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Introduction

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How and why emotions are expressed

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Empirical research on emotion is flourishing. Much of this research has focused on emotional expressions—dynamic patterns of behaviours including facial movements, vocalizations, bodily movements, gaze patterns, gestures and autonomic responses like blushing. However, research to date has primarily focused on perceptions of others' emotional expressions rather than on the production of emotional expressions. This theme issue shifts the focus to the intra-personal level, centring processes in the expresser. Using Tinbergen's ethological framework, this theme issue examines four levels of analysis: mechanisms, development, phylogeny and function. The contributions demonstrate that the production of emotional expression involves distributed, multi-level mechanisms, including appraisal, central emotion circuits and interoceptive signalling, that reciprocally interact to generate emotional expressions. Developmentally, emotional expression production depends both on maturation and learning through social experience. Comparative work illustrates how behavioural indicators allow inferences about emotional states across taxa, revealing both shared and divergent properties of emotions that relate to ecology, social structure and cognitive capacities. Finally, the issue highlights intraindividual functions of emotional expressions alongside their social functions, shedding new light on why emotional expressions have evolved. Here, we synthesize the contributions and set out a new research agenda on how and why emotions are expressed.

This article is part of the theme issue 'Mechanisms, development, phylogeny and functions of emotional expressions'.

1. Introduction

Emotions are central to nearly everything that matters to us: whom we love and befriend, how we spend our time, and how we see ourselves and others. And our emotions shape our behaviour: fear stops us from pursuing risky actions, interest fuels learning, anger mobilizes us to protest, and embarrassment alerts us when our social standing is compromised. The central role of emotion in human life has long been recognized by scholars [1,2], and the past decades have witnessed a rapid expansion in psychology, neuroscience, philosophy, the social sciences and humanities of empirical research and theoretical developments on emotion [3].

While cognitive functions like reasoning and remembering operate hidden inside individuals' minds, emotions are often made visible through verbal and non-verbal expressions—dynamic behavioural patterns including facial and bodily movements, gaze patterns, gestures, vocalizations and visible autonomic responses like blushing or tears [4–6]. Such behavioural and autonomic

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patterns are thought to have initially evolved to aid physiological regulation, to alert the expresser to significant events in the environment and to motivate behaviours to respond to relevant events, thereby facilitating adaptive responses to environmental demands across species [1,7–9]. Over evolutionary time, they have also begun to serve social and communicative functions, because consistent linkage between emotions and their overt manifestations relays important information about an individual's internal state to observers (e.g. [4,7,10–12]). For example, emotional expressions may coordinate social interactions by conveying, intentionally or not, information about the expresser's intentions and internal states. Expressions can thereby elicit appropriate adaptive responses in perceivers, such as sympathy in response to others' distress or appeasement in response to anger [6,11,13,14].

Contemporary research on emotional expressions (mainly in humans) has primarily focused on observers' perceptions of others' emotional expression, with the central research question being the accuracy of inferring emotional states from their expressions. Researchers have also sought to establish how emotional expression perception coordinates social interaction by shaping perceivers' inferences, decisions and behaviours. This work has advanced our understanding of the social and communicative functions of emotional expressions [14]. Yet, while focusing on the recognition and encoding of emotional expression, studies have often overlooked the production of expression and the functions that non-verbal expressions of emotions may serve for the expresser [15].

Although expressing and perceiving non-verbal expressions are two sides of the same coin, there are several reasons why the mechanisms and functions of production cannot be established by studying only perception, and *vice versa* (e.g. [16–18]). First, although action and perception are tightly linked in the brain, affective and cognitive neuroscience shows that they constitute different processes with distinct inputs, outputs and behavioural and physiological goals. Production starts with goals and intentions as inputs and produces motor behaviour and autonomic changes as outputs, whereas perception takes sensory information from the environment as input and produces perceptual representations, such as inferences about others' states or actions [19,20]. Furthermore, imaging studies show overlapping but partially distinct patterns of activation when people express versus observe emotions [21–23]. Lesion studies show that damage to some regions impairs expression but not perception, or *vice versa*. For example, patients with injuries involving the right frontal operculum show impaired spontaneous production (but not comprehension) of emotional prosody, whereas patients with injuries involving the right posterior temporal regions or the thalamus show deficits in the comprehension (but not spontaneous production) of emotional prosody (e.g. [24]).

Second, there is evidence that differentiated emotional expressions, such as laughing, coy smiling, moaning or jealous protesting, emerge already in infancy (e.g. [25–28]). Although infants can distinguish between distinct emotional expressions from early on (e.g. [29]), emotional expression production and their categorization and labelling do not follow the same developmental trajectories in the first years of life [30–33]. This indicates dissociation between production and perception in ontogeny.

Third, examining the production—not just the perception—of emotional expressions in non-human animals, particularly those with bodies vastly different from humans, illuminates the evolutionary diversity of expressive behaviours across species. Studies on production reveal which body movements, postures and modalities a species uses to regulate internal states in relation to the environment, and how these displays are constrained by environmental pressures (e.g. a bird can puff its feathers in display, a dog can wag its tail and other species use entirely different modalities, such as an ant secreting alarm pheromones from glands in their abdomen or head). Comparing such species-specific expressive behaviours allows us to understand how selection pressures have shaped the evolution of the wealth of emotional expression that can be found in the natural world.

Finally, perception studies cannot speak to intra-personal functions of emotional expressions, such as how these expressions regulate internal physiological states, action tendencies of the expresser and self-related processes (e.g. [34]). Dedicated research on emotional expression production and its effects on expressers is, thus, necessary to fully understand the role of emotional expressions in experience and behaviour [15].

In recent years, there has been a steadily growing interest in the study of emotional expression production. Neuroscientific and psychophysiological studies have begun investigating the neural and somatomotor mechanisms that support the production of emotional expressions (e.g. [9,35–40]). Developmental studies are tracking how distinct emotional expressions emerge in human development and how caregivers, peers and culture shape expressions across the lifespan (e.g. [41–47]). Comparative research is investigating whether some emotional expressions are conserved across evolution (e.g. [48–51]). At the same time, intra-personal and regulative functions of emotional expressions are attracting increasing attention [52–54].

Until now, research on emotional expressions has been siloed, with scholars from different disciplines working independently from each other. The present theme issue synthesizes the recent development in psychological, philosophical, biological and neuroscientific work on displaying emotional expressions, and provides an interdisciplinary integration of emotional expression production. We adopt Tinbergen's [55] framework, which distinguishes between four questions to study the ultimate and proximate causes and consequences of behaviour and apply it to the domain of non-verbal expression of emotion.

(a) Mechanisms of emotional expression production. What are the neural, cognitive and somatomotor mechanisms that generate non-verbal emotional expressions? What are the internal and external elicitors of emotional expressions?
(b) Ontogeny of emotional expression production. How do non-verbal emotional expressions emerge and change from infancy through childhood to adulthood? What are the mechanisms of ontogenetic change, including socialization, learning and culture?
(c) Phylogeny of emotional expression production. What are the similarities and differences in non-verbal emotional expressions across species?

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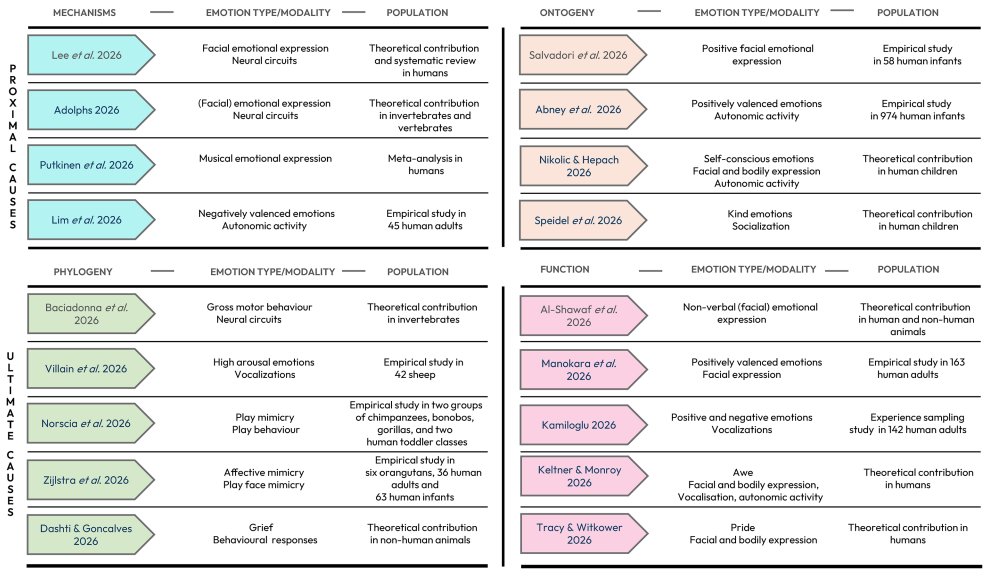

Figure 1. An overview of the contributions in the theme issue.

(d) Functions of emotional expression production. How can the production of non-verbal expressions be functional for the expresser?

