interoceptive cortex, where they prepare the body for movement, prepare the primary sensory systems for perceptions from the external world, and prepare the primary interoceptive system for perceptions from the internal milieu[75]. Meanwhile, afferent prediction error signals from the primary sensory, motor and interoceptive cortex are processed to update ongoing sensations. It is thought that efferent and afferent projections to the primary interoceptive cortex initiate affective sensations such as pleasure, displeasure and arousal[75]. These sensations might ultimately serve an allostatic function by signalling a need to regulate the viscera (displeasure or arousal) versus the achievement of survival needs (pleasure or relaxation)[51,75].

In this framework, adaptive behaviours and affective sensations are a product of allostasis and not of dedicated emotion circuits. Although humans share circuitry for adaptive behaviours with non-human mammals[45], it is not clear that the neural circuitry for an adaptive behaviour represents the conserved neural circuit for a complex mental category such as 'fear' in either humans or non-human animals[46,47,189]. Rather, adaptive behaviours are themselves flexible, situation-dependent actions supported by broadly distributed neural circuitry, not fixed action reflexes triggered by a dedicated circuit[50]. Consequently, some scholars have moved away from the inference that adaptive behaviours are caused by an otherwise unobservable discrete emotional state and instead refer to them as 'survival circuits'[189].

Although the principles of brain evolution remain debated[184,191], these lines of evidence converge to suggest that mammalian brain evolution might not have specifically selected for a set of hardwired emotion categories[50,189,192]. Instead, brain evolution might have selected for efficient allostasis, with the implication that vertebrates, especially mammals, developed neurocircuitry supporting the representation and predictive regulation of the internal milieu (interoception), representation of value (valence and arousal), flexible species-typical adaptive behaviours (feeding, freezing, fleeing, attack, copulation and maternal care[36]) and social learning[193].

Early hominids might have additionally benefited from the evolution of a relatively large brain and therefore a relatively large isocortex, which afforded increasingly abstract allostatic predictions[194] and the ability to learn using memory and language[75,113,189]. These brain features, in combination with a social mode of rearing offspring (including bi-parenting, alloparenting and group care)[194] might have set the stage for the cultural evolution of emotion categories, which built on basic allostatic predictions to meet the unique needs of humans living in large social groups. It follows that to the extent that other non-human animals can pair allostatic states with conceptual representations and transmit them via social learning, they could be said to possess species-specific emotion categories. However, the quality and extent of such categories are probably gated by a species' ability to use symbolic representation, engage in mental inference and the scope of its social learning (see REF.[195]).

neurophysiology with evidence for wide cultural variation within a psychological model that explains both cross-cultural similarity and differences in emotion (see also REFS.[27,28]). First, we discuss prevailing assumptions about the roles of biology and culture in emotion in mainstream psychology. We next review constructionist theories of emotion. These theories posit that emotions emerge from the confluence of biology and culture, but they have rarely outlined the social mechanisms that can transmit emotion categories within and between cultural groups. We use these mechanistic insights to advocate for a cultural evolutionary perspective on emotion that explains how the transmission of genetic and cultural information combine and interact to influence human emotion. This dual inheritance model suggests that emotions are underpinned by neural mechanisms linked to physiological and action regulation, but that discrete emotion categories such as 'anger', 'fear', 'sadness' and 'joy' are cultural artefacts that evolved through social transmission within and between human groups.

Assumptions about biology and culture

Three interrelated assumptions about how biology and culture influence emotion have shaped theory, hypothesis testing and interpretations of empirical data in mainstream psychology, although not without significant criticism.

Universal emotion categories. The first assumption is that there is a set of universal emotion categories that are recognized and communicated by people in every human group[1–4]; these categories are assumed to be functionally, phenomenologically and behaviourally distinct. In this view, an emotion category entails a discrete and modular emotion mechanism that encompasses emotional experiences (feelings) and behavioural expressions (manifestations of the emotion in the face, voice and body)[29,30]. A perceiver's subjective experience of seeing an emotion category displayed in a person's face, voice or body posture is therefore considered a valid index of that person's internal emotional experience. By contrast, a person's symbolic communication about their internal emotional state via language is thought to be an imperfect and biased representation of the underlying state. Yet the emotion categories scholars use to denote scientific constructs typically come from vernacular language (such as the English-language categories 'fear', 'anger' and 'joy').

The assumption of universal emotion categories is reflected in basic emotion theory, sometimes called discrete emotion theory. Basic emotion theorists argue that certain English-language emotion categories are equally meaningful and recognizable in posed facial expressions

across both large Western nations and small-scale societies with little Western contact[6,31–33]. Studies spanning linguistics, sociology, psychology, neuroscience, computer science and medicine continue to assume or seek evidence for a small set of presumably universal emotion categories[1]. However, studies claiming evidence for universal emotion perception have been heavily critiqued because of their demand characteristics and analytic approaches[1,20,34,35].

Distinct biological systems. The second assumption is that each universal discrete emotion evolved as a distinct biological system through individual-level natural selection[29,36]. The biological systems proposed include emotion-specific sets of cranial nerves innervating facial musculature[37], sets of peripheral nerves[38], or brain regions or circuits of connected brain regions[36,39–42]. Studies of non-human animals provided initial evidence for the neural basis of biologically evolved emotions. These studies found relationships between adaptive behaviours that are presumed to be associated with human emotional experiences, such as freezing, fleeing, attacking and maternal care, and the activation of subcortical brain structures. For instance, freezing and fleeing are presumed to be associated with fear and both are associated with activation of the amygdala[43,44] and its connected circuitry (such as the hypothalamus and periaqueductal grey) in non-human animals[36]. Because many of these regions also show increased activation during functional neuroimaging of fearful experiences in humans[45], it is assumed that human fear evolved from the mammalian circuitry for threat-related survival behaviours[29,36].

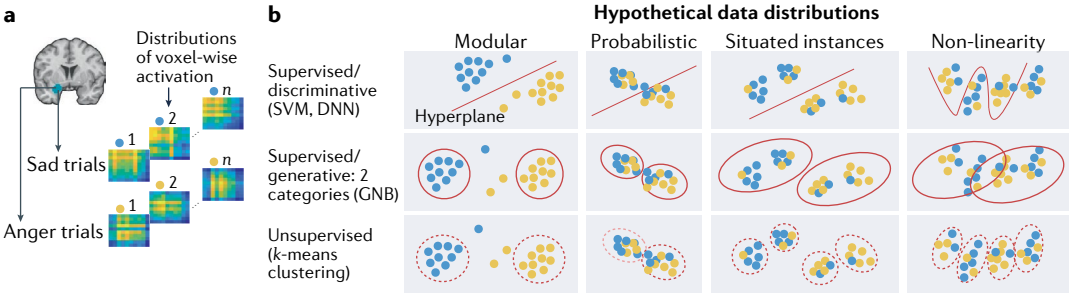
However, critics argue that human emotions involve more than just the circuitry for adaptive behaviours[46,47] (for a discussion, see REF.[3]). First, not all instances of human fear consistently or specifically involve the amygdala, calling into question the notion that the circuitry for freezing and fleeing is necessary for human fear[48,49]. Second, although survival pressures surely shaped the biological evolution of the mammalian brain, these pressures were more likely to select for basic survival processes that are not synonymous with English-language emotion categories[47,50,51]. Thus, basic survival-related behaviours might contribute to, but are not isomorphic with, the complex emotion categories experienced by humans (BOX 1).

