Neuroscience and Biobehavioral Reviews 115 (2020) 378–395

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

Emotional expressions in human and non-human great apes

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ARTICLE INFO

Keywords:
Emotional expressions
Great apes
Comparative psychology
Cognitive control
Evolution

ABSTRACT

Humans and great apes are highly social species, and encounter conspecifics throughout their daily lives. During social interactions, they exchange information about their emotional states via expressions through different modalities including the face, body and voice. In this regard, their capacity to express emotions, intentionally or unintentionally, is crucial for them to successfully navigate their social worlds and to bond with group members. Darwin (1872) stressed similarities in how humans and other animals express their emotions, particularly with the great apes. Here, we show that emotional expressions have many conserved, yet also a number of divergent features. Some theorists consider emotional expressions as direct expressions of internal states, implying that they are involuntary, cannot be controlled and are inherently honest. Others see them as more intentional and/or as indicators of the actor's future behavior. After reviewing the human and ape literature, we establish an integrative, evolutionary perspective and provide evidence showing that these different viewpoints are not mutually exclusive. Recent insights indicate that, in both apes and humans, some emotional expressions can be controlled or regulated voluntarily, including in the presence of audiences, suggesting modulation by cognitive processes. However, even non-intentional expressions such as pupil dilation can nevertheless inform others and influence future behavior. In sum, while showing deep evolutionary homologies across closely related species, emotional expressions show relevant species variation.

During social interactions, individuals exchange information about their emotional states via communicative expressions and behaviours. While they may sometimes do so intentionally, emotion states can also become perceivable without the conscious awareness of the expressor. Among primates, emotion expression appears to be particularly biased towards the visual and vocal channels, probably related to the evolution of full trichromatic vision within primate evolution (e.g. catarrhine versus other groups) along with evolutionarily preserved primate audition (despite anatomical differences across groups) compared to a relative decrease in olfactory sensitivity (e.g. from strepsirrhines to haplorrhines) (for a review, see Liman, 2006). While likely driven by ecological pressures relating to increased foraging capacity, such as the detection of certain leaves and ripe fruits (Surridge et al., 2003), enhanced vision also enables primates to visually detect changes in other's behaviour, including those related to their underlying emotional states. In the current review, we explore the production of emotion expressions in great apes, our closest living primate relatives as they compare to those of humans. Given the face, voice and body are important for expressing internal states, and are thus unsurprisingly the most studied, we focus our attention primarily towards facial, bodily and vocal expressions of emotion. Nevertheless, it is important to acknowledge that other modalities such as olfaction and touch can be important when it comes to expressing emotions and deserve future attention.

In the visual domain, expressions encompass facial expressions (i.e. based on facial musculature, including the ears); other facial information (e.g. based on pupil dilation; tears; sweat; changes in facial temperature (Kret, 2015)); or body posture (i.e. based on bodily muscle activation, movements, and piloerection). The auditory domain concerns vocal utterances, including the pitch and loudness of the voice that may reflect urgency. In this review, we aim to identify evolutionary commonalities and divergences among great apes and humans in communicative aspects of faces, bodies and voices that facilitate the expression and transmission of emotions. Through this

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https://doi.org/10.1016/j.neubiorev.2020.01.027
Received 1 June 2019; Received in revised form 17 January 2020; Accepted 22 January 2020

comparative review, we hope to provide a better understanding of the control that different species can exert over their emotional expression. Moreover, we use the existing literature to explore the extent to which such expressions can be regulated or intentionally controlled. Finally, we will highlight the questions that have remained under-addressed in the literature and provide suggestions for future research.

Before commencing, there are two crucial considerations that we deem important to address when comparing the literature for human and great ape emotional expressions. First is the difference between naturalistic expressions documented for apes versus the largely artificial expressions documented thus far for humans. While we focus on naturalistic data for apes, most studies on human emotional expressions focus on artificial or acted expressions. Access to real human emotional expressions, movement behaviour and vocalizations remains challenging and potentially ethically problematic. Although the problem of posed versus genuinely expressed emotions is crucial and difficult (see Zuckerman et al., 1976), some evidence does however suggest that posed expressions may represent an approximation to genuine emotional expressions (Zuckerman et al., 1976; Wallbott, 1990). Still, a clear downside is that actors tend to produce only stereotypes or exaggerate expressive behaviours, possibly overlooking more subtle cues (Wallbott and Scherer, 1986). Although some descriptions from human ethology have been helpful to fill some of the gaps, we consider it crucial that readers take this point into account when reading this review.

A second point is the challenge in determining whether an emotional expression truly reflects an inner emotional state. This is particularly the case for great apes, but also for humans, where we can only measure emotions to a certain extent, indirectly, and can never get a truly complete and accurate picture. Measuring emotions remains approximating emotions. Combining methods and tapping into underlying psychophysiological measures brings us closer to understanding emotional experiences, and we will come back to this point at the end of this article.

Another aim of this review is to examine the intentional basis of emotion expressions in humans and great apes. Traditionally, emotional expressions have been considered as direct expressions of internal states, implying that they are involuntary, cannot be controlled and are therefore inherently honest (Ekman and Friesen, 1971). Nevertheless, a growing body of research in affective science, including ethological research conducted with animals, challenges this claim, with evidence that emotional expressions in humans, and to some extent in non-human primates, *can* be controlled or regulated. For instance, certain emotion expressions are only expressed when certain audiences are present (Fridlund, 1991; Clay and Zuberbühler, 2012) and helping conspecifics to predict the future behavior of the expressor (Waller et al., 2017). Thus, the exchange of social, emotional information can have different functions and operate at multiple levels of signaler intentionality.

The fact that emotional expressions can be displayed intentionally suggests higher cognitive sophistication. However, even if a species is capable of doing so, this does not mean that it can express all affect states voluntarily, and in all individuals equally. Within the facial expression literature, part of the problem is that most studies have focused on facial muscles while ignoring alternative ways through which emotions can be expressed, such as through blushing or pupil dilation (Kret, 2015). Even less has been researched for bodily and vocal expressions of emotion, including what is known for other animals than humans. To explore this, a comparative investigation, which traces back the phylogenetic history of emotional expressions, is needed.

In the following sections, we take the above-mentioned points into account in order to review the literature on facial expressions, bodily expressions and vocalizations (in that order) in great apes and humans.

1. Facial expressions

1.1. Facial expressions of emotion in humans and great apes

It is well known that the face plays a key role in human communication, and like humans, great apes have a wide range of facial expressions that can be observed in diverse contexts. Moreover, in both humans and great apes, facial expressions are regularly combined with body expressions and vocalisations (which will be addressed in later sections) to provide rich multimodal displays. It has been argued that, similarly to biological categories such as a species, emotions are conceptual categories grouped together by a goal rather than by similar features or a single underlying cause (Barrett, 2016). Supporting that theory, facial expressions, when shown without contextual information such as body language, are difficult to recognize (Aviezer et al., 2008).

Discrete-emotion theories of facial expression, however, suggest that some emotions are innate and hardwired, universal, automatic, and expressed in a specific way across species (Darwin, 1872) and human cultures (Ekman and Friesen, 1971). For example, joy, typically expressed during play, is characterized by a relaxed open mouth, narrowing or closing of the eyes, bursts of laughter, and, as a study in human infants showed, may be accompanied by a temperature drop in the nose region due to heightened arousal (Nakanishi and Imai-Matsumura, 2008). It has been argued that in order for complex systems to be activated comparably across individuals and species, there must be a minimal, hardwired and fixed affect program in the brain (Anderson and Adolphs, 2014). Supporting evidence comes from studies demonstrating that some facial expressions are shown immediately after infants' birth (Fawcett et al., 2016; Meltzoff and Moore, 1983; Rosenstein and Oster, 1997) and by blind people (Eibl-Eibesfeldt, 1989; Galati et al., 1997). Together, this evidence advocates for innate, automatic and universal aspects of emotions with a specific survival function.

One key question is why facial expressions, stereotypical or real, take the specific forms that they do. For instance, when signaling benign intent, why do humans show their teeth and contract the muscles in their cheeks (smiling) instead of frowning and sticking out their tongue? Is there a biological basis and explanation? We cannot answer this question for all expressions, but in experimental work by Lee et al. (2013) some direct benefits for the expressor have been demonstrated. Specifically, the authors demonstrated that enlarging the expressors' eyes in fear has visual perceptual benefits for that person. Also the disgust expression has direct benefits for the expressor; for instance, closing the nostrils in disgust prevents poisonous material from entering the body and the tongue protrusion is a derivate from spitting these out (Chapman et al., 2009). This argues for an intrinsic connection between emotions and specific facial muscle actions. In other words, emotion states contain adaptive properties that apply across emotions and phylogeny (Darwin, 1872; Anderson and Adolphs, 2014). An evolutionary approach to the study of emotional expressions can provide novel insights into the different views on them, and the current review is a step into that direction.

Zooming in on the morphology of the face, humans have evolved communicative faces to facilitate emotion transmission, where the expressive parts are enlarged and accentuated (for a review, see Kret, 2015). There are approximately 42 muscles in the human face that allow for a rich repertoire of expressions (Goodmurphy and Ovalle, 1999). By contracting or relaxing the muscles in different degrees and combinations, they can produce thousands of different messages (Ekman and Friesen, 1976; Ghiselin et al., 1974). Chimpanzees, bonobos and orangutans have strikingly similar underlying mimetic musculature in their faces (Burrows, 2008; Caeiro et al., 2013; Diogo et al., 2009; Diogo, 2018; Parr and Waller, 2006). For a long time, the literature was limited to descriptions of facial expressions in apes, illustrated by drawings or pictures (cf. van Hooff, 1971). Similarities between species were assumed on the basis of these descriptions and the emotional setting in which the facial expression occurred. A weakness of static material is that it does not reflect the dynamics of real expressions. A more elaborate way to study facial expressions across species involves the identification of the facial muscles involved, which can be done with the Facial Action Coding System (FACS). FACS has been developed for humans (Ekman et al., 2002), chimpanzees (Vick et al., 2007), lowland gorillas (Dobson, 2009) and orangutans (Caeiro et al., 2013) as well as other animals, including dogs and horses (Waller et al., 2020). At the basis of the FACS system are specific muscles that can be used independently, so-called Action Units (AUs) that refer to specific muscles innervated by the facial nerve (Caeiro et al., 2013). Activation of some AUs, for example the brow lowering produced by the *Corrugator* muscle, occur in a number of negative emotional expressions. Other muscle actions are uniquely related to one specific emotion. For example, the narrowing and tightening of the red margins of the lips in humans, produced by the *orbicularis oris pars medialis*, is evident only in anger. Often the combination of more than one AU is necessary to clearly signal a single emotion (Ekman, 1992).