Addressing these questions requires input from a range of disciplines. Consequently, contributions in this issue approach these questions from the perspectives of psychology, neuroscience, biology and philosophy. The articles cover a wide range of emotions, from joy and fear to awe and shame. They examine multiple expressive channels ranging from faces to bodily posture, voice and autonomic responses, and they cover species ranging from invertebrates to humans. In this editorial overview, we provide a summary of each of the four sections of the theme issue (mechanisms, development, phylogeny and functions) to address how and why emotions are expressed. An overview of the contributions is presented in figure 1. By bringing these diverse perspectives and methods together, we provide an interdisciplinary overview of current approaches to emotional expression production and highlight new insights and avenues for future research on the role of emotional expression production in human and non-human animal behaviour.

(a) The mechanisms of emotional expression production

Expression production involves coordinated activity of neural, cognitive and somatomotor processes. By investigating how particular patterns of situational appraisals (cognitive evaluations), brain activity and muscle activation give rise to specific expressions in particular contexts, we can map the proximate causes of these expressions—that is, why a given expression occurs in a given context and form. This work builds on the theorizing of Darwin [1], who proposed that salient events elicit internal emotional states that in turn trigger characteristic patterns of expression that evolved from adaptive behaviours. Around the same time, somatic theories of emotion, most prominently that of William James [56], argued that emotional expressions arise directly from peripheral bodily changes, whose perception in turn gives rise to emotional experiences, emphasizing the role of interoception in emotional experience. Contemporary work has expanded these broad ideas to examine how distributed neural systems, interoception, somatosensation and cognitive processes interact in bidirectional and dynamic feedback loops to generate emotional experience and to shape the production of emotional expressions (e.g. [9,19,36,57]).

Emotions can be analysed in terms of three distinct but interacting domains: experience, production and perception. An integrated mechanistic account, therefore, needs to specify how these different processes are coupled and how they can dissociate. Several contributions in the current issue address questions on whether and how emotional experiences relate to emotional expressions. Synthesizing evidence from 49 neuroscientific articles on emotional expression production, Lee and colleagues [16] suggest that emotional experience and emotional expression are at least partly dissociable. They conclude that emotional expressions do not always map directly onto concurrent subjective emotional experiences, and that regulatory mechanisms associated with prefrontal control mediate manifestation of internal experiences as facial expressions. Non-verbal expressions do not thus provide a direct readout of an internal state but are, to varying degrees, regulated. Adolphs [58] takes this discussion further by proposing that emotional expressions can be understood as largely independent of conscious emotional experiences—a perspective that allows us to attribute emotional states to non-human animals and human infants, while remaining agnostic about whether they can consciously feel these emotions.

Emotional expressions do not depend only on internal states, but are also shaped by goals, social rules and contextual associations between emotion-eliciting events, emotional experience and expressive displays [59]. They thus emerge from stimulus appraisals implemented in distributed neurophysiological systems that also integrate information about context. Adolphs [58]

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characterizes this organization as a 'fan-in/fan-out' so that different sensory and contextual signals are first funnelled into a more integrated emotional state (fan-in), which is then expanded back out into a wide range of (coordinated) physiological and expressive responses (fan-out).

One illustration of how cognitive appraisal influences emotional states that is reflected in physiological responses is the contribution of Lim and colleagues [60]. They manipulated emotion regulation strategies of self-distancing and self-immersion during exposure to negatively valanced stimuli and tested the effects on subjective emotional experience and autonomic activity. Their findings demonstrate that cognitive appraisal strategies can causally modulate autonomic activity related to emotion. These results align with recent mechanistic models in which higher-order appraisal and regulation shape bodily states [36] and they illustrate how cognitive regulation strategies are implemented in the process of emotional expression production.

Another recurrent topic in the investigation of the mechanisms of emotional expressions is the link between expression production and perception through perception–action coupling [16,58]. Adolphs [58] highlights mirror systems in the ventral premotor cortex that respond both when an individual performs an action and when they observe another individual performing the same action. Although the ultimate functions of mirror-like responses in the lateral frontal and parietal regions remain debated (e.g. [61]), there is ample evidence on behavioural mirroring or mimicry of emotional (facial) expressions (e.g. [62,63]). Many of the cortical and subcortical structures implicated in emotional expressions, such as the amygdala and cingulate motor cortex, show overlapping activity both when an emotion is expressed and when it is observed, and pattern classifiers trained with brain activity recorded while generating specific expressions can predict the brain activity resulting from viewing the same expressions [23]. These perception–action couplings constitute an important part of the neural processes by which emotional expressions become socially regulated.

Perception–action coupling is also central for musical emotions. Putkinen and colleagues [64] review music as a unique mechanism to induce and share emotions across individuals, including performers and listeners. Music can sustain and deepen affective engagement through repetition and rhythmic entrainment over time, allowing emotions to unfold gradually. The authors' meta-analysis of functional imaging studies also shows that the neural responses to music production and music-evoked emotion overlap, suggesting that music-making engages, to some extent, similar brain networks to those employed in the experience of music-evoked emotions and emotions in general. Music, thus, offers a unique way to study how expressive production, perception and collective synchronization of emotions give rise to neural entrainment across individuals and shared emotional states.

Together, the contributions in the mechanisms section highlight distributed, multi-level mechanisms of emotional expression production, where appraisal, central emotion circuits with fan-in/fan-out organization, and interoceptive signalling reciprocally interact to generate emotional experience and expression. They also demonstrate how perception–action coupling, social context and regulation strategies shape expression production and can decouple expression from the experience.

(b) The ontogeny of emotional expression production

Investigating how the capacity for emotional expression unfolds across human development can help us understand the roles of maturation, social experience and culture, as well as their interactions, in emotional expression production. Theories of emotional development in infancy converge in proposing that all aspects of emotional functions develop throughout infancy and childhood, only reaching adult-like differentiation and complexity through maturation, experience and (implicit) learning of the social contextual factors pertaining to emotions ([65–68]). Most of these theories propose that newborns experience undifferentiated arousal in response to all kinds of strong and salient stimuli, which first becomes differentiated into broadly positive and negative affect and subsequently into a fuller range of distinct emotions: initially so-called 'basic emotions' such as anger and fear during infancy, and later, with further cognitive development, more complex emotions, such as compassion or shame (69; but see, for example, [70,71] for the view that complex emotions may be present earlier in development). Non-verbal emotional expressions are likewise thought to differentiate throughout development, progressing from relatively undifferentiated displays (e.g. smiles representing various forms of positive affect) to more specific expressions tied to specific types of elicitors (e.g. anger expressions linked to goal obstacles) [66].

Maturation is not the only element to affect the development of emotional expressions. Instead, they develop through social interaction, typically with caregivers [72–75]. Repeated social exchanges in which caregivers respond to, mirror, amplify or ignore infants' expressions allow the infants to learn when, how and how strongly different emotions are functional to display. Thus, the ontogeny of emotional expressions includes biological maturation and internal differentiation of affect, as well as co-construction of non-verbal emotional expressions within caregiver–child interactions. Several contributions in this theme issue explore how emotional expressions emerge through dynamic feedback processes in which caregivers and infants simultaneously and continuously influence and are influenced by each other.

The earliest positive emotional expressions in infants typically involve smiling, and they start taking shape in dyadic interactions soon after birth. Salvadori and colleagues [76] report that 8-month-old infants initiate episodes of shared positive emotional expression with an interaction partner more often than four-month-old infants. This developmental change suggests a shift from affect matching (i.e. smiling after their partner smiles) to increasingly agentic use of positive expressions to shape the emotional quality of social exchanges, reflecting more flexible control over emotional expressions to initiate, maintain and up-regulate shared positive engagement. These episodes also appear to support infants' ongoing physiological regulation.

Drew and colleagues [77] in turn show that infants' respiratory sinus arrhythmia (RSA)—a parasympathetic index linked with flexible and context-sensitive regulation of emotion and attention—increases immediately before and during episodes of shared positive affect with the caregiver. This may help infants to sustain engagement in positive social exchanges. Infants' RSA

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did not, however, increase in response to infants' or mothers' positive affect alone. Instead, only mutual positive engagement was accompanied by elevated RSA in the infants, indicating that shared positive affect specifically is associated with infants' parasympathetic engagement. This provides a physiological basis for increasingly flexible and sustained participation in positive social interactions.

As infants develop, they acquire more sophisticated cognitive skills and engage in increasingly complex social situations. Consequently, a broader range of complex emotions begins to emerge. Nikolić & Hepach [78] review the evidence on self-conscious emotions in early development, discussing how embarrassment, guilt, shame and pride emerge. These emotions are suggested to occur when one reflects upon oneself from the perspective of others, and they play an important role in managing individuals' social standing by showing that the expresser is aware of social norms (and violations) and cares about others' opinions of them. The review suggests that children generate expressions of self-conscious emotions similarly and in similar social contexts to adults already in the first years of life, indicating that these emotions emerge earlier in development than previously thought. In addition, self-conscious emotions appear to serve an important function in motivating young children towards prosocial goals. For example, studies on guilt have shown that young children who feel or display guilt engage in more helping and sharing behaviours than children who do not feel or display guilt (e.g. [45,79]), emphasizing the importance of studying these emotions in early childhood.