Researchers are now applying machine learning methods to classify discrete emotion states from behavioural and biological measures including self-report[52,53], facial behaviours[54], vocal acoustics[55], peripheral autonomic activity[52,56] and brain activity[57–59]. The underlying assumption is that above-chance classification of observed data into discrete emotion categories reveals that emotion categories are biologically ingrained. However, critics argue that machine learning techniques cannot reveal the causal mechanisms for any category, and do not reveal patterns consistently and specifically correlated with emotion categories[60,61] (see BOX 2 for a discussion of machine learning in neuroimaging).

Culture influences non-essential processes. The third assumption is that culture influences processes that are not essential to the emotion itself[29]. In this view, cultural processes such as ecology (the physical context inhabited and intergroup contact), norms, values or emotion words might interact with emotions by determining what kinds of stimuli elicit instances of an emotion category, how often someone feels those instances, how intensely they

Box 2 | Criticisms of machine learning approaches to biological mechanisms

Three types of issue arise when using machine learning to reveal the causal biological basis of discrete emotion categories. We focus here on multivoxel pattern analysis of human neuroimaging data, but these points also apply to machine learning in other data modalities (see REFS.[56,60]).



Statistical inference

Machine learning algorithms do not reveal causal mechanisms for a category — they reveal whether patterns of data are correlated with a set of instances of that category. Yet even when certain patterns of neuroimaging data are correlated with instances of an emotion category, the machine learning algorithm used and distribution of the data yield different inferences. To illustrate, the figure shows activation patterns in the amygdala during instances of sadness and anger in a hypothetical experiment (panel **a**), which may produce different underlying data distributions (panel **b**, columns), corresponding with distinct theoretical assumptions. Discriminative algorithms, such as support vector machines (SVM[58,196]) or certain deep neural nets (DNN)[7,14] indicate whether a function (sometimes called a hyperplane) can differentiate between researcher-defined categories at levels better than chance, but do not explicitly reveal the features that led to classification. Supervised generative algorithms (panel **b**, middle row) such as Gaussian naive Bayes (GNB[197]) are similar, but allow for greater interpretation of the features contributing to classification. Finally, unsupervised algorithms[52] (panel **b**, bottom row) inductively discover the number of categories that best explain the data and the features of these categories. If the data distribution associated with instances of a category is modular (panel **b**, column 1), then the algorithm used is inconsequential. But if the distribution is significantly more heterogeneous (panel **b**, columns 2, 3 and 4), different algorithms lead to different conclusions.

Empirical findings

The literature suggests that neural patterns associated with emotions are indeed heterogeneous and not modular. Within a study, supervised approaches can classify neural patterns for a particular emotion category[57–59], but the specific neural patterns do not replicate across studies[52]. Moreover, unsupervised approaches fail to recover so-called universal discrete emotion categories, suggesting that columns 3 or 4 in panel **b** of the figure might best characterize emotion data[52,198].

Theoretical inference

Multivoxel pattern analysis studies also successfully classify neural representations of cultural artefacts that did not evolve biologically, such as vehicles, boats, containers[199,200], and de novo categories[201,202]. Thus, an activation pattern does not necessarily reveal the evolved neuro-physiological mechanisms of an emotion category.

express them, whether they express them privately or publicly, or how they describe their experiences. But these processes do not fundamentally alter the emotion experience itself (see REF.[62]). For instance, it has long been argued that culture primarily influences emotion via 'display tendencies', or a set of norms about how intensely emotions should be described in language[8] and expressed on one's face[19,63,64]. A preprint that has not yet been peer-reviewed[14] draws this conclusion based on a study of Japanese speakers from Japan and English speakers from Europe, Canada and the USA who watched emotionally evocative videos while their facial muscle movements were recorded. The degree of cross-cultural concordance in emotion was assessed by the extent to which Japanese participants' self-reported emotional experiences could be predicted from the recordings of English speakers' facial muscle configurations, and vice versa. Initially, only 0.0001% of the variance in Japanese speakers' self-reports was predicted by English speakers' facial muscle configurations, and 29% of the variance in English speakers' self-reports was predicted by Japanese facial muscle configurations. However, the cross-cultural concordance increased to 45% and 37%, respectively, when statistically controlling for differences in the range and intensity of emotional behaviours within each culture. Considered alone, these findings suggest that people across the globe have fundamentally similar emotion reactions that are partially obscured by culture-specific norms about expression.

However, cultural variation in emotion extends beyond display tendencies to affect the expression, perception and perhaps even the experience of the events described by an emotion category[9]. For instance, the study described above still reveals considerable cross-cultural variation in emotion: even after controlling for differences in intensity between cultural groups, English speakers' facial muscle movements predicted less than half of the variance in Japanese speakers' self-reported emotional experience and vice versa[14]. Furthermore, people ascribe widely different meanings to emotion expressions across cultural groups. Studies of small-scale societies find little evidence that the Himba of Namibia or the Hadza of Tanzania perceive facial[20–23] or vocal[25] behaviours as instances of the English-language categories 'anger', 'disgust', 'fear', 'happiness', 'sadness' and 'surprise.' In fact, individuals from these societies rarely spontaneously use emotion categories to describe the feelings associated with others' facial muscle movements. They instead frequently engage in action identification by making behavioural predictions about other's actions[20,21,23]. Even when members of small-scale societies do perceive emotional meaning in facial muscle movements, they do not necessarily associate them with the categories prescribed by English speakers. For example, in many Western societies, a gasping, wide-eyed facial expression is associated with 'fear', but Trobriand Islanders associate it with 'anger'[23]. When distinct cultural groups do label the same non-verbal cues with putative translational equivalents, the interpretation is not straightforward. Linguistic data suggest that the meanings of English-language emotion categories translate poorly across language families[26]. For instance, the word 'kontan' in Seychelles Creole and the word 'hanisi' in Rotuman are translated to the English word 'love', but 'kontan' also connotes happiness and joy whereas 'hanisi' connotes pity[65]. Although it is possible that linguistic differences do not connote experiential differences, studies showing cross-cultural differences in the neurophysiology of emotional perceptions[66] and experiences[16–18] underscore the fact that culture can influence a range of phenomena including emotion expression, perception, emotional meaning, and the neurophysiological processes underlying emotional experiences.