Apart from the muscles, other characteristics make muscle contractions more or less visible. For instance, in contrast to great apes, humans have less facial hair (especially females), larger eyes, contrasting eye-white, pronounced eyebrows and red-coloured lips, all of which makes their facial expressions more obvious (Kret, 2015). Presumably, humans' large eyes, red lips, and furless skin evolved to promote communication (Schmidt and Cohn, 2001). Facial features may enhance the visibility of facial expressions in apes. This visibility may be enhanced in bonobos by the red color of the inner lips that contrasts with their black faces (de Waal, 1988), in chimpanzees by the distinct light and pink color of their teeth and gums (Vick et al., 2007) and in immature orangutans by the light facial colour of infants (Caeiro et al., 2013). Therefore, in great apes too, some specific facial characteristics may have evolved to enhance communication. In their seminal paper, Kobayashi and Kohshima (1997) demonstrated that of all primates, humans have the most prominent eye whites. Recent empirical evidence however shows that, in contrast to what has been commonly assumed since that work, great apes have as much contrast in their eyes as humans. Chimpanzees' sometimes bright amber or even orange irises stand out clearly from their dark sclera and bonobos' light sclera contrasts greatly with their dark irises. The eye-catching eye-coloration of humans, bonobo's and chimpanzees might have evolved for communicative purposes (Perea-García et al., 2019).

In one of the first, and certainly most widely known experimental attempts to categorize human emotions, six basic expressions of emotion were identified, namely, disgust, fear, happiness, anger, sadness, and surprise. These emotion categories supposedly evolved following challenges that our ancestors faced (Ekman and Friesen, 1976). In later work, other expressions have been added to this list including contempt, amusement, relief, wonder, ecstasy, naches (feeling of a parent/caregiver when witnessing the achievement of their child), fiero (felt when being confronted with a challenge (Ekman and Cordaro, 2011)) and lust (Panksepp and Watt, 2011). To avoid terminological differences, we adopt the view that emotional expressions fall into families or groups. Building upon theoretical models of basic emotions, we consolidated emotions that seem to represent a similar state, despite different labels (Izard, 2011; Levenson, 2011; Panksepp and Watt, 2011). Where possible, the facial muscles identified in FACS will be used to describe and compare human facial expressions with expressions in apes. In the great apes, this has systematically been done in chimpanzees (Parr et al., 2007) and information on the AUs in some facial expressions is available for orangutans (Pritsch et al., 2017). Therefore, most of the comparisons with gorilla's and bonobo's or different types of expressions depend on descriptive studies. Note that not all emotional expressions have been mapped out with the FACS system in humans either.

In the current article and the following eight sections specifically, we focus on facial expressions across humans and great apes. As mentioned before, while the majority of the human literature on emotional expressions focuses on perception and on posed expressions, surprisingly little is known about genuine facial expressions and their function. In the following section, where possible, we will distinguish between expressions that are non-intentional and intentional, which for the purposes of this review refers to expressions that are used to strategically manipulate social situations (Meshulam et al., 2012).

1.2. Disgust and aversion

In humans, disgust is expressed by lowering the brows (AU4), wrinkling the nose (AU9), raising the upper lip (AU10), dropping the jaw (AU26) and protruding the tongue (AU19) (Ekman and Friesen, 1975). Despite the involvement of these multiple AUs, one muscle stands out particularly. This is the *levator labii superioris*, which, by activation, raises the nares, pulls up the infraorbital triangle and wrinkles the sides of the nose. This muscle action does not occur systematically in any other expression (Ekman, 1992). Aversion is shown by all great ape species and by humans alike, in reaction to a bitter taste on the tongue (as shown in infants: Berridge, 2000; Steiner, 2001). The infants showed aversive gapes, head shakes, all with the purpose to eliminate the noxious stimulus from the mouth. In extreme forms, the disgust expression may be accompanied by the gag reflex or throwing up. This facial expression may be non-intentional, representing an honest signal of a direct internal state. In humans, the expression of disgust may have evolved as an intentional signal for others to punish antisocial behaviour (moral disgust: Chapman et al., 2009; Haidt et al., 1997). In a social context, the expression of disgust often signals avoidance behaviour, which mediates social status (Curtis et al., 2011). Further research on the link between moral disgust and disgust related to toxicity and disease showed that the earlier mentioned *levator labii* muscle was similarity activated when exposed to an unpleasant taste, photographs of pollutants, or unfair treatment in an economic game (Chapman et al., 2009). These results suggest that immorality provokes the same disgust expression as a bad taste or smell, which points to their common origin. The cognitive aspect of disgust should also be taken into account. A study showed that people with obsessive-compulsive disorder display greater self-reported disgust, but did not differ in their electrodermal activity or facial electromyographic responses (Whitton et al., 2015). This evidence suggests that the cognitive component greatly contributes to disgust in humans. Whether or to what extent this cognitive aspect impacts disgust expressions is unknown.

Given cross-species differences in cognition, behaviour and ecology, what disgusts a chimpanzee may be different from what disgusts humans, bonobos or orangutans. Köhler (1925/1957) provided details of chimpanzees drinking and licking foul wastewater from a reservoir, smearing themselves with excrement, and engaging in coprophagy. However, he also observed that if chimpanzees stepped in excrement, they frequently used twigs, rags or paper to remove the feces, rather than removing it with their bare hands, suggesting they can experience this emotion. Indeed, a recent experimental study suggests that chimpanzees may sometimes experience a form of disgust. By putting food on feces or other biologically contaminating materials researchers showed that through sight, smell and touch, chimpanzees tended to avoid that food (Sarabian et al., 2017). A presumably shared disgusting taste is that of a bitterness, which plants often have to prevent animals from eating them. Still, taste receptors in mammals are directly related to feeding specializations. Future studies would benefit from using a preliminary assessment before engaging in trials to assess disgust expressions. Unfortunately, the study by Sarabian et al (2017) did not code the facial expressions of the chimpanzees and as far as we know, there is no other work in this direction as it concerns great apes. A similar facial expression called 'the rain face' has recently been described in chimpanzees: "*As soon as a downpour starts, all chimps, young and old, pull an ugly face, pulling their upper lip close to their nose and sticking their lower lip slightly out. Their eyes are semiclosed, their teeth* *visible*" (de Waal, 2019). Like the expression of disgust, the rain face may also, or even primarily, have a protective function, that is, to keep the apes from getting water in their eyes/nose/mouth.

1.3. Fear and anxiety

The expression of fear involves specific combinations of three to six AUs. Humans express this emotion with raised eyebrows (inner brow raise AU1 and outer brow raise AU2), open eyes (upper lid raiser AU5) and an open mouth (lip stretcher AU20, and lip parting AU25) (Ekman et al., 2002). Observers often confuse the expression of fear with surprise (Gosselin and Simard, 1999). Human fear expressions differ from the fear expression in apes that seems limited to the muscles around the mouth. In chimpanzees and bonobos, fear is expressed through bared teeth screams (chimpanzee: AU10 + 12 + 16 + 25 + 27, Parr et al., 2007; bonobo: de Waal, 1988). Chimpanzees also show a bared-teeth yelp and a stretched-pout whimper in submission (van Hooff, 1971). In addition, apes use a silent bared teeth display after aggression and intense settings to show affinity and appeasement (chimpanzee: AU10 + 12 + 25 and AU10 + 12 + 16 + 25: Parr et al., 2007; van Hooff, 1971; bonobo: de Waal, 1988; orangutan: AU10 + 12 + 25, Pritsch et al., 2017).

Another facial expression concerns anxiety or uncertainty. This may seem related to fear, but in chimpanzees it is expressed with a different facial expression, namely whimpering (AU22 in addition to the earlier mentioned AUs 12 and 25) (Parr et al., 2007). No such facial expression has been described in the other great apes.

Research in humans (Marsh et al., 2005) and nonhuman animals alike (Maynard Smith and Price, 1973) demonstrates that fear displays may elicit prosocial responses and approach behaviour and may grade into displays of affiliation including a smile, characterized by contracting the zygomaticus muscle which pulls the corner of the mouth backwards (van Hooff, 1971), which brings us to the next section and group of emotions.

1.4. Affiliation and positive affect

There are multiple facial expressions that fit in the category of 'affiliation and positive affect', each signaling a specific state such as laughter, victory or an affiliative smile. In the section below, we start with the latter and show that there is no such thing as 'just a smile'.

Although smiling is considered an expression of affiliation, it *can* have different meanings, too. One component of the smile, the 'mouth corner up', is shown when tasting something sweet (Steiner et al., 2001). But often, smiles are related to social situations. Research shows that people smile to show subordination (Hecht and LaFrance, 1998), to gain approval (Cashdan, 1998), or to express embarrassment (Goldenthal et al., 1981). Intriguingly, people sometimes smile out of fear or nervousness. Smiling out of embarrassment is a homologue of primate submission displays, because it shares appearances such as withdrawal, often accompanied with a downward glance (Schmidt and Cohn, 2001). Although the smile typically is supposed to receive the label "happy" in psychological lab experiments, humans *use* the smile during greeting; when reassuring others or when communicating a feeling of joy (Kret and Straffon, 2018). For instance, humans may smile when in pain, but not wanting to show that to others and therefore mask their true feeling with this expression. Therefore, people smile to regulate social interactions. This also became clear in a classic experiment. In the experiment, people watched an enjoyable video either alone, with a friend, or with the belief that a friend was viewing the same videotape in another room, while activity of their smiling muscle was assessed with electromyography (Fridlund, 1991). The results showed audience effects whereby smiles were better predicted by social context (more frequently when others were present) than by video content. Importantly, the author reported no relationship between smiling and self-reported happiness. Recently, we obtained similar results in a dating experiment where smiling was not associated with how much they liked their partner, but on the contrary, was associated with politeness or nervousness, without feeling attraction (Prochazkova et al., 2019).

In fact, social smiling is so common that a distinction has been made between the true enjoyment smile, the Duchenne smile, and the social smile, the non-Duchenne smile (Ekman et al., 1990). The Duchenne smile is characterized by activation of the *orbicularis oculi* muscle (AU6), which lifts the cheeks and gathers the skin around the eye and is accompanied by the typical smile produced by the *zygomatic major*, resulting in the apparent oblique stretching of the lip corners (AU 12). The non-Duchenne smile does not narrow expresser's eyes and only includes the stretching and slight opening of the mouth. The majority of the emotion literature makes use of pictures showing people that were asked to smile (i.e. posed). One study compared smiles following this procedure to smiles that were instead spontaneously produced by these actors, in between recording sessions. Results showed that onset and offset speed, amplitude of movement, and offset duration were greater in posed compared to spontaneous smiles (Schmidt et al., 2006).

Researchers have in different ways tried to disentangle genuine from non-authentic smiles and from laughter. Mehu and Dunbar (2008) recorded non-intentional smiles, intentional smiles and laughter during naturalistic group observations that differed in audience composition. The results showed that, when interacting with people of a different age, young men displayed more intentional smiles than laughter as compared to when they were interacting with peers. This supports the hypothesis that humans are able to voluntarily regulate their smile production according to different audiences. Although smiling and laughter may sometimes blur into each other, research in children implies that laughter is associated with play, whereas smiling is associated with different social purposes (Jones and Jones, 1974). A study by Lockard et al. (1977) classified human smiles according to their resemblance to primates' displays where the least intense smiles were similar to a bared-teeth display (front-teeth exposure with sharp mouth corners slightly turned up) and the more intense smiles approximated a play-face expression (open mouth, lower jaw and rounded mouth corners). This study has shown that the most intense forms of laughter and smiling were almost exclusively restricted to social gatherings but did not appear during chance encounters, work meetings or goal-oriented encounters (buying a ticket). The study supports the idea that the human smile originated in the primates' bared-teeth submissive expression and that laughter evolved from the primates' relaxed open-mouth display of play.