Kind emotions, including empathy, self-compassion and gratitude, are also key to prosocial behaviours and are similarly thought to emerge with the development of self-awareness and perspective taking. In this issue, Speidel and colleagues [80] argue that the development of these emotions is supported by 'the Web of Care'—a set of nested, caring relationships and processes including close caregivers and peer relationships as well as broader settings like educational, cultural and community contexts. This framing clarifies how environmental factors at multiple levels are involved, directly or indirectly, in the socialization of emotions.

Together, this section highlights the developmental patterns of emotional expressions, from early expressions of positive affect that are embedded in infant–caregiver interactions, to an increasingly differentiated repertoire of emotional expressions from infancy onwards, as children mature, acquire more sophisticated cognitive skills, accumulate varied social experiences and come to appreciate the complexities of the social world. The contributions underscore the role of caregivers and the broader social environment in tuning the development of emotional expressions, both through immediate responses to children's signals and, through more stable features like the sensitivity and responsiveness of caregivers, educational and community settings.

(c) The phylogeny of emotional expression production

Studying the phylogeny of emotional expressions can reveal which components of emotions are shared across species, which have emerged through distinct evolutionary pathways across species, and which species-specific emotional expressions came into existence following unique adaptations, such as human-specific language and culture. Furthermore, studying emotional expressions across both evolutionarily close and distant species can reveal their mechanistic basis and their effects on behaviour [81], and may also lead to the discovery of new emotion categories that are unknown to humans in other species.

In his seminal work, Darwin argued for continuity in emotional expressions between humans and other animals [4]. He argued that certain expressions were more clearly expressed by other species than humans and also recognized that some species can do things that humans cannot (e.g. with movable ears or hairs that can bristle). Recent studies have established that key brain circuits regulating defensive, appetitive and social behaviour are tightly conserved across species [82]. Many modern animal researchers accordingly adopt a functional, neurobiological definition of emotions, defining them as evolutionarily conserved brain–body states that are triggered by specific classes of stimuli and that organize externally observable emotional expressions, as well as associated cognitive and physiological changes (see [19,81]). For example, studies on facial expressions in primates have revealed consistent facial muscular contractions in response to triggers that are similar to those that elicit the same facial changes in humans [83]. Beyond that, neural and physiological responses to survival-critical emotions such as fear are consistent even across phylogenetically distant species such as humans and rats [84].

There is, however, an ongoing debate about how closely emotion-related physiological and behavioural states measured in animals map onto human psychological categories of emotion. Anderson & Adolphs [81] offered a comparative perspective that posits that certain fundamental properties of emotions, such as action tendencies, are shared across phylogeny, while fine-grained specialization of the affect circuits is species-specific. Human and non-human animals alike can manifest emotional states and express their emotions independently of conscious awareness. Studying these processes on the neural, physiological or behavioural level can therefore unravel their mechanisms and function [81].

On this view, there is no reason to assume that emotions do not exist in a wide range of animal taxa, all the way from humans to invertebrates. In this issue, Baciadonna and colleagues [85] review recent evidence suggesting that some invertebrates manifest basic emotional states, indicated by components of emotions like observable expressions, gross motor behaviours and neural activation patterns. The synthesis is based on a wide range of behavioural indicators, including state-dependent changes in defensive behaviour, freezing, play behaviour, facial and postural changes including head and siphon withdrawal and, in some taxa, acoustic or vibrational signalling. This work reveals scalable, persistent and generalized responses tied to specific emotion-eliciting contexts, which is consistent with commonly proposed criteria for emotional states [81]. Similarly, studies of the brain basis underlying these behavioural changes in invertebrates, particularly those involving monoamine neuromodulators such as serotonin and dopamine, indicate that neuromodulatory systems mediate behavioural shifts related to putative emotional states.

A comparable approach can also be applied to vertebrates. In this issue, Villain and colleagues [86] examined whether high-arousal vocalizations during social and non-social challenges in two diverging sheep lines selected for high or low sociability

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reflect emotions, sociability, or both. They investigated whether these vocalizations encode momentary emotional states versus stable traits, such as sociable temperament. They found that vocal communication associated with high arousal depended on heritable temperamental differences, with highly sociable sheep showing exaggerated vocal responses to social isolation. This finding, in combination with evidence from invertebrates, suggests a more complex picture in which emotional expressions, including vocalizations, reflect not only transient emotional states but also species-specific temperamental traits shaped by breeding.

Behavioural measures, including facial and postural expressions, as well as vocalizations, have been used to study emotions in great apes and humans. These measures have also been extended to examine how emotional expressions are embedded in social interactions and transmitted via emotional contagion. Norscia and colleagues [87] investigated emotional contagion through play behaviours in chimpanzees, bonobos, gorillas and human toddlers. Play is typically associated with positive affect [88], and the 'play face' of non-human primates—characterized by open mouth displays—has been considered homologous to human laughter [89]. Play contagion may enable the sharing of positive playful states between individuals, thereby enhancing social bonding and potentially reducing negative affect after conflicts. Using naturalistic observations, the authors found evidence of play contagion in all species. Contagion was stronger in males than in females, and in younger as compared with older individuals. There were, however, no robust differences in play contagion across primate species, suggesting that communicating intent for mutual play might be an evolutionarily conserved mechanism contributing to social cooperation among hominid species.

Another study in this section investigated emotional contagion through play face mimicry in orangutans, and in human infants and adults [90]. Play contagion and the mimicry of associated facial expressions have been documented in social interactions across many species. Zijlstra and colleagues [90] tested whether such mimicry can also occur outside of live social interaction (i.e. while watching videos of others' play interactions), which would suggest a potential intraindividual function of mimicry, such as facilitating the understanding of others' mental states. Human infants and adults, but not orangutans, showed robust play face mimicry in a non-interactive context. These findings suggest possible boundaries to mimicry and emotion contagion and they point to differences in the evolution and function of mimicry across species. As a highly social species, humans display mimicry in both live and non-live social situations, consistent with broader roles of mimicry beyond immediate social bonding. However, orangutans did not show such mimicry in the absence of direct social interaction, suggesting that in this semi-solitary species, mimicry and emotional contagion may depend more strongly on live social interaction and may primarily serve to manage social encounters. Interestingly, this may be specific to play face, which typically occurs in social interaction, given the evidence that other expressions, such as yawning, are mimicked in orangutans [91].

Whereas these studies focused on positive emotions that are elicited or shared in social contexts, social emotions can also be negative, particularly when social bonds are disrupted or broken. Dashti & Goncalves [92] review grief-like responses across animal species, conceptualizing grief as a conserved, homologically shared emotional response to social loss characterized by active distress and passive depression of an organism. Although grief is sometimes considered uniquely human owing to its complexity [93], observational studies on social loss and mother–infant separation studies point to the possibility that across taxa, grief might be widespread and expressed through withdrawal, vocalizations, anxiety-like behaviours and changes in social interactions. It might have evolved as a mechanism for maintaining social bonds, facilitating learning from social loss and promoting cohesion among the members of a social group.

Together, the studies in the Phylogeny section illustrate how emotional states can be inferred across taxa from behavioural indicators such as facial and postural changes, vocalizations and gross motor behaviours, as well as from neuromodulators. From invertebrates to sheep, great apes and humans, they suggest that some fundamental properties of emotions, such as action tendencies, are at least partially shared across phylogeny. At the same time, they highlight how the elicitors, expression patterns and functions of these emotions can diverge across species, reflecting differences in social structure and cognitive capacities.

(d) Functions of emotional expressions

Practically all emotion theories agree on the idea that emotions function to motivate and guide behaviours, helping organisms adapt to environmental demands (e.g. [1,94–102]). Two major functions have been proposed for emotional expressions: (i) intra-personal functions, whereby expressions prepare the organism to respond adaptively to environmental demands by regulating and guiding behaviours and (ii) social functions, whereby expressions communicate critical information about internal states [12]. These two explanations are not mutually exclusive, and expressions that serve intra-personal regulatory roles can have communicative value as well.

Research has put more emphasis on the communicative role of emotional expressions, arguing that in many contexts their primary function is to convey socially relevant information and influence others' behaviours (e.g. [12,103–106]). Although communicative functions are undoubtedly important, treating emotional expressions primarily or exclusively as communicative signals should come with some caveats.

In the strictly communicative view, emotions should be expressed primarily in the presence of actual (or imagined) observers who can receive the signal. Emotional expressions are indeed modulated by the presence of an audience (e.g. [10,103,107,108]). For example, positive emotional expressions are often enhanced in the presence of others, which may reflect the communicative and affiliative functions of positive emotions (e.g. [109,110]). However, not all emotional expressions are modulated by the presence of an audience (e.g. [111]), and negative emotional expressions are often attenuated in social contexts (e.g. [110,112]). Moreover, subjective emotional experiences are themselves modulated by social settings, so changes in overt expressions do not necessarily imply communicative intent but may simply mirror changes in felt emotions [107]. Also, emotional expressions occur in the

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absence of others (see, for example, [113] in this issue). Individuals may furrow their brows, clench their jaw or slam their laptop lid shut after reading an infuriating email while working at home on their own, tear up when watching a sad movie alone, wrinkle their nose in disgust when encountering a foul odour in an empty room or do a happy dance when finally mastering a difficult task, even if nobody else is around. Emotional expressions, thus, have functions beyond communication and may also serve intraindividual roles in regulating and motivating one's own behaviours.