Constructionist theories of emotion

Over the past century, multiple theories have sought to reconcile the assumptions described above with the conflicting empirical data[67]. The result is a spectrum of emotion theories that differ in their guiding hypotheses[1,67]. At one end are basic emotion theories. Some of these theories explain disconfirming data by citing methodological limitations, such as the lack of spatial resolution in brain-imaging methods[68], the use of univariate (versus multivariate) analyses for revealing emotional 'signatures'[41,69] and the poor ecological validity of laboratory-based studies[7]. Others have redefined hypotheses to suggest that emotions are abstract latent causal mechanisms (such as mechanisms that detect threat[3]), which might not map onto dedicated brain circuitry (for a discussion see REF.[1]). Still others suggest that discreteness will be revealed as 'subtypes' of basic emotions that have yet to be incorporated into theories of emotion[70,71].

At the other end of the spectrum are constructionist approaches that account for disconfirming data by providing an entirely different understanding of the relationships between biology, culture and emotion. These hypotheses are less intuitive than basic emotion predictions, in part because they contrast with core Western philosophical assumptions such as the entitativity of categories (for emotion categories see REFS.[72,73]), either-or logic and linear models of change (see REF.[74] for a discussion of how Western philosophy shapes scientific hypotheses).

Emotion categories are non-entitative. The first assumption of constructionism is that emotions are non-entitative: there is not a consistent 1:1 mapping between specific emotion categories and dedicated, biological mechanisms. Instead, emotions are constructed phenomena that emerge from more basic biological mechanisms that are not specific to any single emotion category. One such mechanism is allostasis (the neurobiological processes that predictively regulate an organism's survival needs, including needs for adaptive action[51]; see BOX 1).

Another mechanism is abstract representation and categorization[75]. The act of placing items into categories leads to non-continuous perception of continuous features (categorical perception), such that within-category differences are perceived as smaller and between-category differences are perceived as larger than objective differences[76]. Categorical perception can be the product of strong perceptual statistical regularities in the stimuli being perceived (for example, most 'dogs' possess perceptual features that 'birds' do not), but it can also arise from learning[76]. Indeed, abstract forms of categorization can imbue objects with functional meaning (for example, a rock and a hammer can both be used to crack open fruit) and impose categorical perception where it is not grounded by strong perceptual statistical regularities[77]. Humans and some non-human animals are able to engage in abstract categorization, meaning that they can see perceptually heterogeneous instances as having a similar function.

Humans also routinely use symbolic language to support the acquisition of, representation of and access to categories[78]. Some constructionist approaches therefore posit a role for language in emotion[62,79,80], whereby access to linguistically supported categories causes categorically distinct experiences to emerge from the multivariate feature space that consists of situated feelings, visceromotor actions, and their associated autonomic responses and facial behaviours (FIG. 1a–c). Consistent with

this hypothesis, emotion word acquisition tracks categorical perception of emotion in facial expressions during early childhood[81] and novel category labels aid acquisition of new facial portrayals of emotion in adulthood[82,83]. In adults, priming linguistic emotion categories also facilitates and biases visual perception of facial portrayals of emotion[84,85], and impaired access to linguistic emotion categories interferes with such perceptions[86–88]. These findings are not unique to visual perception: priming emotion words also influences the subjective experience[89–91] and overt behaviour[90,91] associated with unpleasant affective states.

Rather than being entitative, emotion categories are thought to name populations of instances (FIG. 1c). There is variation in these instances (FIG. 1a), such that no single pattern of physiology[56], behaviour[92], brain states[48,93] or feelings[94] is necessary or sufficient to define all instances of the population, or even a single prototypical instance (FIG. 1a,b). For instance, there is no single situation or relational theme that necessarily or sufficiently defines the meaning of 'anger', even within a single cultural group[95]. Thus, emotion categories are inherently heterogeneous, and adults rely on multi-modal and abstract features to categorize these instances[96,97].

Developmental research is instructive about how adults might accomplish this feat. Starting in infancy, humans rely on broad dimensions such as valence (pleasantness–unpleasantness[98,99]) to categorize emotional instances. However, simply hearing the same word paired with two emotional instances causes infants to subsequently treat those instances as similar[100–103], suggesting that language and socialization help to scaffold categorical perception of emotion. By preschool, children use multimodal information such as the situated features of an emotional instance (for example, interpersonal conflict[104]) and behaviours associated with an emotional instance (for example, aggression[104]) to guide emotion categorization. Around this age, children also start using simple abstract themes (such as having one's goals blocked[105]) to guide categorizations of emotional instances, and their emotion category knowledge continues to become more multi-modal[97] and abstract[96] until early adulthood[100,101,104,106]. Abstract category features help children to perceive diverse affective situations as having similar meanings. In fact, abstract information such as valence, category labels, situations, behaviours and themes all guide preschoolers' categorization of what someone else is feeling better than putative universal facial expressions[104].