The evolutionary origin of the human smile (not laughter) is considered to come from the bared teeth display seen across primates that signals submission or appeasement (van Hooff, 1976). Affiliation and appeasement are expressed in a bared-teeth display in chimpanzees, bonobos and orangutans (Parr et al., 2007, van Hooff, 1971; de Waal, 1988; Pritsch et al., 2017). In some (egalitarian) species this expression has become a mutual greeting signal (Preuschoft and van Hooff, 1997). This indicates a positive sensation and may be non-intentional. However, this AU is also part of the play face that is generally linked to a positively valenced contexts. Indeed, in some instances, the smile and play face grade into one another.

The evolutionary origin of human laughter is considered to be derived from the play face (van Hooff, 1976). Humans and great apes show the play face or relaxed open-mouth face, although with slightly different versions, shown by the specific AUs that are involved (chimpanzee: characterized by AU12 + 25 + 26 or by AU12 + 25 + 27, Parr et al., 2007; bonobo: play face with bared lower teeth and full play face with also bared upper teeth, Palagi, 2006; Demuru et al., 2015; orangutan: AU10 + AU12 + AU25 + AU27, Pritsch et al., 2017; lowland gorilla: play face AU16 + 25 + 26 and full play face AU10 + 16 + 25 + 26; cf. Pritsch et al., 2017). Corresponding movements have been found in human laughter research identified by the raising of the cheeks (AU6), raising of the upper lips (AU10), pulling of the lip corners upwards and backwards (AU12), pressing down of the lower lips (AU16), protrusion of the tongue (AU19), stretching of the lips (AU20), opening of the lips (AU25), dropping of the jaw (AU26), and stretching of the jaw (AU27), and relaxing of the lower lip (AD160) (Matsumoto et al., 2008; Ruch and Ekman, 2001). One commonality between the Duchenne smile and the play face is that the eyes are narrowed.

In great apes, the play face is often paired with panting or laughter and observed in the context of play (Davila-Ross et al., 2015). Play typically carries a positive emotional element (although this may vary depending on the play context and intensity), is more often displayed by immature animals rather than adults and differs from non-playful responses in having no relatively immediate biological result (Beach, 1965; chimpanzees and bonobos: Palagi and Cordoni, 2012). The play face includes a particular kind of open-mouthed gesture, a slack but exaggerated gait, and a marked 'galumphing' in movement (Van Hooff, 1971, 1972).

In humans, lust is considered a profound emotion of strong sexual desire which can be expressed in multiple ways. Descriptive work shows that while women tend to gaze to the right of men they report as being attracted to, men gaze directly at the woman whom they report being attracted to (Grammer, 1990). Ethologist Eibl-Eibesfeldt (1989) has described flirtatious tongue flicking in Yanomami women as a sign of lust, and observed similar behaviour in central European women. Gonzaga et al. (2001) described four expressions of lust: licking, puckering, and touching the lips as well as protruding the tongue. In this work, Gonzaga et al. (2006) found that affiliation cues, including affirmative head nods, Duchenne smiles, positive gesturing with the hands, and leaning toward the partner, correlated with self-reports of love but not desire, while a set of sexual cues (i.e., licking, puckering, touching the lips, tongue protrusions) were rated as desire. Additional cues linked to sexual desire include biting the lips (Givens, 1978) and sucking the lips such that they are rolled into the mouth (Kendon, 1975). A comparison between Asian, Caucasian, and Latino couples during three minute interactions found distinct nonverbal displays but also distinct feeling states, sexual desire and romantic love (Gonzaga et al., 2006).

In humans, the kiss is a sign of affiliation (Eibl-Eibesfeldt, 1989) but is not found in all cultures. Anthropologists believe that kissing can be traced to suckling on the mothers' breast or passing regurgitated food into a baby's mouth (Eibl-Eibesfeldt, 1989). The comparative literature also suggests that human kissing may have a different evolutionary origin than the equivalent behaviours seen in apes, although the two may nevertheless be related. During social greetings, chimpanzees also perform a form of panting on the body of their recipient, which resembles a form 'kissing' (de Waal, 1992). However, while this signal is typically considered as a signal of affiliation and respect towards dominants; unlike human kissing which is associated with socio-positive affiliative interactions, chimpanzee pant-kissing is typically produced primarily during periods of social tension, such as when a subordinate approaches a dominant to appease it or acknowledge its status. However, in such contexts chimpanzee pant-kissing can be performed bi-directionally between the dominant and subordinate, indicative of its affiliative function. In bonobos, the so-called "duck face" (pressing of the lips against each other in a kiss-like expression) is used during affiliative grooming interactions (de Waal, 1988) though typically does not involve physical contact.

During courtships, female gorillas signal sexual arousal with pursed lips (Sarfaty et al., 2012) combined with staring at the male (Hess, 1973), while male mountain gorillas produce a semi-smile (Fossey, 1983, p. 81) characterized by pursed lips with the corners of the mouth backwards and slightly downwards (Hess, 1973). Chimpanzees use the silent pout and a vertical head nod in a sexual context (van Hooff, 1971). The fact that these signals are different suggests that they evolved independently. Human infants also use a pout face to solicit their mother's attention, and a similar facial expression can be found in infant chimpanzees for the same bonding function (Blurton Jones, 1971; van Lawick-Goodall, 1968).

The cultural and species variance in the expression of kissing and sexual arousal speaks against lust being a basic emotion. These differences may relate to the relative importance of facial versus bodily signals of lust. While humans are bipedal, promoting facial displays, apes have quadrupedal locomotion, which may promote bodily displays. Alternatively, these may also be seen as "dialects" since there the shared characteristics of humans with great apes such as the importance of the mouth, may speak for Panksepps' idea of including it in the basic emotion list (Panksepp and Watt, 2011). Similarly, lust can probably be expressed both involuntarily and voluntarily, but further research is needed for firm conclusions.

1.5. Anger and aggression

Humans tend to express anger by frowning and narrowing the eyes (lid tightener, AU7), along with changes in the nostrils, lips, and chin, the brow and brow ridge, both lower and the cheekbones and mouth both raise (AU: $4 + 5 + 7 + 10 + 17 + 22 + 23 + 24$, see Ekman et al., 2002a). In addition, direct eye contact is often observed, which reduces aggressive behaviour (Ellsworth and Carlsmith, 1973). Different studies have shown that humans can intentionally put on an angry face, which has benefits in certain situations. For instance, this expression increases an individual's profits in economic games (Meshulam et al., 2012). A common position is that the anger face is a universal but culturally shaped signal (Matsumoto et al., 2010). From this point of view the angry expression can be decomposed into an arbitrary set of features that we have come to understand as indicators of anger. Yet, a study by Sell et al. (2014) shows that each aspect of the anger face may make the expressor appear physically stronger. Although inducing anger in a laboratory setting is rather difficult, there have been some attempts (e.g. Engebretson et al., 1999). However, as far as we know, there is not a single experimental study that simultaneously measured facial expressions.

Chimpanzees occasionally show bulging lips, indicating attack (van Hooff, 1971), while bonobos show a tense mouth, 'lip press', indicative of retaliative aggressive intent, which may be construed as anger (de Waal, 1988), yet it is not clear how frequently these expressions are being used. For gorillas, no facial expression of anger has been reported, and a description of this expression in orangutans is also lacking. This suggests that great apes do not typically express aggressive intent with a facial expression alone, but likely rely more on vocalisations such as threat barks. As we will elaborate on in the final section of this article, this may be combined with forward movement patterns. Such a multicomponent display may serve as a signal, and a way to impress or intimidate others.

1.6. Surprise

Humans express surprise with an open mouth and raised eyebrows. Ekman and Friesen (2002) proposed that surprise is expressed by specific combinations involving two to four AUs (AU: $1 + 2 + 5 + 25$). These are the raised inner and outer brow, the raised upper eyelid, and the open mouth, which are the same as in fear, with the exceptions of the lowered brow and the stretched lip. In addition, surprise has a lower intensity of the upper eyelid raising. The intensity of the raising of the upper eyelid tends to be subtle in surprise, whereas it can have various intensities in fear (Ekman & Friesen, 2002). As far as we know this expression has not been systematically analysed in people actually experiencing surprise.

In ape species, no separate facial expression has been reported that describes excitement or surprise. An interesting avenue for future research is to record facial expressions following unexpected events. Using looking time paradigms, researchers can decipher whether the outcome of an experiment was indeed unexpected (see for instance Krupenye et al., 2016).

1.7. Sadness and grief

The facial display for sadness is characteristic by the inner brow raiser, brow lowerer and lip corner depressor (AU1 + AU4 + AU15) (Ekman & Friesen, 2002). It has been proposed that emotions are context-bound and promote adaptation when they are endorsed in the situational contexts for which they have evolved (Keltner and Haidt, 1999). For example, the expression of tears in grief may provoke sympathy from others that helps the bereaved to deal with the loss. Hasson (2009) proposed that emotional tears have a signaling function and are not only cues. Practically speaking, there are two inevitable results of tearful crying. First of all, tears diffuse light and blur vision. Furthermore, tears reduce the perception of gaze direction and pupil size by other individuals (Provine et al., 2009). Therefore, tears could handicap the ability to see clearly, and therefore also the ability to accurately respond to dangerous interactions (Hasson, 2009). This increases vulnerability to attacks. While tears may help attackers, at the same time tears can be 'appeasement signals' attracting help from others and reducing defensive actions. By blurring vision, tears weaken effectiveness of both attack and defense. Emotional tears are shed generally in response to emotionally intense social events (Provine et al., 2009). The reason why tears are relatively difficult to control or fake is because they are related to genuine, intense emotional states. Considering that human beings are social animals with strong social relationships, the signaling function of tears to repeal danger is highly plausible (Hasson, 2009). In addition, crying is a behaviour designed to incite help from others. However, the trigger that induced the crying behaviour modulates helping behaviour (Hendriks et al., 2008).

No clear description has been made regarding facial expressions of this emotion in apes, however it is well recognised that apes do not produce tears. Humans produce tears with lacrimal glands located above their eyes that are modulated by sympathethic and parasympathethic nerves. Monkeys and apes do have these glands, which are innervated by parasympathetic nerves. Bora et al. (2009) argue that a possible explanation to why humans produce tears and apes do not is due to reduced number of insular spindle neurons. This seems possible because tearful crying and insular spindle neurons both appeared relatively recently in human evolution. Nevertheless, when observing another ape expressing distress, such as following a social conflict, great apes will sometimes approach to offer friendly contact which functions to reduce the recipient's distress (Clay et al., 2018). In this regard, the suite of emotion expressions signaling distress in great apes appears to be adequate to eliciting necessary behaviours in receivers, such as comforting contact, without the need for further elaborated signals.