Furthermore, congenitally blind individuals spontaneously produce similar patterns of facial expressions to sighted people [114]. And although there are differences in acoustic features of affective vocalizations between deaf and hearing people, many affective vocalizations of deaf individuals are reliably recognized as emotional states by subjects with normal hearing [115]. Thus, at least some aspects of emotional expressions do not depend on species-typical perceptual learning and are therefore unlikely to be purely acquired social signals, speaking against a strictly communicative role of emotional expressions.

The intraindividual functions of emotional expression have, however, remained elusive. One reason for this, as Al-Shawaf and colleagues [116] argue in this issue, is that it is often difficult to disentangle intra- from interpersonal function: it is rarely clear when a non-verbal expression primarily prepares an individual for action, when it primarily serves to inform or influence others, and when it simultaneously fulfils both roles. On their view, this ambiguity reflects the logic of natural selection, specifically inclusive fitness, which operates at the level of genes rather than an individual. Because the genetic interests of a single organism often overlap with those of other related conspecifics, intra-individually functional behavioural and skeletomuscular changes may become relevant signals for conspecifics, promoting the selection of accurate decoding. Emotional expressions are thus likely to frequently serve both intra-individual and social functions simultaneously; for example, envy communicates desired goals and status concerns to others, while simultaneously motivating the individual to do better [116].

In this issue, Manokara and colleagues [17] propose that by studying the spontaneous production rather than mere perception of emotion, we can capture aspects of emotional expressions that may be missed in perception studies. Whereas perception studies may allow for the identification of emotional expressions that are signals, serving communicative functions, expression studies can additionally identify cues that may be inherent parts of an expression and serve intraindividual functions, but are not documented in perception studies because human judges do not detect them. They examined how 22 positive emotions are displayed on the face when induced naturally and found 13 patterns of facial behaviour that were uniquely related to specific positive emotions, such as interest, determination and elation. By mapping facial movements related to particular spontaneously induced positive emotions, this work reveals a richer and more differentiated expressive repertoire than may be apparent from perception studies alone.

Vocalizations related to different emotions can similarly inform functional theories of emotion. In this issue, Kamiloğlu [113] examined the situational cues and psychological characteristics associated with the production of emotional vocalizations in daily life using a seven-day experience sampling study. She found that the frequency of different vocalizations varied substantially across contexts (e.g. public spaces versus interaction with close others) and that all vocalizations were reported to occur more often in social situations than when alone. Yet, many emotional vocalizations also occurred when alone, indicating that they serve intraindividual functions, beyond social communication. In terms of social norms, laughter and sighs were rated as most appropriate, whereas screams and retching sounds were rated as least appropriate in daily life, perhaps owing to their differing functions. Laughter signals prosocial motivation and affiliation absent of non-threatening intent, while sighing may serve an intraindividual emotional regulatory function by enabling release of muscle tension and stress through prolonged exhalation. Both may be perceived as more appropriate than screams and retches, which reflect high-intensity alarm signals that trigger strong emotional reaction in others. By linking specific vocalizations to typical social contexts and perceived appropriateness, this study helps inform functional accounts of different emotional vocalizations.

The next two contributions in this issue focus on two specific emotions and their functions in more detail: awe and pride. Keltner & Monroy [117] review evidence for a distinct multi-modal expression of awe—an emotion that occurs in response to something that is perceived as vast and beyond current knowledge. They discuss studies showing that awe is associated with a distinct multi-modal non-verbal expression (raised eyebrows, widened eyes, an open mouth, jaw drop, stillness of the body, vocal bursts such as 'whoa' or 'wow' and goose bumps) that probably serves an intra-personal function of facilitating information processing. For example, widening the eyes and raising the eyebrows can increase the visual field and sensory intake, facilitating the detection of unexpected features. At the same time, awe is also deployed in cultural forms, such as music, story, dance and visual art, allowing individuals not only to express awe but also to share conceptual knowledge of the emotion, arriving at a shared understanding of awe. Their analysis demonstrates how a distinct emotion can recruit multi-modal expressive patterns and cultural forms to support both intraindividual and social functions.

The final contribution in this issue focuses on another distinct positive emotion, pride, that centres on achievement and social status. Tracy & Witkower [118] argue that an emotional expression that benefits its expresser serves an intraindividual function, even when the benefits are accrued through the communicative function of the expression. They describe that a prototypical expression of pride (an extended and upright posture, head tilted upward and a small smile) benefits the expresser in transforming achievements into higher social status. Individuals who display pride communicate their achievements to others and receive more attention, a greater allocation of resources and higher-quality mates, gaining prestige.

Taken together, these studies invite a nuanced view on the functions of emotional expressions. Rather than treating expressions exclusively as social signals, they show that different expressions may simultaneously serve intraindividual and social functions. Furthermore, by studying the production of emotional expressions, these studies reveal a rich, context-sensitive expressive repertoire that may not have emerged from perception studies alone.

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2. General discussion

Empirical and theoretical contributions in this issue examine non-verbal emotional expressions at different levels of analysis, including mechanisms, ontogeny, phylogeny and function. These contributions also speak to each other directly in several ways. First, one level of analysis can generate hypotheses about phenomena at another level of analysis. For example, theories about the function of a specific emotional expression can generate hypotheses about its proximate mechanisms. If blushing serves an intraindividual function to alert the individual that their social status is at stake [78], then blushing should be more likely to be elicited when one's social status is threatened than when it is not and should recruit neural mechanisms associated with self-referential processing. And if functionalist accounts also propose a social function—that blushing serves as a signal to appease others, and is not a by-product of underlying affective processes—then blushing should be more likely to appear in the presence of an audience than in its absence. As another example, knowledge about mechanisms can generate hypotheses about ontogeny. If kind emotions, such as gratitude, require estimating appropriate reciprocity [119], then gratitude should emerge in development only once children begin to understand reciprocity [80].

Second, the same non-verbal emotional expression and related phenomena can be studied from different angles. Our issue provides several examples. One example is vocalizations that were studied from phylogenetic [86] and functional levels [113] of analysis. Vocalizations are particularly interesting to study from different levels of analyses, because they show stronger cross-species continuity and early emergence in human development compared with other modalities, such as facial expressions. Understanding how vocalizations operate in non-human animals, how they emerge and change during early human development, and when different vocalizations are most likely to occur in adults' daily lives can offer a more comprehensive understanding of why certain vocalizations appear in some but not other situations, and in some but not other species.

Mimicry is another example of a phenomenon warranting multi-level analysis. Affective mimicry can be seen as a context for the elicitation of non-verbal emotional expressions: one organism's emotional expression serves as an elicitor of a similar emotional expression in an interaction partner. From this perspective, we can ask how mimicry evolved and when and why it occurs in different species. Two studies in the current issue examine affective mimicry across non-human primate species, as well as human infants, toddlers and adults [87,113]. Integrating findings across species and across development can shed light on the evolution of mimicry, on its elicitors and functions and on how these may differ across species and change over the course of ontogeny. For example, mimicry may serve additional or more differentiated functions in humans, who are a highly social species, and it may, therefore, be expected to occur more frequently and in a wider range of situations, modulated by social context and goals. The observation that affective forms of mimicry are present early in human development but that their frequency and form change with age and that some forms of mimicry are more or less frequent across species can further distinguish aspects of mimicry that are more strongly constrained by biological mechanisms from those that are more shaped by learning and experience.

Finally, our issue demonstrates that a single study can test hypotheses from different levels of analysis (e.g. comparing emotional expressions of human and non-human animals during different developmental periods). This is important because with such designs we can test hypotheses about the proximal and ultimate mechanisms of emotional expressions. Moving forward, we can design, for example, studies on the effects of the presence of an audience (strangers versus close ties) on the expressions of smiles (and related brain activity) in non-human animals as well as humans of different ages to study not only whether smiles serve affiliative social functions across species (ultimate mechanism), but also their mechanisms and developmental changes (proximate mechanisms) as well as whether the mechanisms and functions change across species and development.

(a) Where we are and where we are heading in the study of emotional expression

Research on the production of emotional expression has flourished in the past decades, and there is now accumulated knowledge across disciplines. However, this research has been fragmented, with studies done independently from each other in different disciplines and typically published in specialist journals, making the synthesis of current knowledge challenging. An interdisciplinary integration is therefore much needed [3,6]. This theme issue is an attempt to bring together research on emotional expressions that focuses on the expresser, examined from different levels of analysis and their synthesis. We hope that this issue will demonstrate that it is not only possible, but also necessary, to study emotional expressions across different disciplines if we are to move the field forward, and that it will inspire more affective scientists to go beyond a single level of analysis when studying emotional expressions. Only then will we be able to address not only how or why emotional expression occurs in a given moment, but also how its form and occurrence are constrained by evolutionary design and biology, and at the same time, modulated by context, learning and culture.

To further the field, we need to overcome limitations present in much of the current work on emotional expression. The abundance of studies on emotion perception partly stems from pure convenience factors—it is substantially easier to get evaluations and ratings from pre-curated images, audio clips or videos of expressions in the laboratory or in online experiments than to meticulously record the behavioural, neural or physiological responses of individuals producing emotional expressions when truly embedded in an emotional situation, especially in naturalistic settings. Current advances in remote sensor technology [120] and automatic extraction of social signals for digital inputs [121], however, provide promising opportunities for mapping the mechanisms of emotional expression in the wild.