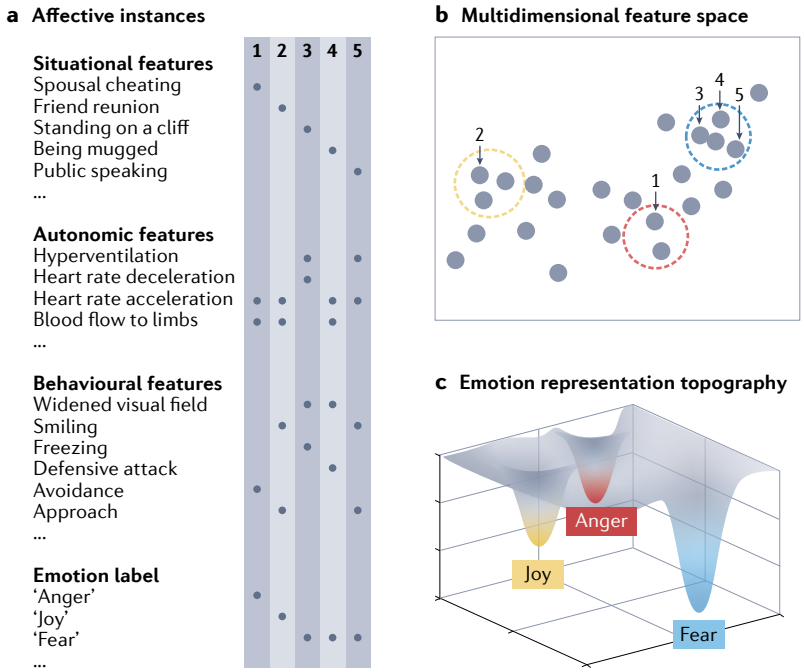


Fig. 1 | **A constructionist framework of emotion representation. a** | Emotion categories name populations of situated instances with features that vary between categories (anger, joy and fear) and within categories (different instances of fear). For example, an instance of anger at spousal cheating (column 1) shares some features with joy at a reunion with a friend (column 2) and fear while being mugged (column 3). Instances of fear evoked by different situations also differ in their features (columns 3, 4 and 5). **b** | Emotions emerge from multidimensional feature space, and the similarity between emotional instances can be represented as the distance between grey circles in that feature space. **c** | Emotion feature space is warped by experience and concept use. Experience of many similar instances and socially learned categories creates a mnemonic category, which are visualized as shaded attractor-basins. Attractor-basins guide how people interpret future situated instances and warps people's perceptions of similarity between these instances.

If emotion categories name heterogenous populations of instances united by abstract features, it follows that those instances might be categorized into quantitatively or qualitatively different categories across[20,21,24,26,66], or even within[102,107,108], cultural groups. The constructionist approach predicts that when a person understands a culturally familiar emotion concept, they will experience, express and perceive instances of that category with greater intensity and frequency[80] than if they lacked that emotion category. Lack of a culturally familiar emotion concept should in turn prevent people from showing categorical experiences, expressions and perceptions of that emotion[9,83,108]. These hypotheses explain why ethnographic fieldwork has documented many emotion categories that are unique to particular cultural or linguistic groups[9,109,110]. They also explain why participants from different cultural groups associate translational equivalents of English-language emotion categories with different situational, experiential and behavioural features[9,15].

Emotion categories cannot be reduced to biologically evolved modules. A second assumption of constructionism is that emotion categories cannot be exclusively reduced to neurobiological products of genetic evolution. Genetic evolution provided humans with many important ingredients for the construction of emotion categories, including allostasis, abstract categorization and social learning (the capacity to communicate and acquire information via social interaction[111]). These biologically evolved capacities (BOX 1) might combine to create emotions, but emotions are not reducible to any single one[48,75,112,113].

There might be some core similarities in emotions across cultural groups based on a shared set of biologically evolved capacities. The fact that emotions are based in allostasis suggests that brain regions involved in visceromotor regulation and representation of prior experiences should be consistently involved in emotions, and indeed this is the case[48,62,76,113]. Brain regions involved in generating and representing visceromotor actions such as the amygdala, anterior cingulate cortex, insula, basal ganglia and

brainstem are consistently activated during human emotions[49], even if their patterning differs across instances of the same emotion category within and between cultural groups[16–18]. Because affective sensations (pleasantness–unpleasantness and arousal–quiescence) are a product of allostasis (BOX 1), emotions should be described by these qualities across cultural groups, even if qualities associated with specific emotion categories differ. Indeed, valence and arousal predict the semantic groupings of emotion categories in all language families[26].

In addition, the predominance of categorical thinking in healthy humans might lead people around the world to experience and perceive affective states as categorical, even if the features that comprise affective categories (as in FIG. 1a) differ across cultural groups. Indeed, across studies and modalities, categorical solutions best capture people's understandings and experiences of emotions[14,20,26], even when the categories or their features differ substantially across cultural groups[22,27]. For instance, studies of facial perception reveal that emotion categorization is common across cultural groups, but that the emotion categories themselves are culturally variable[24,114]. One study assessed which dynamically moving facial actions participants from the UK and China associated with the English-language emotion categories 'anger', 'disgust', 'fear', 'joy', 'sadness' and 'surprise' and their Mandarin translational equivalents. UK and Chinese participants perceived four common categories of facial actions that were primarily differentiated by their valence, arousal and dominance. The first involved smiling and was associated with positive valence, high arousal and dominance; the second involved lowered brows, closed eyes, pressed lips, and was associated with negative valence, both high and low arousal, and submission; the third involved raised lids, an open jaw, and was associated with both positive and negative valence, high arousal, and both high and low dominance; the fourth involved a wrinkled nose, tightened eyes, and was associated with negative valence, high arousal, and high dominance[24]. However, there were also culturally distinct categories of emotion expression. For instance, UK and Chinese participants both perceived culture-specific facial action patterns associated with English-language categories 'joy', 'disgust', 'fear' and 'surprise' and their Mandarin translational equivalents. Culture-specific facial action patterns were also associated with categories that did not have translational equivalents in the other cultural group (such as 'depressed' in English and 'storm of anger' and 'feel well' in Mandarin)[24]. These findings suggest that people from different cultural groups construct different emotion categories around facial muscle movements.

Emotion categories are acquired socially. A third assumption of constructionism is that emotion categories are acquired socially (FIG. 2). Human infants have limited ability to engage in allostasis and require others to help regulate their survival for much of early life[115]. Through these early interactions, human caregivers regulate infants' distress and pleasure and transmit information about the emotion categories relevant to their culture through facial mimicry, joint attention and language[115–117]. As infants progress to toddlerhood, they begin to learn through experiences with the world and shared language how to differentiate their own internal sensations and others' behaviours into culturally relevant emotion categories[9,28,118]. Through this developmental process, children begin to understand and regulate their own internal states, communicate them to others, and learn which emotion categories are culturally normative and valued[9,98,117]. Even in adulthood, acculturation to a new society involves learning the host culture's emotion categories; the wellbeing of transplants to new societies is predicted by the extent to which they understand their new culture's emotion categories[119].

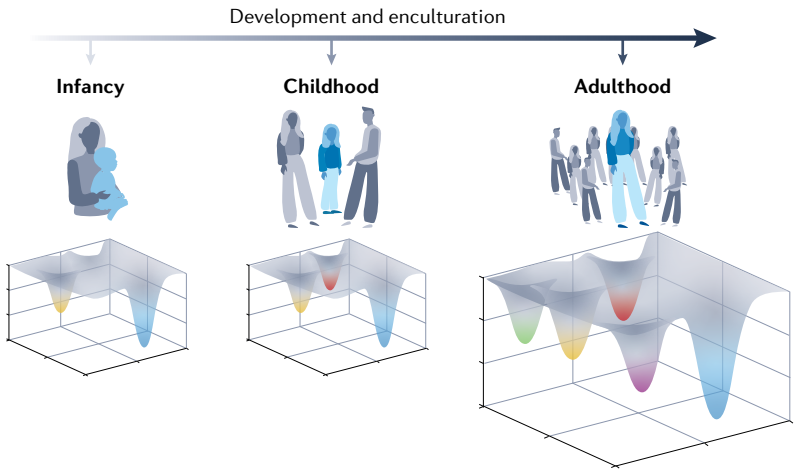


Fig. 2 | **The impact of social learning on emotion across development.** Across development, social learning opportunities influence people's exposure to situated instances and the social categories that people use to make meaning of and communicate these instances. The figure depicts representations of valence in infancy (where the source of social learning is the primary caregivers), the development of emotion concepts in early childhood (when sources of social learning might expand to multiple caregivers, teachers and peers), and an adult emotion concept topography which varies by individual (where sources of social learning are the many other adults in one's own and other cultural groups).