1.8. Intentional facial expressions

Ekman et al. (1997) have repeatedly stressed that there is a need to differentiate between non-intentional emotional expressions and intentional facial actions. The fact that people exaggerate, inhibit, fake, and hide their emotions according to social context (Bonanno et al., 2004; Srivastava et al., 2009) suggests that at least some facial expressions have a certain degree of intentionality.

Not much is known about intentional facial expressions in apes. The faces of enjoyment and disgust after sweet and bitter tastes suggest that these specific facial expressions are involuntary (Berridge, 2000). There are some indications that great apes do have control over some facial expressions that signal social intentions. Research in bonobo play faces indicates that they are more often used when the interactant is facing, and thus seeing the other individual (Demuru et al., 2015). In orangutans, when seeing the other, the play faces are more intense (Waller et al., 2015). This suggests that bonobos and orangutans may be able to control the display of this facial expression. The approach, which borrows measures of intentionality from the gesture literature (e.g. Demuru et al., 2015), may be fruitful to determine whether great apes have control over their facial expressions. Moreover, they may be aware of their facial expressions and their effect on others. An anecdote of a gorilla female indicates that while a facial expression is possibly involuntary, the expresser may be aware of it nonetheless, and tries to hide the signal. This specific gorilla female hid a play face behind her hand (Tanner and Byrne, 1993). Similarly, chimpanzee males that had unclear dominance relationships hid their fearful teeth-baring from their opponent by turning away. In addition, in one case a male was seen to push his lips back over his teeth with his fingers and only after he succeeded in this during the third trial did he turn to his opponent (de Waal, 1986). Thus, great apes may be able to control what others notice from their facial expressions. Altogether, apes may know the effect of their facial expressions and may have some control in expressing them, but systematic research on this topic is still needed.

The view that facial expressions are automatic and direct reflections of inner emotional states has been criticized. For example, Waller et al. (2017) propose that facial expressions are indicators of future behavior – but do not necessarily accommodate current affective states. A similar theoretical position has been proposed by Crivelli and Fridlund (2018) who wrote that facial expressions are *"not semantic read-outs of internal states such as emotions or intentions, but flexible tools for social influence. Facial displays are not about us, but about changing the behavior of those around us".* We partly agree with these accounts in the sense that some emotional expressions may serve as functional regulators. Indeed, as we have shown, some emotional expressions can be intentional, for instance, to inform or deceive bystanders, suggesting that they can have a communicative purpose and both the expressor and the observer may be aware of them. At the same time, emotional expressions may reflect inner sates. The fact that facial expressions can be used to influence receiver behaviour does not preclude them from also reflecting internal states. Moreover, many emotion expressions are expressed in isolation, without the presence of conspecifics, which is not consistent with the proposal of Crivelli and Fridlund (2018). From an evolutionary perspective, while a facial expression may be proximately triggered by an internal or external stimulus, it may, ultimately, be under positive selection for its ability to influence others (Tinbergen, 1963). In this respect, facial expressions can have strong effects on receivers, regardless of their intentionality. The main difference being that the less purportedly intentional a facial expression is -i.e. one less prone to audience effects, quicker to trace from the trigger, and beyond the expresser's control, such as pupil dilation- the closer they reflect expresser's affective state.

1.9. Autonomic expressions

In the previous section, we provided examples of facial expressions caused by changes in the activation or deactivation of AUs. However, there is more to facial expressions than the facial muscle actions. Autonomic expressions such as pupil size, blushing and sweating are linked to arousal states and to emotions (De Melo and Gratch, 2009) and potentially perceivable by observers (Kret and De Dreu, 2017; Kret et al., 2014; Kret, 2015; Prochazkova & Kret, 2017), even by young infants (Kelsey et al., 2019; Aktar et al., 2020). These physiological responses reflect autonomic nervous system activity and are non-intentional, yet potentially informative for observers.

In addition to reflections of ambient light, pupil size reflects arousal, which is for instance increased when observing emotional others (Bradley et al., 2008; Kret et al., 2013). Generally, people with large pupils are perceived more positively than people with small pupils (Kret et al., 2015; Kret, 2018; van Breen et al., 2018). Since pupil size is affected by emotions it could be used as an additional measure to distinguish automatic emotional expressions from intentional facial actions. It must be noted though, that a strong mood-induction manipulation during which pupil size is being measured, is currently lacking from the literature. Again, most research focused on emotion perception rather than on what happens in the body during the production of an emotion.

Facial heat is another autonomic signal that gives insight into genuine emotions and can be perceived by others. Individuals' skin gets perfused with oxygenated blood when they experience a strong emotion and is non-intentional (Drummond and Bailey, 2013; Drummond and Lazaroo, 2012). Depending on the social situation, it may signal shyness and embarrassment, or anger and aggression (Dijk et al., 2009b, 2009a; Shearn et al., 1990). The evolutionary reasons for blushing are not well understood, but it has been shown that it reflects people's concern with how they are regarded by others; embarrassing, anxious or low self-esteem (Leary and Meadows, 1991). Blushing is related to self-focused attention and observed, for instance, in people who worry about how they come across (Lanzetta et al., 1982). Kim et al. (2012) used infrared thermography to measure changes in the facial temperature of people who scored high or low on self-focused attention. The results showed that people who score high on self-focused attention increased their facial skin temperature more than the low self-focused group, and also showed longer recovery from blushing episodes. Thermal imaging techniques have been proven to be effective in deception detection in mock-crime scenarios (Pavlidis et al., 2000). These results provide valuable information by showing that self-awareness plays a role in emotional expressions.

Thermal imaging also seems a useful tool for measuring emotion states in great apes. In one experiment, chimpanzees were tested in three conditions in which they were presented with playback sounds or videos of fighting conspecifics. The nasal temperature of chimpanzees dropped significantly when exposed to this emotional material as compared to a control condition (Kano et al., 2016). Another study used this novel technology to study the effect of positive and negative emotions in different monkeys and two Western lowland gorillas by focusing on four facial areas (the peri-orbital area, the nose bridge, the nose tip, and the upper lip). Monkeys and apes were filmed during positive interactions with toys and during tickling and for negative emotions during food delay and teasing. In the positive condition, the results indicated a drop in the nose tip temperature and a tendency of an increase in the periorbital temperature. For the combined food delay and teasing condition, the results showed an increase in the upper lip temperature (Chotard et al., 2018). Whether these changes can be perceived by conspecifics is unknown.

These findings are important as they suggest that distinctive physiological reactions are connected with a primordial primate emotion system. Further studies are needed to confirm this. Also, as far as we know, blushing has never been investigated in great apes and it would be possible to do so using this technique if researchers manage to induce embarrassment. However, self-awareness implied for feelings of shame and embarrassment may be beyond what we might expect for great apes.

1.10. Conclusion about facial expressions

In previous sections we showed that emotions are expressed through different communication compartments, namely, facial muscle movements and physiological reflections on someone's face. During a social interaction, emotions are likely to be expressed through the interaction between these channels (Kret, 2015). Altogether, there are a number of facial expressions related to aversion, fear, affiliation and play which appear to be shared by both humans and great apes. Other facial expressions appear to be derived in our own species, including those associated with emotions of lust, anger and frustration. Some emotions may be linked to a facial expression in only one species. This was found for excitement and anxiety. This indicates that not all emotional expressions are conserved. Some emotional expressions may be unique for a certain species. For instance, crying or blushing has thus far only been observed in humans. Non-invasive physiological techniques such as thermal imaging and pupillometry provide a promising avenue to investigate affective responses across species. By adding information from these alternative physiological sources, in the close future we may be able to compare emotional expressions between species with higher accuracy, as we will no more be dependent on facial muscle movements alone.

2. Bodily expressions

2.1. Bodily expressions of emotion in humans and great apes

Compared to the facial modality, but in line with vocalizations, bodily expressions can be perceived from great distance. The advantage over vocalizations is that individuals can choose to signal a silent message to a specific onlooker without informing other group members or predators. In bodily expressions, orientation and movement can be part of the expression and these parameters play a greater role than in facial expressions and vocalizations.

The literature in human psychology that addresses bodily expressions (also known as 'body language') focuses mostly on *perception*, leaving the topic of their *production* underrepresented. William James (1932) conducted the first experiments on body posture. Although he did not sample naturalistic postures in real emotional situations, he took a bottom-up approach by photographing a mannequin in 347 positions, without instructing her to express emotions. An instruction-free approach is important, and lacking in most recent studies, which is a limitation, as instructions may reduce the natural variance in expressions, yielding exaggerated or stereotyped expressions. Moreover, what people think their body posture should look like in a certain emotional situation might be different from what it actually would look like, and may be colored by cultural norms. In the study, participants were asked to characterize what the posture signified and what attitude was expressed. Next, the position of the head, trunk, feet, knees and arms were quantified. The principal determinant was the position of the arms, and the hands in particular. Other early experimental studies using hypnotic techniques to induce emotions have shown that some are accompanied by specific postures (e.g., Gidro-Frank and Bull, 1950; Bull and Gidro-Frank, 1950). Apart from these scientific and perhaps somewhat semi-scientific attempts to analyze body language, bodily expressions are widely applied in arts such as in paintings, sculptures, theater and dance. Dance composers use movement quality descriptors such as speed, smoothness, tension, and force to quantify movements (e.g., Labanotation technique: Hutchinson, 1961; Laban 1956, 1975). As far as we know, scientific studies using standardized emotion induction techniques (e.g. the Trier Social Stress Test (Kirschbaum et al., 1993), have not systematically analyzed participants' body language meanwhile. What has been done mainly, is the analysis of *actors*' body language while imagining themselves being in an emotional situation.

In the literature on the production of emotional body language, authors typically describe the postures or movements of professional actors portraying specific emotions, sometimes in a scenario-based interaction setting coached by a professional theater director (as in Dael et al., 2012). Ignoring fingers and toes, and treating the spinal column as three separate joints at the neck, chest and abdomen, there are fifteen major joints in the human skeleton with a total of twenty-nine degrees of freedom (ankles, knees, elbows and the chest are monaxial, wrists are biaxial, and shoulders, hips and the head/neck and abdomen 'joints' are triaxial) (Coulson, 2004). Apart from measuring the angle of, for instance, the upper arm at the joint of the shoulder, motor variables are also obtained from the *moving* body. By attaching physiological instruments to the muscles (e.g., electromyography, accelerometer), these systems provide accurate indicators of motoric movement (e.g., Coombes et al., 2007; Huis in 't Veld et al., 2014; van Boxtel & de Gelder, 2014). Motion tracking is another example of a technique providing objective measures of body movement, for example gait (Omlor and Giese, 2006), and emotional arm movements (Pollick et al., 2001). Finally, using a body-sway platform, it has been demonstrated that highly anxious people freeze when looking at an angry other (Roelofs et al., 2010). All these techniques are typically used in controlled laboratory settings in humans, are obtrusive, and limit behavioral freedom. Based on acted expressions, several methods have been developed to code movements. For instance, the Body Action and Posture coding system provides a time-aligned micro description of body movement on an anatomical level (different articulations of body parts), a form level (direction and orientation of movement), and a functional level (communicative and self-regulatory functions) (Dael et al., 2012).