Research on the perception and production of emotional expression is often treated as two separate lines of work and conducted largely independently from each other. However, to understand the mechanisms and functions of emotional expression, we need to integrate perception and production within a single framework. For example, when investigating cross-cultural differences in

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emotional expressions, most studies focus on differences in the perception of emotional expressions. These studies typically use the same set of expressions across cultures and then implicitly assume that emotional expressions are produced in the same way in different cultures, such that any observed differences across cultures stem from cultural differences in how we perceive emotional expressions. Yet, emotional expressions may be differently expressed across cultures, both qualitatively and quantitatively [122–125]. It is therefore important to study how emotional expressions are actually produced in different cultural contexts and how these potentially different expressions are then perceived by observers from different cultures. Only by jointly studying perception and production can we determine whether cross-cultural differences reflect differences in signals themselves, perception or both.

There is also an increasing focus on studying emotional expression outside of Western cultures, including small-scale societies, mostly from psychologists (e.g. [126]). Yet, to account for the dynamic nature of culture, avoid ethnocentrism and build theories and hypotheses that do not rely on Western ways of thinking, collaboration with scholars from other disciplines, such as anthropology and sociology, as well as with scholars from non-Western backgrounds, is much needed to gain a better understanding of cultural influences on emotional expressions [127].

In addition, most research on the production of emotional expression has been conducted with adults, and our understanding of when and how different emotional expressions emerge over the course of human development is still limited. Most developmental studies focus on the production of facial expressions for a small set of emotions, such as joy and fear in infants (e.g. [30]). However, a wide range of emotional expressions emerges and can be studied in infancy, toddlerhood and across early and middle childhood (e.g. [78,80]). Longitudinal studies and studies comparing children of different ages will inform our understanding of how a rich repertoire of emotional expressions develops in humans and how this development is influenced by maturation, socialization and learning.

Similarly, comparative studies on the production of emotional expressions are needed to shed light on the environmental pressures that shaped emotional expressions. At present, it is challenging to map similar expressions across human and non-human animal research. In the human literature, the emphasis has traditionally been on the face, but in non-human animal research, especially in work on invertebrates and some vertebrates, such as fish and birds, the focus has often been on gross motor behaviours. To truly understand emotional expressions from a multi-species perspective, it will be important to study other species in their own right and identify aspects that are shared as well as those that are unique to particular species. Some steps have already been taken toward greater comparability. For example, facial action coding systems (FACS) have been developed and validated not only for adult and infant human faces, but also for non-human primates and several domestic species (i.e. multi-species or animal FACS; for an overview, see [128]). Comparable work on body posture and motion, as well as vocalizations, could further facilitate our understanding of emotional expression across species (e.g. [49,129]).

Furthermore, there is a growing focus on integrating different modalities in emotion expression research, but this work has mostly concentrated on emotion perception (e.g. [130–132]). Examining multiple modalities, such as facial expression, body posture and movement, vocalization, smell and physiological measures, in research on emotional expression production could shed light on how expressions in different modalities relate to each other and whether they cluster differently under different circumstances, possibly reflecting distinct emotion profiles [133,134]. At present, it is still debated whether vocalizations or facial expressions are unique to specific emotions. Moving forward, it will be important to investigate whether different constellations of expressions across modalities can distinguish one emotion from another and how these multi-modal patterns vary across contexts, development and phylogeny and culture.

Finally, recent developments of new technologies, including wearables, computer vision methods, experience sampling protocols and portable neuroimaging such as functional near-infrared spectroscopy (fNIRS), now allow us to study emotional expressions and related neural mechanisms as they occur outside the lab, in everyday life. This enables the design of studies with more ecologically valid tasks that more closely reflect the circumstances in which emotional expressions occur in real life, and moves us away from highly controlled, decontextualized tasks in the lab. A common criticism of human emotion research, and especially of emotion perception research, is the use of highly posed, decontextualized emotional expressions in the lab that do not transfer well to real life, where signals are more ambiguous, temporal dynamics differ and context matters (e.g. [135]). A shift towards studying emotions in real-world settings will allow us to gain a better understanding of when, how and why emotions are expressed in everyday life.

3. Conclusion

This theme issue brings together psychologists, neuroscientists, biologists and philosophers to examine the production of non-verbal emotional expressions using Tinbergen's four levels of analysis: mechanisms, ontogeny, phylogeny and function. The contributions in the issue demonstrate that the production of emotional expression involves distributed, multi-level mechanisms, including appraisal, central emotion circuits with fan-in/fan-out organization and interoceptive signalling, that reciprocally interact to generate emotional expressions and experience. The development of emotional expression production depends both on maturational processes (e.g. acquiring necessary cognitive skills) and on learning through social experience. Comparative work allows us to infer emotional states from behavioural indicators across taxa, suggesting that some fundamental properties of emotions are at least partially shared across phylogeny, whereas other properties diverge across species in ways that reflect differences in ecology, social structure and cognitive capacities. Finally, the issue highlights the importance of studying the intraindividual functions of emotional expressions alongside their social functions to fully understand why emotional expressions have evolved.

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Synthesizing these different levels of analysis allows for a richer understanding of how the form and occurrence of emotional expressions are constrained by evolutionary design and biology, and at the same time, modulated by context, learning and culture. We call on affective scientists to consider these different levels of analyses, to integrate research on production and perception, and to employ naturalistic tasks and multi-modal measures in their work to move the field of non-verbal emotional expression production forward.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.
Data accessibility. This article has no additional data.
Declaration of AI use. The University of Amsterdam AI chat was used for language editing only; all intellectual contributions are the authors' own.
Authors' contributions. M.N.: conceptualization, writing—original draft; M.E.K.: conceptualization, writing—review and editing; L.N.: conceptualization, writing—review and editing; D.S.: conceptualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.
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References

1. Darwin C. 1965 *The expression of the emotions in man and animals*. Chicago, IL: University of Chicago Press.
2. Wundt W. 1897 *Outlines of psychology*. (Translation published 1998.) Bristol, UK: Thoemmes Press.
3. Dukes D *et al.* 2021 The rise of affectivism. *Nat. Hum. Behav.* **5**, 816–820. (doi:10.1038/s41562-021-01130-8)
4. Keltner D, Sulloway FJ. 2026 Principles of emotional expression: reassessing Darwin's evolutionary account. *Evol. Hum. Behav.* **47**, 106861. (doi:10.1016/j.evolhumbehav.2026.106861)
5. Kret ME. 2015 Emotional expressions beyond facial muscle actions. A call for studying autonomic signals and their impact on social perception. *Front. Psychol.* **6**, 711. (doi:10.3389/fpsyg.2015.00711)
6. Sauter DA, Russell JA. 2024 What do nonverbal expressions tell us about emotion? In *Emotion theory: the Routledge comprehensive guide. Volume I: History, contemporary theories, and key elements* (ed. A Scarantino), pp. 543–560. London, UK: Routledge. (doi:10.4324/9781315559940-28)
7. Keltner D, Sauter D, Tracy J, Cowen A. 2019 Emotional expression: advances in basic emotion theory. *J. Nonverbal. Behav.* **43**, 133–160. (doi:10.1007/s10919-019-00293-3)
8. Levenson RW. 2003 Blood, sweat, and fears. *Ann. N. Y. Acad. Sci.* **1000**, 348–366. (doi:10.1196/annals.1280.016)
9. Nummenmaa L, Glerean E, Hari R, Hietanen JK. 2014 Bodily maps of emotions. *Proc. Natl Acad. Sci. USA* **111**, 646–651. (doi:10.1073/pnas.1321664111)
10. Parkinson B. 2005 Do facial movements express emotions or communicate motives? *Pers. Soc. Psychol. Rev.* **9**, 278–311. (doi:10.1207/s15327957pspr0904_1)
11. Scarantino A. 2017 Do emotions cause actions, and if so how? *Emot. Rev.* **9**, 326–334. (doi:10.1177/1754073916679005)
12. Shariff AF, Tracy JL. 2011 What are emotion expressions for*? Curr. Dir. Psychol. Sci.* **20**, 395–399. (doi:10.1177/0963721411424739)
13. Ashkanasy A, Manstead A. 2008 Functions of emotion from an organizational perspective. In *Research companion to emotion in organizations* (eds NM Ashkanasy, CL Cooper), pp. 605–616. Northampton, MA: Edward Elgar Publishing.
14. van Kleef GA, Côté S. 2022 The social effects of emotions. *Annu. Rev. Psychol.* **73**, 629–658. (doi:10.1146/annurev-psych-020821-010855)
15. Morningstar M, Nault DR, Lundell-Creagh R, daSilva EB. 2026 Expresser effects in research on emotion communication: expanding our understanding of inter-individual differences in nonverbal expression of emotion. *Affec. Sci.* **7**, 27–40. (doi:10.1007/s42761-025-00316-x)
16. Lee S, Hwang S, Kim JM. 2026 From seeing to showing: toward a neuroscience of emotion production. *Phil. Trans. R. Soc. B* **381**, 20250136. (doi:10.1098/rstb.2025.0136)
17. Manokara K, Teulings I, Cong Y, Kamiloğlu RG, Fischer A, Sauter DA. 2026 More than just smiling: how 22 positive emotions are spontaneously expressed on the face. *Phil. Trans. R. Soc. B* **381**, 20250133. (doi:10.1098/rstb.2025.0133)
18. Sauter DA. 2010 Are positive vocalizations perceived as communicating happiness across cultural boundaries? *Commun. Integr. Biol.* **3**, 440–442. (doi:10.4161/cib.3.5.12285)
19. Adolphs R. 2017 How should neuroscience study emotions? By distinguishing emotion states, concepts, and experiences. *Soc. Cogn. Affect Neurosci.* **12**, 24–31. (doi:10.1093/scan/nsw153)
20. Rizzolatti G, Craighero L. 2004 The mirror neuron system. *Annu. Rev. Neurosci.* **27**, 169–192. (doi:10.1146/annurev.neuro.27.070203.144230)
21. Hennenlotter A, Schroeder U, Erhard P, Castrop F, Haslinger B, Stoecker D, Lange K, Ceballosbaumann A. 2005 A common neural basis for receptive and expressive communication of pleasant facial affect. *Neuroimage* **26**, 581–591. (doi:10.1016/j.neuroimage.2005.01.057)
22. Saarimäki H, Nummenmaa L, Volynets S, Santavirta S, Aksiuto A, Sams M, Jääskeläinen IP, Lahnakoski JM. 2025 Cerebral topographies of perceived and felt emotions. *Imaging Neurosci.* **3**, imag_a_00517. (doi:10.1162/imag_a_00517)
23. Volynets S, Smirnov D, Saarimäki H, Nummenmaa L. 2020 Statistical pattern recognition reveals shared neural signatures for displaying and recognizing specific facial expressions. *Soc. Cogn. Affect Neurosci.* **15**, 803–813. (doi:10.1093/scan/nsaa110)
24. Ross ED, Monnot M. 2008 Neurology of affective prosody and its functional–anatomic organization in right hemisphere. *Brain Lang.* **104**, 51–74. (doi:10.1016/j.bandl.2007.04.007)
25. Colonnesi C, Bögels SM, de Vente W, Majdandžić M. 2013 What coy smiles say about positive shyness in early infancy. *Infancy* **18**, 202–220. (doi:10.1111/j.1532-7078.2012.00117.x)
26. Hart SL, Behrens KY. 2013 Affective and behavioral features of jealousy protest: associations with child temperament, maternal interaction style, and attachment. *Infancy* **18**, 369–399. (doi:10.1111/j.1532-7078.2012.00123.x)