The cultural evolution of emotion

The assumptions of constructionism suggest that emotion categories can be modelled as cultural artefacts that are transmitted via social learning within and between cultural groups[75,120–122]. Cultural artefacts are units of cultural information including languages, beliefs, behaviours, technology, art and social systems that are constrained by human psychological and physiological capacities, and vary based on the needs, resources and ancestral histories of a specific group[123–125]. This notion is also consistent with the cultural evolutionary concept of 'cognitive gadgets'[126], or psychological phenomena that build on basic human abilities, but evolve under local cultural and ecological pressures. For instance, tool use requires basic human cognitive abilities such as causal and abstract reasoning, but humans from different societies have created widely different tools, even when these tools are designed to serve similar functions[127]. Relatedly, cooperation relies on basic mammalian behaviours that increase reproductive fitness, such as kin selection and reciprocal altruism, but there is wide variation in the norms and institutions that regulate cooperation across human groups[128].

As cultural artefacts, emotions should be targets of cultural evolution. Cultural evolution is a theoretical framework premised on the idea that human variation is the product of both genetic inheritance and social learning[123–125,129]. In many models,

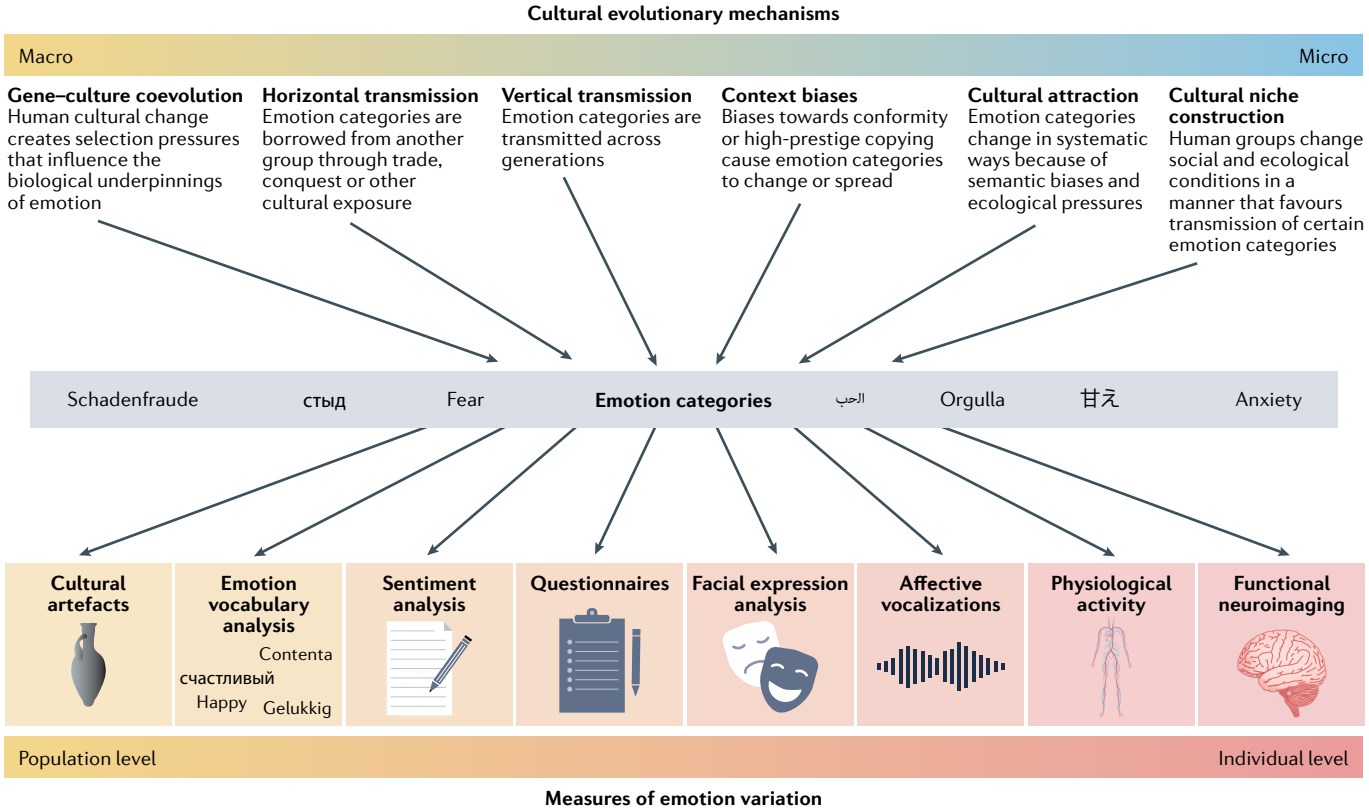


Fig. 3 | **Cultural evolutionary mechanisms of emotion.** Top: Cultural evolutionary mechanisms underlying emotion variation. Mechanisms listed towards the left are more likely to produce variation at the population level, and mechanisms listed towards the right are more likely to produce variation at the individual level. Bottom: Measures of emotion variation along a continuum from measures that exclusively capture population-level variation in emotion to those that exclusively capture individual-level variation.

the transmission and proliferation of cultural artefacts is guided by the Darwinian principles of competition, inheritance and variation[123]. Models of cultural evolution have been applied to understand cultural variation in psychological phenomena such as prosociality[128], theory of mind[125], personality[130] and religious belief[131], but few scholars have specifically articulated the role of cultural evolutionary mechanisms in emotion (but see REFS.[27,28,117,132]). Although constructionist[9,76] and related[133] approaches have hypothesized a role for cultural learning in emotion, they have not formally incorporated mechanisms of cultural evolution into their theories.