Taking a different methodological approach, the field of biology provides descriptions of bodily expressions of emotion and how they are produced in naturalistic contexts. Typically, behavioural observations are coded with help of ethograms. Darwin's work (1872) provides the earliest and still one of the best examples of the literature on body expressions in humans and other animals. Two important differences between the bodies of humans and apes is the bipedalism of the former, and the hairiness of the latter. These differences have natural consequences for emotional expressions. The current section aims to discuss how emotions are being expressed by the body in humans and great apes and, if known, whether these expressions are under intentional control, under partial control or fully automatic. When considered relevant, certain gestures are covered as well. The remaining of this section is divided into subsections, each addressing one emotion type.

2.2. Disgust and aversion

Darwin (1872) described two emotional expressions fitting into the category 'disgust/ aversion'. Specifically, he defined disgust as "*Gestures as if to push away or to guard oneself, spitting, arms pressed close to the sides, shoulders raised as when horror is experienced"* (pp. 257, 260). For contempt, he had the following description: "*Turning away of the whole body, snapping one's fingers"* (pp. 254–256). Wallbott (1998) employed a slightly different description of a disgust expression. According to his report, *"moving the shoulders forward, the head downward and crossing the arms in front of the body*" are characteristics of this emotion. This discrepancy illustrates that emotions are not expressed in one singular way through the bodily channel. Because of all the bodily joints, the variance in expression forms is much richer compared to the facial modality, as we will also demonstrate further in the following sections.

Disgust and aversion are emotions with strong sensations in the body, yet most experimental studies on bodily expressions in humans exclude these categories. An early study investigated the perception of a range of emotions or physical states from dynamic point-light displays (consisting of lights that were positioned on twelve joints) of two female actors. The movements ranged from clear emotional states including the aversive category contempt, to drunkenness or dancing and much in between. Using a six alternative forced choice methodology, agreement rates ranged between 71% for fear and contempt to 96% for happiness (Walk and Homan, 1984). Intriguingly, the study did not describe *how* the movement patterns looked like or how the two actors were instructed to perform them. Instead of point light displays, another study used a small wooden doll (of the type that is typically used by painters as a model of the human body) to investigate the perception of the common six basic expressions of emotion from body posture. This study marked joint rotations and weight transfer values for each of the emotion categories. In the disgust category, the weight transfer was backwards, which was driven by the chest and head which were tilted backwards (avoidance), the arms reached forward and the abdomen twisted to one side. Again, on the basis of what exactly these parameters were chosen remains unclear. The results showed that participants were equally likely to categorize disgust postures as fear as disgust. In fact, many participants never correctly identified disgust (Coulson, 2004).

There are a couple of other emotion perception studies that included emotions from this category, but describing these in detail is beyond the scope of this review (for a review, see de Gelder et al., 2010); for a comparison between humans and chimpanzees, see Kret et al. (2018). An overall finding is that accuracy rates of disgust are low, especially when movement parameters are excluded (e.g., in the case of photographic stimulus materials). There may be no static body posture for disgust other than the act of retching. Disgust may therefore be primarily communicated through the face, although further research is needed to determine whether certain dynamic features of the body also contribute. Perhaps the body and facial expressions must be combined to have a more precise and less confounding representation of disgust. Another possibility is that, given the low recognition rates, this emotion is difficult to act, possibly because people have only little intentional control over it. Studies investigating the human body when people are truly experiencing disgust are lacking in the literature but needed.

As far as we know, body expressions of disgust or contempt have not been systematically investigated in great apes. In a survey provided to ape experts, short anecdotes have been given about this emotion (Case et al., 2019). For example: "*in one instance several individuals poked at and then jumped back from a rotten pumpkin"* (western lowland gorillas in captivity). "*In a few instances, I observed individuals put feces to their faces and quickly pull back their upper lip and quickly put down or throw the feces away from them. Additionally, they would wipe their hand on the wall/floor directly after*" (bonobos in captivity). "*I saw an adult male step in feces and then pick up a stick to wipe it off his foot. Usually, though, I see the chimps vigorously shaking a body part until the offending waste is shaken off.*" "*Chimps will sniff at unfamiliar objects, including food and feces. When there is an unpleasant smell, they pull away in the way we would. I've never seen extreme disgust though - no gagging behavior, for example*" (common chimpanzees in captivity). Anecdotally, author MK also observed similar behaviour in a captive chimpanzee performing a computerized task. The alpha male Akira was rewarded with a piece of apple via an automated feeder after a correct trial. One day the reward was perceived as unpleasant, seemingly because the alpha's finger had a bad odor. After several bad experiences where he picked up the apple, brought it to his mouth and then noticed the smell after sniffing, he switched hands. None of these anecdotes describe how this putative emotion state of disgust is expressed via the body but from the above descriptions it seems that like humans, apes avoid the trigger that elicited disgust.

It is possible that we need to conclude that there is no clear bodily expression of disgust in either humans or apes and that different disgust-inducing contexts yield different actions. Clearly, more research is needed to verify this presumption.

2.3. Fear and anxiety

One overarching feature of the expression of fear and anxiety is that individuals experiencing these emotions tend to make themselves small and withdraw from the trigger (the latter being a commonality with disgust). Crouching has the effect of communicating subordinate status without provoking an aggressive encounter. Indeed, subordination displays appear non-threatening as they make the organism appear smaller, weaker and juvenile (Eibl-Eibesfeldt, 1989). This behaviour may have evolved from generalized concealment, flight-intention, or a self-protective posture, but could also connote a reluctance to attack by reducing the perceived body size (Weisfeld and Beresford, 1982). The latter relates to Darwin's earlier-mentioned point about opposite emotions being expressed in opposing ways ('dominance-large', which is the focus of the next section, and 'subordinance-small'). A common tendency or even ritualized custom is that of subordinate humans abasing themselves before their superiors with lowered head and slumped shoulders (van Lawick-Goodall, 1968; Maclay and Knipe, 1972; Eibl-Eibesfeldt, 2017). Eibl-Eibesfeldt (2017) observed that in human children, the loser of a staring contest typically lowered the head, which inhibited aggression and often elicited comforting, friendly behaviour in the winner. It has also been demonstrated that the combination of head bow and shoulder slump, as well as supination and kneeling, effectively inhibited further attack in children (Ginsburg, 1980).

Research has shown that individuals sometimes freeze when facing an imminent threat (for instance, Roelofs et al., 2010). Freezing usually precedes the fight or flight reaction when a sudden threat appears because it is a more rapid response (with fight or flight being driven by a neuro-hormonal response) and reduces movement to reduce detection probability, making it highly adaptive. Freezing is characterized by immobility of the body and heart rate deceleration, but richer descriptions of the posture are lacking in the literature. Posed bodily expressions of fear are generally recognized well; in a study where student actors posed four different emotions, the accuracy rate for fear was 93% on average (De Gelder and Van den Stock, 2011). This shows that it is possible to act this expression. The fact that these expressions are modulated by context, have clear effects on observers and can be acted convincingly, shows that the expression can, but does not have to be, intentional.

In chimpanzees, submission is expressed through crouching, flinching, shrinking and parrying (van Hooff, 1971). Within a chimpanzee community, rank is important for individuals and there are numerous ways of displaying it. Dominant males attempt to make themselves bigger (which will be discussed in the next section), especially when subordinates approach with submissive gestures. The dominant may literally step over the subordinate who covers his head after bowing several times first. A female may shove her genitals into his face as a sign of submission (Vannelli, 2015). Another expression that is frequently described in the primatology literature is scratching. Scratching is commonly associated with the presence of psychological and physiological stress (Maestripieri et al., 1992; Schino et al., 1991; Troisi, 1999) and is contagious (Laméris et al., 2020).

2.4. *Affiliation and positive affect*

"*Joy, when intense, leads to various purposeless movements-to dancing about, clapping the hands, stamping, etc., and to loud laughter*" (Darwin, 1872, p. 195).

In humans, laughter is typically observed during play and when something unexpected happens. This can be during tickling, but also after an unexpected outcome of a joke. A characteristic of laughter is that the muscles relax and individuals lose control over them, sometimes even the one that controls the bladder. A parallel can be made here with crying, where individuals also have little control over their bodies and where some muscles relax and others tense. Joy or happiness can be acted with the body, but this is more difficult than producing a smile on command. In the earlier described BEAST body database, this expression was recognized for 85%, which is about 10% lower than the other three emotional body categories in that study. The expressions happiness and anger were oftentimes confused (de Gelder and van den Stock, 2011). It must be noted though, that in most emotion perception studies, the category happiness equals 'victory', which is a different emotion than the one that elicits laughter and where the muscles are tense rather than relaxed.

In apes, playful intentions are especially visible in their movement patterns. In chimpanzees this can involve play chase, gymnastics, grasping, poking and gnaw-wrestling (van Hooff, 1971). When wrestling and tickling each other, they show similar bodily movements as humans, where the muscles also relax and where control is hard.

In the literature, it is hard to find a bodily equivalent of the affiliative smile. The closest description comes from an analysis of dance movements. The study showed that when playing a warm or friendly character, ballet dancers tend to take relatively rounded postures (Aronoff et al., 1992).

Another expression of a positive emotion is that of lust or sexual attraction. During courtship behavior individuals try to enhance their physical attributes. Stereotypically this means that males present themselves as masculine and dominant, and females as feminine and submissive. Gender specific differences in non-verbal behaviour have been identified between romantically interested men and women Grammer (1990). For example, when a woman showed interest in a man, she would tilt her head, and in doing so expose her neck, which is a weak spot of the body. Also the presenting of the behind during dance or walking movements attracts males' attention to the vulnerable parts. Therefore, this behaviour is thought to signal both sexual interest and submission. In contrast, an interested man would display more dominant behaviours, such as leaning forward into the intimate space of the woman or putting his arms behind his neck. The man would thereby appear larger and more dominant (i.e., the so-called 'head akimbo'). When the woman averted her gaze, the interested man would follow her head direction and thus by doing so, mimic her. Another study found that open body postures predicted higher dating success, especially for men. It is thought that open postures display dominance and higher status (Vacharkulksemsuk et al., 2016). One way of 'opening' the body, is by folding the hands behind the head, presenting the armpits. This is a posture one can find in fashion magazines a lot, but has also been described and depicted in a bonobo (Pollick and de Waal, 2007). Chimpanzee females present their hindquarters (van Hooff, 1971). Gorilla females invite the male by taking a tense stance, while staring at the males with pressed lips Hess, 1973; Sarfaty et al., 2012), holding out their hand or presenting their hindquarters (Hess, 1973). Paralleling a vertebrate-wide plan, human courtship expressivity in general relies on nonverbal signs of submissiveness and affiliation. The adoption of a submissive pose enables a person to convey an engaging, non-threatening image that triggers the approach of potential mates (Givens, 1978). Chimpanzees express excitement through the head nod that also indicates lust (van Hooff, 1971). This latter emotion state also often involves presenting genitals.