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27. Reddy V. 2000 Coyness in early infancy. *Dev. Sci.* **3**, 186–192. (doi:10.1111/1467-7687.00112)
28. Scheiner E, Hammerschmidt K, Jürgens U, Zwirner P. 2002 Acoustic analyses of developmental changes and emotional expression in the preverbal vocalizations of infants. *J. Voice* **16**, 509–529. (doi:10.1016/S0892-1997(02)00127-3)
29. Wu Y, Muentener P, Schulz LE. 2017 One- to four-year-olds connect diverse positive emotional vocalizations to their probable causes. *Proc. Natl Acad. Sci. USA* **114**, 11896–11901. (doi:10.1073/pnas.1707715114)
30. Camras LA, Shutter JM. 2010 Emotional facial expressions in infancy. *Emot. Rev.* **2**, 120–129. (doi:10.1177/1754073909352529)
31. Nguyen TT, Nelson NL. 2021 Winners and losers: recognition of spontaneous emotional expressions increases across childhood. *J. Exp. Child Psychol.* **209**, 105184. (doi:10.1016/j.jecp.2021.105184)
32. Riddell C, Nikolić M, Dusseldorp E, Kret ME. 2024 Age-related changes in emotion recognition across childhood: a meta-analytic review. *Psychol. Bull.* **150**, 1094–1117. (doi:10.1037/bul0000442)
33. Widen SC, Russell JA. 2008 Children acquire emotion categories gradually. *Cognitive Development* **23**, 291–312. (doi:10.1016/j.cogdev.2008.01.002)
34. Kamiloğlu RG, Sauter DA. 2024 Sounds like a fight: listeners can infer behavioural contexts from spontaneous nonverbal vocalisations. *Cognition Emotion* **38**, 277–295. (doi:10.1080/02699931.2023.2285854)
35. Ashhad S, Kam K, Negro CAD, Feldman JL. 2022 Breathing rhythm and pattern and their influence on emotion. *Annu. Rev. Neurosci.* **45**, 223–247. (doi:10.1146/annurev-neuro-090121-014424)
36. Critchley HD, Garfinkel SN. 2017 Interoception and emotion. *Curr. Opin. Psychol.* **17**, 7–14. (doi:10.1016/j.copsyc.2017.04.020)
37. Goldin PR, McRae K, Ramel W, Gross JJ. 2008 The neural bases of emotion regulation: reappraisal and suppression of negative emotion. *Biol. Psychiatry* **63**, 577–586. (doi:10.1016/j.biopsych.2007.05.031)
38. Nummenmaa L. 2022 Mapping emotions on the body. *Scand. J. Pain* **22**, 667–669. (doi:10.1515/sjpain-2022-0087)
39. Philippot P, Chapelle G, Blairy S. 2002 Respiratory feedback in the generation of emotion. *Cognition Emotion* **16**, 605–627. (doi:10.1080/02699930143000392)
40. Nikolić M, di Plinio S, Sauter D, Keysers C, Gazzola V. 2024 The blushing brain: neural substrates of cheek temperature increase in response to self-observation. *Proc. R. Soc. B* **291**, 20240958. (doi:10.1098/rspb.2024.0958)
41. Camras LA, Oster H, Campos JJ, Bakemand R. 2003 Emotional facial expressions in European-American, Japanese, and Chinese infants. *Ann. N. Y. Acad. Sci.* **1000**, 135–151. (doi:10.1196/annals.1280.007)
42. Kret ME, Venneker D, Evans B, Samara I, Sauter D. 2021 The ontogeny of human laughter. *Biol. Lett.* **17**, 20210319. (doi:10.1098/rsbl.2021.0319)
43. Malti T, Keller M. 2010 The development of moral emotions in a cultural context. In *Emotions, aggression, and morality in children: Bridging development and psychopathology* (eds WF Arsenio, EA Lemerise), pp. 177–198. Washington, DC: American Psychological Association. (doi:10.1037/12129-009)
44. Messinger DS, Cassel TD, Acosta SI, Ambadar Z, Cohn JF. 2008 Infant smiling dynamics and perceived positive emotion. *J. Nonverbal. Behav.* **32**, 133–155. (doi:10.1007/s10919-008-0048-8)
45. Nikolić M, Brummelman E, de Castro BO, Jorgensen TD, Colonnesi C. 2023 Parental socialization of guilt and shame in early childhood. *Sci. Rep.* **13**, 11767. (doi:10.1038/s41598-023-38502-1)
46. Wass S, Phillips E, Smith C, Fatimehin EO, Goupil L. 2022 Vocal communication is tied to interpersonal arousal coupling in caregiver-infant dyads. *eLife* **11**, e77399. (doi:10.7554/eLife.77399)
47. Kamiloğlu RG, Sun R, Bos P, Huber F, Attema JJ, Sauter DA. 2024 Tickling induces a unique type of spontaneous laughter. *Biol. Lett.* **20**, 20240543. (doi:10.1098/rsbl.2024.0543)
48. Briefer EF. 2012 Vocal expression of emotions in mammals: mechanisms of production and evidence. *J. Zool.* **288**, 1–20. (doi:10.1111/j.1469-7998.2012.00920.x)
49. Kamiloğlu RG, Çalışkan C, Slocombe KE, Sauter DA. 2023 Threat vocalisations are acoustically similar between humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Bioacoustics* **32**, 679–692. (doi:10.1080/09524622.2023.2250320)
50. Kim Y, Kret ME. 2022 The emotional expressions and emotion perception in nonhuman primates. In D Dukes, AC Samson, EA Walle (eds.), *The Oxford Handbook of Emotional Development* pp. 129–145. Oxford Academic. (doi:10.1093/oxfordhb/9780198855903.013.20)
51. Kret ME, Tomonaga M, Matsuzawa T. 2014 Chimpanzees and humans mimic pupil-size of conspecifics. *PLoS One* **9**, e104886. (doi:10.1371/journal.pone.0104886)
52. Gračanin A, Vingerhoets AJJM, Kardum I, Zupčić M, Šantek M, Šimić M. 2015 Why crying does and sometimes does not seem to alleviate mood: a quasi-experimental study. *Motiv. Emot.* **39**, 953–960. (doi:10.1007/s11031-015-9507-9)
53. Susskind JM, Lee DH, Cusi A, Feiman R, Grabski W, Anderson AK. 2008 Expressing fear enhances sensory acquisition. *Nat. Neurosci.* **11**, 843–850. (doi:10.1038/nn.2138)
54. Vlemincx E, Van Diest I, Van den Bergh O. 2016 A sigh of relief or a sigh to relieve: the psychological and physiological relief effect of deep breaths. *Physiol. Behav.* **165**, 127–135. (doi:10.1016/j.physbeh.2016.07.004)
55. Tinbergen N. 1963 On aims and methods of ethology. *Zeitschrift für Tierpsychologie* **20**, 410–433. (doi:10.1111/j.1439-0310.1963.tb01161.x)
56. James W. 1884 On some omissions of introspective psychology. *Mind* **9**, 1–26. (doi: 10.1093/mind/os-IX.33.1)
57. Prochazkova E, Prochazkova L, Giffin MR, Scholte HS, De Dreu CKW, Kret ME. 2018 Pupil mimicry promotes trust through the theory-of-mind network. *Proc. Natl Acad. Sci. USA* **115**, E7265–E7274. (doi:10.1073/pnas.1803916115)
58. Adolphs R. 2026 Comparative neuroanatomy of emotion expression: from flies to human. *Phil. Trans. R. Soc. B* **381**, 20250135. (doi:10.1098/rstb.2025.0135)
59. Scherer KR, Moors A. 2019 The emotion process: event appraisal and component differentiation. *Annu. Rev. Psychol.* **70**, 719–745. (doi:10.1146/annurev-psych-122216-011854)
60. Lim W, Savage H, Longley B, Critchley HD, Dalgleish T, Nord C. 2026 The impact of emotion regulation strategies on experiential and physiological responses to negative emotional videos. *Phil. Trans. R. Soc. B* **381**, 20250138. (doi:10.1098/rstb.2025.0138)
61. Rizzolatti G, Sinigaglia C. 2010 The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat. Rev. Neurosci.* **11**, 264–274. (doi:10.1038/nrn2805)
62. Hess U, Fischer A. 2014 Emotional mimicry: why and when we mimic emotions. *Soc. Personal. Psych. Compass* **8**, 45–57. (doi:10.1111/spc3.12083)
63. Duffy KA, Chartrand TL. 2015 Mimicry: causes and consequences. *Curr. Opin. Behav. Sci.* **3**, 112–116. (doi:10.1016/j.cobeha.2015.03.002)
64. Putkinen V, Rassouli M, Nummenmaa L. 2026 Emotional expression through music. *Phil. Trans. R. Soc. B* **381**, 20250131. (doi:10.1098/rstb.2025.0131)