We suggest that cultural evolution is a useful framework for understanding variation and structure in emotion across cultural groups and timescales (FIG. 3). We introduce three claims about culture and emotion categories derived from theories of cultural evolution. These claims suggest hypotheses about how cultural groups develop emotion categories, how groups come to possess similar (versus distinct) categories, and how these categories change and diversify over time. These claims also challenge longstanding assumptions about universality in emotion across cultural groups and human history. The cultural attraction and dual inheritance models we draw from are sometimes viewed as in opposition to each other[134], but we believe they offer useful and compatible hypotheses about the cultural evolution of emotion.

Emotions are cultural artefacts that are sensitive to forces of attraction. Our first claim is that emotion categories are culturally transmitted artefacts, not unlike human languages, beliefs, behaviours, technologies, art forms and social systems. As outlined above, the notion that emotion categories are cultural artefacts is consistent with constructionist theories: emotion categories are grounded in the neurobiology of allostasis but socially devised around culture-bound situations, meanings and goals[26,75,117,120].

Models of cultural attraction raise plausible hypotheses about how the earliest humans first formed emotion categories. Cultural attraction describes the probable favouring of specific cultural information owing to psychological or ecological factors that bias adoption and transmission of such information[135,136]. Theories of cultural attraction have been applied to the spread of religious beliefs or common features in narratives[137,138], but emotion categories might also be targets of cultural attraction.

Certain emotion categories could form over time via cultural attraction in human groups if particular allostatic predictions frequently occurred in certain salient situations. Cultural attraction could therefore explain both similarities and differences in the type, number and meaning of emotion categories across cultural groups. For instance, many cultural groups use more differentiated and numerous negative emotion categories than positive emotion categories[139], which might stem from a bias to categorize and communicate more frequently about instances of allostatic dysregulation as opposed to instances when needs are met. The more differentiated categorization of unpleasant states might even help humans to regulate those states via intrapersonal or interpersonal processes, which might in turn select for and accelerate the rate of cultural evolution of negative emotion categories over and above positive

emotion categories. An inherent bias towards social information[140] might also lead cultural groups to form categories around the allostatic predictions that occur most frequently in common social situations. Cultural attraction might therefore explain why some core relational themes[141] such as loss or norm violation are widespread across cultural groups without assuming that they are linked to the biological evolution of discrete emotion categories (as in basic emotion accounts[29]). These core relational themes might have been salient to multiple human cultural groups as a product of common social or environmental contexts, resulting in translationally equivalent emotion categories across groups[26]. Consistent with cultural attraction, groups with more similar cultural values[142] and environments[7,26,143] are more likely to share an understanding and expression of emotion categories.

Emotions are cultural artefacts that are socially learned. Models of cultural attraction might explain why there are emotion categories with similar themes across many human groups. However, the focus on psychological biases or environments common to human experiences in these models does not explain the cultural variation observed in emotion categories. For instance, the Japanese emotion category 'amae' has no equivalent in the USA, even though humans in Japan and the USA both experience allostasis and social living and have similar climates and ecologies. As another example, emotional experiences in response to the same events are described differently by Chinese Americans versus European Americans even though both groups live in the USA[54]. Even when cultural groups use emotion categories with similar core relational themes, those categories often have unique meanings and associations[26]. For instance, anger is linked to violations of norms in multiple human groups, but people show culture-specific ways of expressing and regulating anger. European American college students (who tend to identify with cultural norms of independence such as agency) frequently respond to anger by trying to change the situation. By contrast, more interdependent Asian American students (who tend to identify with cultural norms of group unity) are more likely to report engaging in behaviours that allow them to adjust to others' expectations during anger[143]. Dual inheritance models are better equipped than cultural attraction models to explain these cultural differences because they suggest that social learning can lead to persistent cultural variation, even when humans possess similar psychological biases or when cultural groups inhabit similar ecologies. Dual inheritance models can also explain cumulative cultural evolution (the ability of cultural innovations to build on themselves over time), which results in more widespread cultural variation in human than non-human animal groups.

As socially learned categories, language may be especially important to the acquisition of emotion categories within individuals and their transmission between individuals. Language may have allowed early humans to symbolically represent their allostatic experiences, communicate them to other members of their social group using a single familiar word, and coordinate and socially regulate one another's allostasis[144,145]. For contemporary humans, language supports the development and representation of emotion categories across the lifespan[79,118]. Computational modelling also supports the role of language in the development and transmission of category knowledge amongst members of a social group. For instance, artificial intelligence agents programmed to learn colour categories through interaction with the environment develop their own idiosyncratic categorizations of colour. However, when agents are programmed to additionally communicate with one another via shared language, the group develops a single set of shared perceptual categories[146]. No such analysis exists for emotion categories, but developmental evidence is consistent with the notion that social learning guides the development of emotion categories: children's understanding of emotion concepts and ability to discriminate among emotional facial expressions develops gradually from infancy to childhood, correlates with their understanding of emotion category words, and is longitudinally predicted by their caregiver's use of such words in child-directed speech[118,147,148] (but see REF.[149] for an alternative view).

If emotions are linguistically mediated and socially learned cultural artefacts, then one method of studying the cultural evolution of emotion categories is to examine language phylogenies across human history[150]. It is difficult (if not impossible) to trace human behaviours or physiological activation back in time. However, language phylogenetic trees that trace the ancestry of human languages[151] can be used to determine the origin of words for certain concepts and to examine how those words and their cognates (words that share written and spoken form) have evolved over time (for example, proliferating or becoming infrequent). There are no studies of the lexical evolution of emotion words in such phylogenies, but basic comparisons of languages in the same families yield preliminary insights into the emergence and evolution of emotion categories. For example, basic etymologies suggest that the English word 'sad' evolved from the Old English 'sæd' (which probably meant sated or weary), which in turn evolved from the Proto-Germanic cognate *sathaz (which probably meant sated) and the Proto-Indo-European root *sa (to satisfy)[152]. Examining emotion words in language phylogenies cannot reliably trace historical differences in how humans perceived and experienced affective instances. However, they can suggest how affective instances might have been labelled and communicated by different cultural groups over history and which ones might have been important to those groups. Language phylogenies might also be useful for detecting historical divergences in the categorization and representation of different emotion categories.

Formal analyses of emotion category words across language phylogenies could be used to quantify and predict semantic changes in and the temporal emergence of certain emotion categories across human history. For instance, the Proto-Indo-European language is thought to have been spoken around 4500–2500 BCE and 'sad' appears to have taken on its more modern meaning ("expressing or marked by sorrow or melancholy") around the fourteenth century[152]. Future work could examine which cultural factors precede the emergence of the modern form of 'sad' or other emotion categories across different languages. Complementary work could examine shifts in the non-linguistic representation of emotion categories in cultural artefacts such as art or photographs over time. For instance, one study demonstrated contemporary differences in the intensity of emotional facial and bodily expressions as depicted in popular children's picture books in the USA and Taiwan[153]. Future research could examine whether such artistic depictions shifted across time within and between cultural groups.