2.5. *Anger and aggression*

Dominance is an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation (Drews, 1993). It is important to note that there can be no dominance without another individual, which makes it different from say, an expression of fear, which can be induced by a non-social trigger in the environment. When in states of aggressive dominance, individuals make themselves as physically big as possible (Darwin, 1872). Men especially, stand with their legs further apart and spread them when they sit. Women occupy less space: they neither stand with legs spreads, sit with their thighs opened, nor do they spread their arms while sitting (Eibl-Eibesfeldt, 1989).

Pride, a subtly expressed self-conscious human emotion, is reflected in a particular movement pattern and set of body configurations that is shared with the expression of dominance, anger and aggression. Specifically, this expression includes the head that is tilted slightly back, an expanded posture, and arms akimbo with hands on hips (Tracy and Robins, 2004). In Wallbotts examination (1998) of this emotion, actors expressed pride with their arms crossed in front of their chest, making the biceps stand out. By responding to success with behaviors that expand the body, individuals advertise their accomplishment, to ensure their continued status and acceptance within their social group. The pride expression meets one of the central criteria for functional universality, that is, a psychological entity that evolved to serve a particular adaptive function. This has been demonstrated in a study showing that it is displayed similarly across cultures in the same contexts and situations, even by the blind (Tracy & Matsumoto, 2008).

As mentioned earlier, anger shares commonalities with the expression of pride. Humans are capable of acting anger by adjusting their body posture. Generally, these postures are comparably better recognized than the expression of fear (de Gelder and van den Stock, 2011). In a study, the expressive postures of ballet dancers were analyzed. Researchers found that angular postures tended to be adopted when playing the role of a threatening character (Aronoff et al., 1992). When it comes to the expression of victory, things get fuzzier. In the expression of victory, the arms play an important role, and are held high up in the air. In humans, this expression can often be seen in sports contests. In the BEAST expression set, this expression gets the label “happy” and is not surprisingly often mixed with the category “anger” (De Gelder and Van den Stock, 2011).

“A young female chimpanzee, in a violent passion, presented a curious semblance to a child in the same state. She screamed loudly with wide open mouth, the lips being retracted so that the teeth were fully exposed. She threw her arms wildly about, sometimes clasping them over her head. She rolled on the ground, sometimes on her back, sometimes her belly, and bit everything within reach.” (Darwin, 1872, page 140). What Darwin describes here is a tantrum most parents of toddlers will recognize, but, in humans, is a behaviour that disappears over the course of typical development. With the stretching of the arms, an individual makes himself tall and visible. But the lying on the floor shows that, although triggered by anger or frustration, this is not a dominant posture and different, for example, from the way human adults express anger, that is, by frontal body lean or movements, muscle tension, and the clenching of the fists (Dael et al., 2011). This example illustrates that it is not always trivial to categorize emotional expressions and that they often represent mixed feelings.

During chimpanzee dominance displays, piloerection or bristling of hairs is often observed. This reflexive response of the sympathetic nervous system is seen in reaction to cold, shock, or fright but is also part of threat or agonistic display. Chimpanzees stand up straight and sometimes walk bipedally, they may sway-walk, show arm-sways, stamp and stamp-trot (van Hooff, 1971). Dominant primates are frequently described as exhibiting relaxed, expansive movements, and subordinates as showing attenuated, inhibited movements (Reynolds and Reynolds, 1965). In display, gorillas have been described to strut (Schaller, 1965) and chimpanzees to swag (van Lawick-Goodalt, 1968). Clear parallels can be found in studies with humans. Dominant adult humans appear more relaxed than subordinates (Mehrabian, 1968). In a longitudinal study, boys who had been ranked by peers as "'tough" or dominant in agonistic encounters, in early grade school were observed to have erect posture in high school. Further, high school students who were judged by peers as successful by group standards tended to have erect posture. Finally, erectness of posture was related to performance on a college examination, with students’ posture changing in erectness upon their receiving their grade (Weisfeld and Beresford, 1982).

These largely similar results in humans and apes are consistent with the hypothesis that human competition for social success is based upon a biological capacity for dominance hierarchy. That said, people lack the kind of structures that many other primates use in display. Although the structures used in display may differ from species to species, it is remarkable that man has no erecting hair, colored skin, callosities, or dramatic actions of ears or scalp (Washburn and Hamburg, 968, p. 474). The kinds of gesture that communicate threat in the nonhuman primates have been shifted to the face (Kobayashi and Kohshima, 1997), the hands (freed by bipedalism and made important by tools), and to language. Strength is important but not enough for dominance. Strategies such as deception, bluffing and the formation of coalitions can overcome it (Vannelli, 2015). In humans, dominant postures are often accentuated with clothing, which can be a form of bluffing (Burgoon and Dunbar, 2006).

2.6. Surprise

Similar to disgust body expressions, in the human literature, the production of the expression of surprise has received little attention. Perception studies show that recognition rates tend to be relatively low (de Gelder et al., 2010). There is no explicit research on this emotion in apes, apart from anecdotes from writings of de Waal and Goodall.

2.7. Sadness and grief

Darwin noted that *“the appearance of dejection in young orangs and chimpanzees, when out of health, is as plain and almost as pathetic as in the case of our own children. This state of mind and body is shown by their listless movements, fallen countenances, dull eyes, and changed complexion”* (Darwin, 1872, page 136). Further on in his book, he writes the following: *“Persons suffering from excessive grief often seek relief by violent and almost frantic movements. But when their suffering is somewhat more mitigated, yet prolonged, they no longer wish for action, but remain motionless and passive, or may occasionally rock themselves to and fro. The muscles become flaccid and the head hangs”* (page 176). This rich description is consistent with experimental work showing that individuals in dysphoric mood move differently than those in a positive mood. Using a motion capture system, a study found that patients suffering from major depression or undergraduates who had listened to sad music had a reduced walking speed, arm swing, and vertical head movements compared to matched controls or students who had listened to positive music. Moreover, depressed and sad walkers displayed larger lateral swaying movements of the upper body and a more slumped posture (Michalak et al., 2009). In another study, a pianist was asked to play the same excerpt with different emotionally expressive intentions. Results showed that this especially influenced the velocity of head movements, which were slower when the pianist was trying to make the excerpt sound sad (Castellano et al., 2008).

Changes in a person’s breathing pattern might also be signs of emotion and may be visible to observers. Sighing, for example, is something people do almost every day, but this behavior has hardly ever been investigated in the psychological, and let alone the primatology literature. People tend to associate sighing mainly with negative, low-intensity and deactivated emotional states (Teigen, 2008). That study further revealed that observed sighs are primarily perceived as signs of sadness, whereas own sighs are more often believed to express a state of “giving up”.

There is no systematic analysis of sad body expressions in apes. However, a chimpanzee that lost its mother has been described to show less locomotion and a slumped posture (Goodall, 1986), suggesting a parallel in how this emotion is expressed in humans.

2.8. Autonomic expressions

It is well known that emotions alter physiological activity, for example inducing a higher state of arousal. This, in turn is related to changes in heart rate, breathing, and may also induce bodily changes that *can* be perceived by others such as sweat, goosebumps or the coloration of the skin resulting from the widened diameter of the blood vessels (Cacioppo et al., 2007). For example, many people are nervous while giving a speech to an audience. While some get red stains in the neck, others may get dark circles under their armpits on their shirt (De Melo, and Gratch, 2009). Extreme, high arousal emotion states such as laughter or fear can cause the bladder to empty. These responses have thus far not been systematically studied in connection to emotion and it is not known which of these, apart from piloerection, appear in apes.

2.9. Conclusion on body expressions

As is the case for facial expression research in humans, and in stark contrast with great ape research, the study of human body expressions has mostly focused on posed expressions and on perception rather than on production. In general, research on bodily expressions of emotion is also limited when it comes to great apes. For instance, the question whether apes express disgust with their bodies, has not been investigated yet, as is the case for several other emotions.

A consistent finding in human body expression perception studies is that anger, happiness and sadness are most accurately recognized, with surprise and fear somewhat lower, and disgust frequently failing to reach statistically significant levels. In fact, there may be no specific static body posture for disgust other than the act of retching. Disgust may therefore be primarily communicated through the face. Fear and surprise, and to a lesser extent disgust, are emergency responses whose bodily expression may have more to do with velocity and form of movement than postural configuration. The different emotions vary on the level of movement activity, with 'elated joy' and 'hot anger' being high in activity, and 'fear' and 'pride' low (Wallbott, 1998).

Apart from the bodily configuration and movement characteristics, another relevant point is that of viewpoint. Whether an expressor is facing an interaction partner or not, can matter for how it comes across. For instance, if the expressor's head is directed at a social partner, this probably reflects a socially-motivated emotion. In the case of 'hot anger', the targeted individual has to be on guard. The orientation of the head can be compared with eye gaze in facial expressions.

Future research should investigate how posture (including head orientation) and movement contribute collectively or independently to the attribution of emotion. In addition to mapping out the relative roles of posture and movement, research is needed to define its exact temporal pattern, and how these may vary across different emotions in humans and great apes. To that extent, recordings should be made of people experiencing extreme emotions. Reality television programs can actually be useful to that extent. People sign up to be exposed to emotional events, get back in touch with a lost parent, get to face their greatest fear or have to compete for scarce sources on a remote island and do not mind being watched. It may not be impossible to ask their permission to analyze their expressions during these events.

The specific topic of body language within the great-ape literature is scattered and contains gaps, especially when it comes to certain emotions.

3. Vocalisations

3.1. Vocal expressions of emotion in humans and great apes

While the mechanisms underlying primate vocal behaviour remain a source of debate, there nevertheless appear to be notable overlaps in form, function and patterns of production of primate and non-verbal human vocalisations, suggestive of shared evolutionary history. In terms of expression of emotion, non-verbal vocalisations in humans, such as laughter, screaming and crying, show closer links to animal vocalisation expressions than speech (Owren and Bachorowski, 2001; Rendall et al., 2009). For instance, both the acoustic structure and patterns of production of non-intentional human laughter have shown parallels to those produced during play by great apes, as discussed below (Owren and Bachorowski, 2003; Ross et al., 2009). In terms of underlying mechanisms, research is indicative of an evolutionary ancient system for processing such vocalisations, with human participants showing similar neural activation in response to both positive and negative affective animal vocalisations as compared to those from humans (Belin et al., 2007). Moreover, the human capacity to detect emotionality in animal vocalisations is not only restricted to mammalian calls. Filippi et al. (2017) recently showed that human participants could reliably discriminate the emotional intensity of amphibian and reptile vocalisations as well as those from mammals, which in terms of acoustic properties, was associated with higher fundamental frequency and SCG ratios (spectral centre of gravity). The findings are suggestive of an evolutionarily ancient system for processing the emotional content of vertebrate vocalisations.

In the following sections, we review some work that investigates vocal expressions of emotion in humans and great apes. A central question for comparative affective science is whether nonhuman animals, including great apes, are even able to experience and thus consequently express the same array of emotions identified for humans. For instance, can a chimpanzee experience grief, jealousy or pride or is such an assertion a highly anthropomorphized claim? Given the controversy of such a question, and the paucity of research dedicated to addressing it, we conservatively restrict our review to functional affective categories for which there is established empirical evidence in the comparative literature.