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65. Campos JJ, Barrett KC. 1984 Toward a new understanding of emotions and their development. In *Emotions, cognition, and behavior* (eds CE Izard, J Kagan), pp. 229–263. New York, NY: Cambridge University Press.
66. Camras LA. 2024 How do emotions develop in children? In *Emotion theory: the Routledge comprehensive guide* (ed. A Scarantino), pp. 527–546. London, UK: Routledge.
67. Holodynski M, Friedlmeier W. 2005 Ontogenesis of emotions and their regulation. In *Development of emotions and their regulation: an internalization model*, pp. 113–216. Boston, MA: Springer. (doi:10.1007/0-387-23295-8_4)
68. Lewis M. 2000 The emergence of human emotions. In *Handbook of emotions* (eds M Lewis, JM Hariland-Jones pp. 265–280. New York, NY: The Guilford Press.
69. Lewis M. 2007 Self-conscious emotional development. In J. L. Tracy, R. W. Robins, J. P. Tangney (eds.), *The self-conscious emotions: Theory and Research* pp. 134–149. New York, NY: Guilford Press.
70. Draghi-Lorenz R, Reddy V, Costall A. 2001 Rethinking the development of "nonbasic" emotions: a critical review of existing theories. *Dev. Rev.* **21**, 263–304. (doi:10.1006/drev.2000.0524)
71. Reddy V. 2003 On being the object of attention: implications for self–other consciousness. *Trends Cogn. Sci.* **7**, 397–402. (doi:10.1016/S1364-6613(03)00191-8)
72. Boiger M, Mesquita B. 2012 The construction of emotion in interactions, relationships, and cultures. *Emot. Rev.* **4**, 221–229. (doi:10.1177/1754073912439765)
73. Messinger DS, Fogel A. 2007 Interactive development of social smiling. In *Advances in Child Development and Behavior* (ed. RV Kail), pp. 327–366. San Diego, CA: Academic Press.
74. Parkinson B. 2012 Piecing together emotion: sites and time-scales for social construction. *Emot. Rev.* **4**, 291–298. (doi:10.1177/1754073912439764)
75. Wass SV, Smith CG, Clackson K, Gibb C, Eitzenberger J, Mirza FU. 2019 Parents mimic and influence their infant's autonomic state through dynamic affective state matching. *Curr. Biol.* **29**, 2415–2422.E4. (doi:10.1016/j.cub.2019.06.016)
76. Salvadori EA, Messinger DS, Cobo-Lewis A, Colonnesi C. 2026 Smiling in time: the interactive development of infant smiling with mothers, fathers, and strangers. *Phil. Trans. R. Soc. B* **381**, 20250142. (doi:10.1098/rstb.2025.0142)
77. Drew A, Sheinkopf SJ, Mitsven SG, Seifer R, Lester BM, Tronick EZ, Messinger DS. 2026 Mutual positive engagement with mother is uniquely associated with increases in human infant heart rate variability. *Phil. Trans. R. Soc. B* **381**, 20260004. (doi:10.1098/rstb.2026.0004)
78. Nikolić M, Hepach R. 2026 The expression of self-conscious emotions and their motivational and communicative function in early development. *Phil. Trans. R. Soc. B* **381**, 20250134. (doi:10.1098/rstb.2025.0134)
79. Donohue MR, Tully EC. 2019 Reparative prosocial behaviors alleviate children's guilt. *Dev. Psychol.* **55**, 2102–2113. (doi:10.1037/dev0000788)
80. Speidel R, Orlitsky T, Shulz MS, Malti T. 2026 Developing kind emotions in caring environments. *Phil. Trans. R. Soc. B* **381**, 20250141. (doi:10.1098/rstb.2025.0141)
81. Anderson DJ, Adolphs R. 2014 A framework for studying emotions across species. *Cell* **157**, 187–200. (doi:10.1016/j.cell.2014.03.003)
82. Zych AD, Gogolla N. 2021 Expressions of emotions across species. *Curr. Opin. Neurobiol.* **68**, 57–66. (doi:10.1016/j.conb.2021.01.003)
83. Kret ME, Prochazkova E, Sterck EHM, Clay Z. 2020 Emotional expressions in human and non-human great apes. *Neurosci. Biobehav. Rev.* **115**, 378–395. (doi:10.1016/j.neubiorev.2020.01.027)
84. de Waal FBM, Andrews K. 2022 The question of animal emotions. *Science* **375**, 1351–1352. (doi:10.1126/science.abo2378)
85. Baciadonna L, Macri C, Baracchi D, Giurfa M. 2026 Exploring emotional expression in invertebrates: mechanisms, functions, and phylogeny. *Phil. Trans. R. Soc. B* **381**, 20250146. (doi:10.1098/rstb.2025.0146)
86. Villain AS, Boissy A, Douls S, Renaud-Goud P, Mialon M-M, Hazard D, Briefer EF. 2026 Vocal encoding of heritable sociability prevails over emotions in sheep bleats *Phil. Trans. R. Soc. B* **381**, 20250143. (doi:10.1098/rstb.2025.0143)
87. Norscia I, Collarini E, Cordoni G. 2026 The play fever: individual and group factors influence the contagion of play behaviour within social hominid groups. *Phil. Trans. R. Soc. B* **381**, 20250144. (doi:10.1098/rstb.2025.0144)
88. Panksepp J. 2011 The basic emotional circuits of mammalian brains: do animals have affective lives? *Neurosci. Biobehav. Rev.* **35**, 1791–1804. (doi:10.1016/j.neubiorev.2011.08.003)
89. Davila-Ross M, Dezecache G. 2021 The complexity and phylogenetic continuity of laughter and smiles in hominids. *Front Psychol.* **12**, 648497. (doi:10.3389/fpsyg.2021.648497)
90. Zijlstra T, Riddell C, Nikolic M, Kret M. 2026. The development of play face mimicry: Comparative insights from human infants, adults, and orangutans. *Phil. Trans. R. Soc. B* **381**, 20250142. (doi:10.1098/rstb.2025.0142)
91. van Berlo E, Díaz-Loyo AP, Juárez-Mora OE, Kret ME, Massen JJM. 2020 Experimental evidence for yawn contagion in orangutans (*Pongo pygmaeus*). *Sci. Rep.* **10**, 22251. (doi:10.1038/s41598-020-79160-x)
92. Dashti S, Goncalves A. 2026 On the nature of grief: uncovering the evolutionary roots of loss across the animal realm. *Phil. Trans. R. Soc. B* **381**, 20250147. (doi:10.1098/rstb.2025.0147)
93. Brinkmann S. 2018 The grieving animal: grief as a foundational emotion. *Theory & Psychology* **28**, 193–207. (doi:10.1177/0959354317747051)
94. Adolphs R, Mlodinow L, Barrett LF. 2019 What is an emotion? *Curr. Biol.* **29**, R1060–R1064. (doi:10.1016/j.cub.2019.09.008)
95. Campos JJ, Mumme DL, Kermoian R, Campos RG. 1994 A functionalist perspective on the nature of emotion. *Monogr. Soc. Res. Child Dev.* **59**, 284–303. (doi:10.1111/j.1540-5834.1994.tb01284.x)
96. Dewey J. 1895 The theory of emotion. *Psychological Review.* **2**, 13–32. (doi:10.1037/h0070927)
97. Ekman P. 1992 Facial expressions of emotion: new findings, new questions. *Psychol. Sci.* **3**, 34–38. (doi:10.1111/j.1467-9280.1992.tb00253.x)
98. Frijda NH. 1992 The empirical status of the laws of emotion. *Cognition and Emotion* **6**, 467–477. (doi:10.1080/02699939208409699)
99. Izard CE. 2011 Forms and functions of emotions: matters of emotion–cognition interactions. *Emot. Rev.* **3**, 371–378. (doi:10.1177/1754073911410737)
100. Levenson RW. 1999 The intrapersonal functions of emotion. *Cognition and Emotion.* **13,** 481–504. (doi: 10.1080/026999399379159)
101. Scarantino A. 2024 Motivational theories of emotions in philosophy and affective science. In *Emotion theory: the Routledge comprehensive guide*, pp. 429–466. New York, NY: Routledge.
102. Scherer KR. 2009 The dynamic architecture of emotion: evidence for the component process model. *Cognition and Emotion.* **23**, 1307–1351. (doi:10.1080/02699930902928969)
103. Fridlund AJ. 1991 Sociality of solitary smiling: potentiation by an implicit audience. *J. Pers. Soc. Psychol.* **60**, 229–240. (doi:10.1037/0022-3514.60.2.229)
104. Hess U, Thibault P. 2009 Darwin and emotion expression. *Am. Psychol.* **64**, 120–128. (doi:10.1037/a0013386)
105. Keltner D, Tracy J, Sauter DA, Cordaro DT, McNeil G. 2016 Expression of emotion. In *Handbook of emotions* (eds M Lewis, JM Haviland-Jones, L Feldman Barrett pp. 467–482, New York, NY: Guilford Press.