Environments shape emotion transmission. Building from the claim that emotion categories are cultural artefacts that are transmitted via social learning, our next claim is that the social and ecological environment influence their transmission. As in biological evolution, cultural evolutionary models consider the surrounding social and ecological

environment to be a significant source of variability that predicts which cultural artefacts are transmitted[123]. Groups transmit cultural information across generations (FIG. 2) via vertical transmission. Yet cultural groups also constantly learn from each other via horizontal transmission[154,155].

An important prerequisite for the horizontal transmission of emotion is exposure to other cultural groups, which is itself dictated by the environment those groups live in. Horizontal transmission can occur due to migration, conquest or trade, all of which allow social groups to transmit cultural artefacts to one another. For instance, groups in close geographic proximity, who have more frequent opportunities for intergroup contact, are more likely to show similarities in emotion than groups that are geographically distant. Language families in close geographic proximity are more likely to share semantic meanings for emotion categories than more distant language families[26,156]. Geographic proximity between groups also predicts cross-cultural similarity in the emotion categories that people perceive in facial muscle movements[157] and the patterns of facial muscle movements that they spontaneously produce in response to emotionally evocative situations[7]. In some cases, horizontal transmission is evident when cultural groups overtly borrow concepts from others. For example, the German concept 'schadenfreude' (a novel compound word meaning "pleasure derived by someone from another person's misfortune") now appears in the English Oxford Dictionary[158]. These findings suggest that as human groups interact and adopt cultural practices from one another, they might also update their conceptualizations of emotion categories or even adopt new ones. This suggests that studies using internet media to study emotions[7] might overestimate the degree of cross-cultural equivalence in emotion because they sample from data uploaded by internet users, who are more likely than non-internet users to be exposed to the emotions of other cultural groups around the world. Cross-cultural equivalence in emotion across geographically distant groups might therefore grow over time as technology affords more horizontal transmission.

Human interactions with their environment can also influence cultural transmission via cultural niche construction, which describes how cultural groups create niches that favour the evolution of certain kinds of cultural information. For example, historical migration patterns might affect how groups express emotions facially because nonverbal signals helped heterogeneous ethnic groups to interact. Humans who live in places with greater historical migration rates tend to make more overt and easily interpretable facial expressions of emotion[159] (in particular expressions of affiliation, such as smiling or laughter) than do humans who live in places with lower historical migration rates[19,63]. Other studies suggest that historical migration patterns away from one's cultural group to unsettled areas might have affected groups' understanding of 'happiness', perhaps because living in unsettled lands requires cultural adaptations such as individualism and self-autonomy. People whose ancestors migrated to these regions in Japan and the USA are more likely than their counterparts to endorse ideals such as personal agency and tend to conceive of 'happiness' as an emotion associated with individual achievement and pride rather than collective wellbeing[160]. Adaptations to the environment such as a change in subsistence strategy also influence cultural adaptations and could in turn affect social transmission of emotion. In China, adoption of group-based rice farming versus individual-based wheat farming is associated with increases in cultural individualism[161]. Future work should examine how these and other changes to the cultural niche predict variation in the social transmission of emotion categories.

Finally, gene–culture coevolution represents a final underexplored means by which environmental factors could influence the cultural evolution of emotion. Gene–culture coevolution occurs when certain cultural practices amplify the transmission of certain genes and vice versa. For instance, gene–culture co-evolution explains why people whose ancestors hailed from dairy farming groups possess genes that help them to digest dairy, whereas other humans do not[162]. These effects extend to other biological phenomena such as the ability to metabolize alcohol and starch[162], historical changes in the average age of menopause[163], and the prevalence of asthma and pollen allergies[164]. With respect to emotion, some scholars have proposed that the short allele of the 5-HTTLPR serotonin transporter polymorphism co-evolved with cultural collectivism and affects group differences in the prevalence of mood disorders[165]. Other studies cite the role of the DRD4 dopamine receptor gene in explaining group-based differences in risk-taking and pleasure seeking[166,167]. This research is still in its infancy and needs to expand beyond the focus on single genetic polymorphisms to explain population differences in emotion categories[16]. Nevertheless, it is plausible that gene–culture coevolution has exerted a hidden influence on group differences in emotion.

Transmission biases change emotions. Our fourth claim is that emotion categories might change through the act of transmission. Just as genes mutate because of DNA copying errors during cell division, cultural artefacts might mutate and shift as they are passed on through vertical or horizontal transmission. For instance, evidence from natural language processing suggests that emotion categories such as 'sad', 'awe', 'joy', 'fear' and 'anger' changed substantially in meaning in English and French books from the 1890s to the 1990s[132]. Emotion transformation during transmission is consistent with theories of cultural attraction whereby some information is more likely to be socially transmitted and learned than others[135]; it is also consistent with dual inheritance theories of cultural evolution[123] whereby selection pressures influence which information is inherited. There is little research on how and why emotion categories mutate over time, but theories of cultural evolution point to at least two transmission biases that influence this process: content and context biases.

Content biases explain why the meaning of certain emotion categories might predispose those categories to remain stable or change over time. Like cultural attraction, some information might be more resistant to change because it is particularly salient to members of a cultural group. For instance, concepts deemed most prototypical of emotional feelings by English-speaking raters from the USA were less likely to change in meaning over the twentieth century than emotion concepts deemed less prototypical[132], perhaps because prototypical emotion concepts have clearer cultural functions that make them more resistant to change. By contrast, anger at immorality ('moral outrage')[168] might be an example of an emotion category that has expanded in meaning over time, in part owing to its culturally attractive social value (signalling of ingroup membership)[168] in modern heterogeneous cultures and in part owing to shifts in the meaning of other related concepts, such as moral harm[169].

The valence of emotion concepts might also serve as a content bias. A preprint that has yet to be peer-reviewed shows that negatively valenced words have changed meaning more than positively valenced words over the last 10,000 years[170]. Because words are rarely dropped from a lexicon

once created, this might be another pathway to the greater prevalence of negative than positive emotion categories in many human languages[139]. By extension, the greater prevalence of negative emotion categories in language might prompt people to categorize and experience negative states as more differentiated than positive states[171]. These findings raise the novel hypothesis that negative emotion concepts have more culturally variable meanings than positive emotion concepts.