Another key question, still extensively debated, is whether primate vocalisations are primarily expressions of the caller's emotional state or whether they also convey referential information about the external world (Owren et al., 2010; Rendall et al., 2009; Seyfarth and Cheney, 2003, 2010). Generally, two views have been contrasted. Historically, the more dominant assumption is that primate vocalisations are essentially read-outs of underlying emotional states rather than providing referential information about the world (e.g. Bickerton, 1990; Marler et al., 1992; Tomasello, 2010; Hammerschmidt and Fischer, 2008). The more contemporary view is that while primate vocalisations are expressions of the signaller's underlying emotional state (unlike truly arbitrary signals used in human language), such vocalisations may also functionally refer to aspects of the external world, such as classes of predators, types of food and social relationships (reviewed in Townsend and Manser, 2013). In this regard, vocal signals may simultaneously convey information about both internal and external states (Seyfarth et al., 2010); something which is discussed further below in Section 3.5.

3.2. Fear and anxiety

There are numerous parallels in how great apes and humans respond to danger and threat using vocal expressions of negative affect. Like most other socially-living animals, great apes produce loud and distinctive alarm calls when encountering predators, a context where the producer is presumably in a fearful or aroused state (Zuberbühler, 2006). Chimpanzees and bonobos produce loud barks known as waa-barks or wieuw-barks during predator encounters (Marler and Tenaza, 1977; de Waal, 1988) as well as softer vocalisations (chimpanzee hoo; bonobo peep), which may be intended for more immediate audiences, discussed further below (Schel et al., 2013; Crockford et al., 2013; 2015; Clay et al., 2015).

The high-amplitude alarm calls of great apes, presumably evolved for long-distance communication, are high in frequency, have sharp onsets, dramatic fluctuations in frequency and amplitude contours, as well as non-linear vocal features; all properties which Rendall et al. (2009) argue have evolved to be aversive to receivers, making them difficult to habituate to (Hammerschmidt et al., 1994; Owren and Rendall, 2001; Rendall et al., 2009). Gorillas produce both barks and hoots in response to alarm, although to date alarm calling in gorillas has received little attention (Salmi et al., 2013). Wild orangutans produce at least four distinct alarm call types, the kiss squeak, grumph, gorkum, and complex call, which they can combine together into vocal sequences as well as modify using auditory-hand gestures (Hardus et al., 2009; Lameira et al., 2015, 2016). A recent study suggested that orangutans may be capable of delayed vocal reference, something which indicates an overlay of cognitive control of these affectively-based vocalisations (Lameira and Call, 2018). In a playback study, wild Sumatran orangutan mothers appeared to suppress alarm calls for up to 20 min until the predator was out of sight, with vocal delay varying as a function of perceived danger for their infant. Four predictions for arousal-based mechanisms were not met, which suggests production of such alarm calls may have been under cognitive control, rather than being purely reflexive.

Intriguingly, chimpanzees and bonobos also produce softer alarm calls during predator encounters, which may be subject to intentional control and intended for specific audiences (Schel et al., 2013; Bermejo and Omedes, 1999; Clay et al., 2015). For example, a recent experimental study revealed that wild chimpanzees produce 'alarm hoo' 'waa bark' vocalisations to intentionally inform naïve receivers about the presence of predators (Schel et al., 2013). Alarm hoos differ acoustically to those produced in other contexts, such a travel; which may reflect differences in underlying affective states but can functionally inform receivers about the eliciting context (Gruber and Zuberbühler, 2013). In bonobos, the acoustic structure of peeps produced during alarm contexts overlapped with those produced in neutral and positive contexts, suggesting that such calls may not be bound to expressing specific affective states and require additional contextual cues in order to be understood.

Compared to great ape alarm calls, humans are more likely to produce a range of fear-based vocalisations in predator contexts, such as screams, whimpers and moans. It is notable that human fear screams also display similar characteristics, with sharp onsets, high frequencies and their noisy (or non-linear) dynamics, properties which are highly aversive to listeners and are known to activate the amygdala, which is involved in danger processing (Arnal et al., 2015). In primates, it has been demonstrated that alarm calls can be effective in deterring predators as well as for preparing receivers to respond appropriately to impending danger (Zuberbühler et al., 1999), something also likely to be the case for humans (Arnal et al., 2015). Recent research has also shown that the acoustic properties of human screams can be reliably detected within noisy environments, something presumably indicative of having evolved in noisy environments, such as dense forests, where there is a strong adaptive pressure to reliably signal danger (Nandwana et al., 2015).

It is worth noting that compared to a rich literature on primate alarm calls recorded under natural conditions, most research on human vocal expressions has been conducted using artificial vocal stimuli produced by actors (e.g. Scott et al., 1997; Sauter and Eimer, 2010). This is despite evidence that suggests that such 'acted' emotional vocalizations are acoustically and neurally distinct from their non-intentional equivalents (Anikin and Lima, 2017; Ackermann et al., 2014; Simonyan, 2014) and can reliably be distinguished as such by receivers (McLellan et al., 2010). In order to understanding the mechanisms underlying the production and perception of vocal expressions of emotion in our own species, future research using naturalistic stimuli is necessary for inclusion, particularly for making informed evolutionary comparisons.

Regardless of the confound in human research of posed versus automatic vocal expressions, converging research highlights relevant overlaps in the production and perception of human screams and cries compared to great ape screams produced in response to social threats, anxiety and distress. Similarly, in human babies cries produced in response to different arousal states show distinct acoustic structures which receivers appear to use as a proxy of the signaler's emotional experience (Kersken, 2012). In chimpanzees and bonobos, victim screams appear to convey a rich array of information about the aggressive encounter, such as about the severity of the attack, the identity of the caller and the social role played within the aggression (victim or aggressor) (Slocombe and Zuberbühler, 2006; Slocombe et al., 2009; Clay et al., 2015). Consistent with an affective explanation, screams produced during more severe aggressive attacks are louder, higher in frequency and noisier in acoustic structure (Slocombe and Zuberbühler, 2006; Clay et al., 2015). Victim screams also differ acoustically to those produced when in the aggressor role, with the latter being more pointed in acoustic form (Slocombe and Zuberbühler, 2006). Victim chimpanzees also appear to be sensitive to audience composition, producing louder and longer screams when individuals equal to or higher in rank to the aggressor are present in the audience (Slocombe and Zuberbühler, 2006), suggestive of strategic call production. In bonobos, acoustic structure is also explained by the psychological property of social expectation, whereby victims receiving aggression that could not have been readily predicted produced screams that were higher in pitch, amplitude and longer in duration (Clay et al., 2015. Again, this finding suggests while such calls are likely an honest signal of caller arousal, call production can also be shaped by a cognitive dimension.

In addition to screams, chimpanzee and bonobos also commonly produce pout moans and whimpers to signal their distress and/or fear (de Waal, 1988; Marler and Tenaza, 1977). These signals commonly produced by juveniles and infants with the context of maternal care, such as requesting contact and or food. Thus, given their association with juvenility, the function of these types of vocalisations appears to express submission, distress and benign intent. While there has thus far been little attention into the production of these calls by mature individuals, research recent research has shown that within the context of maternal requests, bonobo infants regularly combine pout moan vocalisations with specific gestures in order to increase their functional specificity (Genty, 2019). These data suggest that even from a young age, pout-moans may already be under some intentional control, with these vocalisations produced to fulfill certain goals, rather than being purely expressive of internal states.

3.3. Affiliation and positive affect

While social play may have different underlying functions and reflect different motivational states, it nevertheless seems to be the most obvious context in which expressions of affiliation and positive affect can be explored in animals. As with screams, there appear to be notable overlaps in the form and function of laughter in great apes and humans (Ross et al., 2010; Owren, 2007; Gervais and Wilson, 2005; Provine, 2004; Todt and Vettin, 2005; Trivedi and Bachorowski, 2013), suggesting a shared evolutionary history. Ross et al. (2009) examined the acoustic structure of tickle-induced vocalizations from immature orangutans, gorillas, chimpanzees, and bonobos, as compared to those of human infants. Results revealed large spectral overlap in the acoustic structure of human and great ape laughter, however, there were some differences. Compared to great apes, humans produce significantly more voiced sounds and exclusively egressive vocalisations (produced during exhalation), whereas the other great apes produce both egressive and ingressive sounds (exhalation-inhalation phases). These results suggest that although tickling-induced laughter in humans is acoustically distinct from great ape laughter, the differences more likely reflect a gradual evolutionary transition, rather than being novel inventions. In this regard, automatic tickle-induced human laughter most likely derived from egressive vocalisations produced during tickling play in the last common ancestor we share with great apes (Ross et al., 2009).

In terms of function, laughter in great apes (and humans) is associated with the signaling and promotion of social bonding, social tolerance and positive emotion contagion (Scott et al., 2010; Provine, 2004). Nevertheless, while laughter within the play context is typically associated with corresponding positive affect, it may not always be the case. As shown in a recent review of play in dogs (Sommerville et al., 2017), play may serve an array of different functions unrelated to affiliation, including motor development and social cohesion, and can also occur in a range of positive as well as negative contexts, such as in periods of social tension, such as waiting for food and periods of social crowding (Yamanashi et al., 2018; Palagi et al., 2006). As discussed by Adriaense et al. (this issue) a recent review revealed also that a systematic investigation documenting the relationship between positive affect and play remains outstanding (Ahloy-Dallaire et al., 2018). In this regard, care is needed when interpreting the affective basis of play and its functions.

For humans, regardless of its underlying functions, we find evidence of laughter in every human culture; moreover, universal consistency in its acoustic structure (Provine, 2004). Research has also revealed the presence of two kinds of human laughter: *automatic or unintentional* laughter is triggered by external events such as tickling, whereas *intentional* laughter is under active cognitive control (Gervais and Wilson, 2005). As with other intentional emotional signals, intentional human laughter shows distinct acoustic properties compared to non-intentional laughter, reflecting different underlying production systems and a differing evolutionary history (Bryant and Aktipis, 2014; Lavan et al., 2016; McGettigan et al., 2013). Vocal emotion expressions are influenced by the vagal system, which extends to the recurrent laryngeal nerve (Ludlow, 2012). Thus, underlying arousal can directly impact the vocal apparatus, resulting in increased vocal fold tension, subglottal air pressure, and glottal adduction rate, along with possible irregular vibration regimes of vocal fold tissue. Consequently, non-intentional laughter is generally higher in pitch, louder, faster in burst rate and more unvoiced (Bryant et al., 2018).

Consistent with a separate evolutionary histories account of automatic versus intentional laughing, one study revealed that across 21 different cultures in 6 world regions, human participants could reliably distinguish non-intentional (i.e. naturalistic) laughter from volitional laughter (Bryant and Aktipis, 2014). Compared to volitional laughter, non-intentional laughter shows higher values on acoustic correlates of physical arousal, including higher fundamental frequencies, shorter burst duration, a greater ratio of unvoiced to voiced elements and a higher rate of intervoiced intervals (Bryant and Aktipis, 2014; Lavan et al., 2016; Wood et al., 2017).