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106. Niedenthal PM, Brauer M. 2012 Social functionality of human emotion. *Annu. Rev. Psychol.* **63**, 259–285. (doi:10.1146/annurev.psych.121208.131605)
107. Fischer AH, Manstead ASR, Zaalberg R. 2003 Social influences on the emotion process. *European Rev. Social Psychol.* **14**, 171–201. (doi:10.1080/10463280340000054)
108. Heesen R, Szenteczki MA, Kim Y, Kret ME, Atkinson AP, Upton Z, Clay Z. 2024 Impact of social context on human facial and gestural emotion expressions. *iScience* **27**, 110663. (doi:10.1016/j.isci.2024.110663)
109. Kraut RE, Johnston RE. 1979 Social and emotional messages of smiling: an ethological approach. *J. Pers. Soc. Psychol.* **37**, 1539–1553. (doi:10.1037/0022-3514.37.9.1539)
110. Lee V, Wagner H. 2002 The effect of social presence on the facial and verbal expression of emotion and the interrelationships among emotion components. *J. Nonverbal Behav.* **26**, 3–25. (doi:10.1023/A:1014479919684)
111. Riddell C, Nikolić M, Kret ME. 2025 Putting the social in emotions: the effect of audience presence on pride and embarrassment across Ontogeny. *Dev. Sci.* **28**, e70024. (doi:10.1111/desc.70024)
112. Jakobs E, Manstead ASR, Fischer AH. 2001 Social context effects on facial activity in a negative emotional setting. *Emotion* **1**, 51–69. (doi:10.1037/1528-3542.1.1.51)
113. Kamiloğlu RG. 2026 Vocal display rules in everyday life: when is it appropriate to laugh, sigh, or scream? *Phil. Trans. R. Soc. B* **381**, 20250151. (doi:10.1098/rstb.2025.0151)
114. Valente D, Theurel A, Gentaz E. 2018 The role of visual experience in the production of emotional facial expressions by blind people: a review. *Psychon. Bull. Rev.* **25**, 483–497. (doi:10.3758/s13423-017-1338-0)
115. Sauter DA, Crasborn O, Engels T, Kamiloğlu RG, Sun R, Eisner F, Haun DBM. 2020 Human emotional vocalizations can develop in the absence of auditory learning. *Emotion* **20**, 1435–1445. (doi:10.1037/emo0000654)
116. Al-Shawaf L, Lewis D, Acevedo E. 2026 The functions of emotion and emotion expression at multiple levels of analysis *Phil. Trans. R. Soc. B* **381**, 20250150. (doi:10.1098/rstb.2025.0150)
117. Keltner D, Monroy M. 2026 The expression of awe: evolutionary origins and cultural elaborations of a basic emotion. *Phil. Trans. R. Soc. B* **381**, 20250148. (doi:10.1098/rstb.2025.0148)
118. Tracy J, Witkower Z. 2026 The interpersonal and intrapsychic functions of the pride expression. *Phil. Trans. R. Soc. B* **381**, 20250149. (doi:10.1098/rstb.2025.0149)
119. Kini P, Wong J, McInnis S, Gabana N, Brown JW. 2016 The effects of gratitude expression on neural activity. *Neuroimage* **128**, 1–10. (doi:10.1016/j.neuroimage.2015.12.040)
120. Hu X, Sgherza TR, Nothrup JB, Fresco DM, Naragon-Gainey K, Bylsma LM. 2024 From lab to life: evaluating the reliability and validity of psychophysiological data from wearable devices in laboratory andambulatory settings. *Behav. Res.* **56**, 1–20. (doi:10.3758/s13428-024-02387-3)
121. Santavirta S, Wu Y, Suominen L, Nummenmaa L. 2025 GPT-4V shows human-like social perceptual capabilities at phenomenological and neural levels. *Imaging Neurosci.* **3**, IMAG.a.134. (doi:10.1162/IMAG.a.134)
122. Cordaro DT, Sun R, Keltner D, Kamble S, Huddar N, McNeil G. 2018 Universals and cultural variations in 22 emotional expressions across five cultures. *Emotion* **18**, 75–93. (doi:10.1037/emo0000302)
123. Cowen AS *et al.* 2024 How emotion is experienced and expressed in multiple cultures: a large-scale experiment across North America, Europe, and Japan. *Front Psychol.* **15**, 1350631. (doi:10.3389/fpsyg.2024.1350631)
124. Lindquist KA, Jackson JC, Leshin J, Satpute AB, Gendron M. 2022 The cultural evolution of emotion. *Nat. Rev. Psychol.* **1**, 669–681. (doi:10.1038/s44159-022-00105-4)
125. Mesquita B, Frijda NH. 1992 Cultural variations in emotions: a review. *Psychol. Bull.* **112**, 179–204. (doi:10.1037/0033-2909.112.2.179)
126. Witkower Z, Tracy JL. 2020 We don't make WEIRD faces: a brief history of emotion expression research in small-scale societies. *Evol. Hum. Behav.* **41**, 454–455. (doi:10.1016/j.evolhumbehav.2020.06.005)
127. Crivelli C, Jarillo S, Fridlund AJ. 2016 A multidisciplinary approach to research in small-scale societies: studying emotions and facial expressions in the field. *Front Psychol.* **7**, 1073. (doi:10.3389/fpsyg.2016.01073)
128. Waller BM, Julle-Daniere E, Micheletta J. 2020 Measuring the evolution of facial 'expression' using multi-species FACS. *Neurosci. Biobehav. Rev.* **113**, 1–11. (doi:10.1016/j.neubiorev.2020.02.031)
129. Segalin C, Williams J, Karigo T, Hui M, Zelikowsky M, Sun JJ, Perona P, Anderson DJ, Kennedy A. 2021 The Mouse Action Recognition System (MARS) software pipeline for automated analysis of social behaviors in mice. *eLife* **10**, e63720. (doi:10.7554/eLife.63720)
130. Aviezer H, Trope Y, Todorov A. 2012 Holistic person processing: faces with bodies tell the whole story. *J. Pers. Soc. Psychol.* **103**, 20–37. (doi:10.1037/a0027411)
131. D'Mello SK, Bosch N, Chen H. 2018 Multimodal-multisensor affect detection. In *The Handbook of Multimodal-Multisensor Interfaces: Foundations, User Modelling, and Common Modality Combinations - Volume 2* (eds S Oviatt, B Schuller, PR Cohen, D Sonntag, G Potamianos, A Krüger), pp. 167–202. New York, NY: Association for Computing Machinery/ Morgan & Claypool. (doi:10.1145/3107990.3107998)
132. Pelachaud C. 2009 Modelling multimodal expression of emotion in a virtual agent. *Phil. Trans. R. Soc. B* **364**, 3539–3548. (doi:10.1098/rstb.2009.0186)
133. Keltner D, Cordaro DT. 2017 Understanding multimodal emotional expressions: recent advances in basic emotion theory. In *The science of facial expression* (eds J-M Fernández-Dols, JA Russell), pp. 57–75. Oxford, UK: Oxford University Press.
134. Scherer KR, Ellgring H. 2007 Multimodal expression of emotion: affect programs or componential appraisal patterns? *Emotion* **7**, 158–171. (doi:10.1037/1528-3542.7.1.158)
135. Barrett LF, Adolphs R, Marsella S, Martinez AM, Pollak SD. 2019 Emotional expressions reconsidered: challenges to inferring emotion from human facial movements. *Psychol. Sci. Public Interest* **20**, 1–68. (doi:10.1177/1529100619832930)

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