In contrast to content biases, context biases explain the success of social transmission as a function of who expresses cultural information. One of the most powerful context biases in cultural evolution is prestige bias — the tendency to disproportionately learn social information from prestigious individuals. Prestige bias has been applied to explain the evolution of food taboos[172] and 'runaway' patterns of maladaptive cultural evolution such as cult behaviour[129]. Little research has explicitly addressed this hypothesis in emotion, but some findings are suggestive. For example, one person's emotional state can subtly shift the emotional state of others via facial mimicry, autonomic nervous system activation and brain activity (emotional contagion)[173]. Prestige bias in emotion might occur when a prominent individual's emotional expressions exert greater emotional contagion effects and greater subsequent expression of that emotion category. For example, one study found that Twitter followers are more likely to mimic the language and affective valence of prominent politicians' and celebrities' posts than that of other users[174]. A valuable extension of this work could test whether certain emotional facial expressions, vocalizations or conceptualizations are sensitive to prestige bias.

A second context bias is the conformity bias, which suggests that frequently encountered emotion categories or expressions might be learned at a greater rate than infrequently encountered emotion categories or expressions. Conformity-biased transmission has been supported by many studies. When users' Facebook newsfeeds were manipulated to contain more pleasant emotional content, their subsequent posts became more pleasant and vice versa for negative content[175]. Other studies suggest that the expression of positive emotions in song lyrics and literature has decreased over the past century, whereas the expression of negative emotions has remained stable or increased[176,177]. Studies of acculturation also capture conformity bias by showing that the immigrants' self-reported emotion experiences become more like native citizens' self-reports over time, and this effect is explained by degree of exposure to the host country[143,178]. Canadian and East Asian perceivers are able to accurately guess the extent to which East Asian immigrants have acculturated to Canada on the basis of their facial expressions of emotion[179]. Conformity-biased transmission might even influence the rate at which new emotions are adopted. New technology adoption follows an s-shaped curve, in which new technologies are first adopted slowly and then become rapidly integrated as people begin to view these technologies as normative[180]. Future work might examine whether the diffusion of novel emotion categories, or categories that are newly borrowed from one cultural group to another, follow a similar s-shaped curve.

Box 3 | **Tools for addressing cultural evolutionary hypotheses**

General resources

D-PLACE: Aggregates data on cultures' evolutionary histories, ecologies, sociocultural structures and geographic locations into one repository with rich metadata on sources of information, including previously established phylogenetic trees; ideal for merging metadata into project-specific datasets of cultural groups.

- Historical Migration Data: Information on current-day and historical size of the immigrant population by country of settlement.
- Gallup analytics: A compilation of multiple open access datasets including global data on ecological and cultural variables such as urbanization, hunger rates, safety and security, as well as some behavioural data such as altruism rates and risk perceptions (we note that some data offered by Gallup requires an access licence).

Linguistic resources

- World Loanword Database: Contains vocabularies of 1,000–2,000 entries for 41 languages, as well as the likelihood that these words were borrowed from other languages.
- CLICS: Contains data on concept colexification (when semantically related concepts are named with the same word) from over 2,000 languages, which is useful for analyses of semantic meaning (as in REF.[26]); basic Python scripts for computing colexification networks can be found on the Open Science Framework.
- Glottolog: A reference catalogue of the world's languages, providing expert classifications, geolocations and references for more than 7,000 spoken and signed languages.
- Concepticon: A reference catalogue of concepts that are typically used in cross-linguistic studies, offering definitions, links to datasets in which the concepts were used, and additional metadata on psychological categories (norms, ratings and relations).
- Common Crawl: A repository of open-source web data that is ideal for natural language processing.

Behavioural resources

- eHRAF World Cultures: A database of ethnographic material spanning hundreds of cultural groups. All ethnographies are tagged with subject metadata, which allows for targeted searches.
- Ethnographic Atlas: A set of quantitative variables describing cultural practices for 1,291 diverse societies with global coverage.
- Natural History of Song: Contains ethnographic descriptions of songs from 60 cultures; also contains features of songs from 86 societies that were gathered through field recordings.
- Gallup 2017 Global Emotions Report: A set database of adults' self-reported positive and negative daily experiences in 2016 across 142 countries.
- Context–facial behaviour correlations. Degree to which emotional contexts correlate with emotional facial behaviours by country[7].
- Historical long-migration heterogeneity and emotional behaviour. Datasets from REF.[63] containing country-level and USA state-level long-migration historical heterogeneity and measures of emotional expression and experience from the 2017 Gallup Global Emotions Report.

Conclusion

In this Perspective, we laid out a new approach that marries constructionist theory with models of cultural evolution to articulate hypotheses about how emotions emerge from the confluence of biology and culture. This approach, when paired with methodological shifts towards more global data and increasingly sophisticated computational tools (as in REFS.[7,14,26,132]), promises to yield insights into how emotion categories emerge in cultural groups, how they evolved throughout history and how they might change in the future.

A cultural evolutionary approach enables researchers to move beyond questions

about how many universal emotions there are to more nuanced questions. For example, do some emotion categories have more historically durable meanings than others? When do emotion categories show punctuated (versus gradual) change across human history? When does cultural contact lead to changes in emotion perceptions, expressions or experiences? Will increases in globalization predict greater transmission of emotion categories and thus greater universality in emotion across groups in the future? More generally, a cultural evolutionary approach can move the science of emotion beyond the tired nature-versus-nurture debate to explain how culture and biology continually interact to influence emotion and the human experience.

Cultural evolutionary research on emotion is in its infancy. We know of very little research on the subject apart from the findings we reviewed here. This might be due to relatively siloed research traditions: emotions have most frequently been the topic of study in psychology and neuroscience, whereas cultural evolution has more frequently been applied in population genetics, comparative linguistics and anthropology. We hope that future research will apply cultural evolutionary mechanisms to questions about emotion and formulate new cultural evolutionary hypotheses that build on our preliminary proposals.

New methods and measurement strategies also make this an exciting time to apply cultural evolutionary hypotheses to the study of emotion. Until even a few years ago, it was difficult to address questions about emotion on a global scale. Innovations in computation have made this possible: scholars can now analyse data including videos of human behaviours[7,14], self-reports from participants[181] or digitized global databases[182]. It is now possible to test cultural evolutionary questions about emotion using a diverse set of methods and measures, including cultural artefact analysis, emotion vocabulary analysis, sentiment analysis of written or spoken language, questionnaire self-reports, analysis of facial and bodily behaviours, analysis of affective vocal acoustics, physiological activity and brain activation (FIG. 3). These tools are increasingly available to all researchers regardless of location or discipline. Furthermore, open access databases have compiled features that describe different cultural groups[183]. BOX 3 outlines some open-access resources that can be used to address hypotheses about the cultural evolution of emotion.

The future is bright for a cultural evolutionary model of emotion. As this research progresses, we look forward to understanding more about what is common to human experiences, perceptions and expressions of emotions around the world, and what makes them different.

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