While yet to be researched in humans, the discovery of food represents another context thought to reflect underlying positive affect in great apes and other primates (Clay et al., 2010). As with a number of other animals and birds, chimpanzees, bonobos and gorillas all produce distinctive vocalisations during the discovery and consumption of food. Chimpanzees produce the ‘rough grunt’ in response to food, a low-amplitude noisy call which shows significant acoustic gradation towards foods of differing perceive quality, something which is meaningful to receivers (Slocombe and Zuberbühler, 2005; Slocombe and Zuberbühler, 2006). Consistent with an arousal based explanation, grunts given to high quality foods are highest in pitch as compared to grunts given to lower quality foods. Nevertheless, chimpanzee food grunts appear to be under some intentional control and learning; they are more likely to be given in response to specific audiences, such as close social partners and dominants (Slocombe et al., 2010), and individuals also appear to be able to modify their acoustic structure in order to converge with those of other group members (Watson et al., 2015). Together, these results highlight their apparent function in signaling and/or promoting social affiliation. Bonobos produce an array of five different call types in response to the discovery of food: barks, peeps, peep-yelps, yelps and grunts (Clay and Zuberbühler, 2009), with variation in sequence structure providing reliable cues to perceive food quality as compared to individual calls. As with chimpanzees, the highest frequency calls within their food call repertoire – barks and peeps - are primarily produced towards highly preferred foods, suggestive that such calls are reliable indicators of internal arousal. Recent research has revealed the presence of acoustically distinctive food calls in gorillas, known as singing or humming (Luef et al., 2016). Such vocalisations seem to play an important role in communicating positive affect and signaling food presence among group members, something which may function to promote social cohesion and affiliative bonds.

3.4. Threat and aggression

As with humans, great apes produce an array of vocalisations to express agonistic intent during aggressive interactions. During mild threats, chimpanzees, bonobos and gorillas all produce grunt vocalisations to signal discontent and aggressive intent, which may be combined with retraction of the teeth, indicative of biting, along with arm raises/flapping and/or body lunges (Marler and Tenaza, 1977; de Waal, 1988; Clay and Zuberbühler, 2011; Salmi et al., 2013). During and following higher intensity aggression, chimpanzees and bonobos often produce shrill bark vocalisations (chimpanzee ‘waa’ bark; bonobo ‘whistle bark’) akin to those produced during predator encounters (Crockford and Boesch, 2003; Fedurek et al., 2015; de Waal, 1988). These barks may be produced by the aggressor but also by the victim in response to the aggression as well as bystanders observing the encounter who produce such barks to signal support (Newton-Fisher, 2006; Wittig et al., 2013). A recent study by Fedurek et al. (2015) revealed that in wild chimpanzees, waa barks served a dual social strategy for victims, serving both to attracting support from allies in the audience as well as to repel their aggressors from further attack by signaling readiness to retaliate. Similar patterns are shown in the production and perception of vocal expressions of anger produced by humans, which also show similar acoustic properties as those observed in great apes (Johnson et al., 1986; Johnstone and Scherer, 2000; Scherer, 2003). In both human and non-human great apes, such vocalisations can provide informative cues to the signaller’s motivational state which can help receivers predict their future behaviours as well as providing cues to underlying social dynamics.

3.5. Affect, reference or both?

A key question when considering great ape vocalisations (or any animal) as compared to the arbitrariness of human language is whether signals given in response to external events are primarily expressions of the caller’s affective state or also convey referential information about the external world (Owren et al., 2010; Rendall et al., 2009; Seyfarth and Cheney, 2003). While extensive discussion of this debate is beyond the scope of this review, briefly dipping into the discussion is relevant when considering the emotional basis of human and animal vocalistions. Thus far, the general assumption has been that, unlike human speech, primate vocalisations are essentially read-outs of underlying emotional states, subject to little to no intentional control or learning (e.g. Bickerton, 1990; Marler et al., 1992; Tomasello, 2010; Hammerschmidt and Fischer, 2008). This reflects neurological and behavioural evidence that their vocal repertoires, as well as patterns in call production, are typically stable across populations (taking into account environmental variation) and show similar patterns in ontogenetic development (Hammerschmidt and Fischer, 2008 but see Crockford et al., 2004). The apparently ‘involuntary’ nature of animal vocalisations has traditionally been contrasted with intentional and referential nature of human speech (Bickerton, 1990); nevertheless, a growing body of research suggests that such conclusions may be inaccurate.

Seminal research in the 1980′s on the alarm calls of vervet monkeys challenged the idea that animal vocalisations are only read-outs of internal states with evidence that alarm calls can functionally refer to different predator classes and trigger specific adaptive responses in receivers (Seyfarth et al., 1980). Since this study, there is growing evidence that a range of animal species, including great apes, can produce distinct vocalizations that convey referential information about events and objects in the world (for a review see Townsend and Manser, 2013). As discussed above, both chimpanzees (*Pan troglodytes*; Slocombe and Zuberbühler, 2005, 2006) and bonobos (*Pan paniscus*; Clay and Zuberbühler, 2009; 2012) produce referential calls during feeding contexts to convey referential information about food quality. The hoos of chimpanzees also have been shown to refer to different behavioural events, such as preparation for travel as compared to rest and alert contexts (Crockford et al., 2018). In this sense, such vocalisations appear to communicate both affective and referential information to receivers.

Although the cognitive mechanisms driving production of such calls remain unclear (Macedonia and Evans, 1993), recent research suggests that great ape vocalisations may be subject to greater flexibility and intentionality (Crockford et al., 2012) than has been previously assumed (e.g. Zuberbühler, 2005, 2008). For instance, there is accumulating evidence that great apes can sometimes control, modify and target their vocalizations (Genty et al., 2014) and take into account the knowledge state of their receiver (Crockford et al., 2012; Schel et al., 2013; Lameira, 2018). Two studies have shown that wild chimpanzees can adjust their alarm call production depending on whether their receiver was already informed about the presence of a predator or not, and they were also more likely to produce alarm calls to naïve rather than informed receivers (Crockford et al., 2012; Schel et al., 2013). A study in captivity suggested that chimpanzees may also be able to adjust the structure of existing referential food vocalizations through a process of vocal learning (Watson et al., 2015).

Research suggests that the ‘peep’ vocalisation of wild bonobos may be potentially less fixed to internal emotional states. Wild bonobos produce peeps across a huge array of emotional contexts spanning a full range of emotional valence states (positive-neutral-negative) (Clay et al., 2016). Importantly, the acoustic structure of peeps produced in presumably negative arousal states (such as fleeing from aggression or in response to a predator) cannot be acoustically distinguished from those produced in positive valence contexts, such as the discovery of food or during grooming. These data highlight great vocal flexibility in the expression of emotion in this species and that the capacity to produce calls across different emotional contexts has evolutionary roots that predate the evolution of speech.

There is also evidence that great apes, especially orangutans, can partially control their breathing and articulator apparatus, resulting in the production of both voiced and unvoiced novel calls (Lameira, 2017). Captive chimpanzees, bonobos and orangutans have been shown to voluntarily produce atypical, voiceless calls (e.g. ‘raspberries’) in order to gain the attention of human caregivers/other conspecifics (e.g. orangutans (Lameira et al., 2015); chimpanzees (Hopkins et al., 2007); bonobos (Taglialatela et al., 2003), some of which have been acquired through social learning (Taglialatela et al., 2012). The extent to which free-living great apes flexibly control their vocalizations requires further investigation. However, recent studies suggest they hold greater capacities in intentional vocal production than previously assumed (Gruber and Zuberbühler, 2013; Crockford et al., 2012; 2015; 2017).

4. General discussion

4.1. Expressions compared

Emotional expressions are frequently used in humans and all great ape species by means of facial, bodily or vocal channels. Given their close phylogenetic relationship, the presence of an expression in all ape species suggests that it was also present in the last common ancestor. Studying similar types of communicative signals or non-intended expressions in closely related species allows one to determine homologies, i.e., shared evolutionary ancestry (Preuschoft and van Hooff, 1997). In this review, we identified both similarities and differences between humans and great apes (chimpanzees, bonobos, gorillas and orangutans) in emotional aspects of their faces, bodies and voices and the extent of their control over these modalities. Nevertheless, it is important to note that, the occurrence of similar expressions and or behaviours (e.g. kissing) does not necessarily imply the same underlying mechanisms, evolutionary history or affective state.

Our review indicates that humans and great ape facial expressions are based on a similar underlying mimetic musculature in their faces; although such further research using Facial Action Coding System (FACS: Ekman et al., 2002; see also Waller et al., 2020) is needed to pinpoint the extent of evolutionary homologies or divergence. Thus far, gorilla and orangutan facial expressions need to be described consistently and a systematic description of facial expressions with FACS has only started recently.

Despite some overlap, there is a notable divergence of human facial features compared to other apes. Human faces are remarkably expressive and, correspondingly, humans are highly attuned to facial information (Kobayashi and Kohshima, 1997). It is likely that features such as pronounced eyebrows, eye whites and redder lips facilitate the transmission of emotional expressions and may have evolved to do so (Kret, 2015). While enhanced in our species, some of these facial features may also have evolved to enhance the visibility of facial expressions in other ape species, including pink lips in bonobos, pink chimpanzee and bonobo gums and light facial colour of orangutans’ infants.

More broadly, we find some key similarities between humans and great apes emotional displays. First, the nose wrinkle is a prototypical facial expression of disgust that is present in both humans and chimpanzees in response to bitter tastes (Steiner et al., 2001). Second, both humans and apes express fear and anxiety through open mouth. Yet, while chimpanzees and bonobos express fear mainly through bared teeth (van Hooff, 1971), humans additionally express fear with raised eyebrows and wide eyes. This indicates conserved components in the facial expression, with some divergences. The body postures concern making the body smaller and are conserved. Similarly, patterns in vocal expressions such as pitch, loudness and duration, seem conserved.

Third, affiliation is expressed in all great ape species by relaxed open mouths and laughter. While some smiles may be associated with positive affect, they may also express anxiety or fear, such as the bared teeth display during appeasement (de Waal, 1988; Pritsch et al., 2017). Laughter appears to be a conserved hominid expression related to play and shows a number of similarities and some seemingly derived differences, both in facial expression and breathing patterns (Sauter et al., 2019). Humans seem to have an elaboration in muscles involved both smile and laughter expressions which may also be due to the grading of smiling and laugher in a continuous signal (van Hooff, 1971).

In both humans and great apes, individuals use their mouth and bodily presentations to indicate sexual attraction and intent, yet there are clear differences in the expression between humans and apes. Research shows that gorillas signal sexual intent with pursed lips and a grin-like ‘semi-smile’, which may be equivalent to humans’ lip biting and smiling. By contrast, human flirtatious signaling is highly diverse, including behaviours such as eye contact, nodding, licking, puckering, touching the lips, and tongue protrusion (Gonzaga et al., 2006; Givens, 1978). Thus, while some common features are found, species-specific expressions are present.

Fourth, while common among humans, facial expressions of anger and aggression appear rarer in great apes (and are not yet described for gorillas and orangutans). Apart from the bulging lips, indicating attack (chimpanzees (van Hooff, 1971), and bonobos’ lip press, indicative of retaliative aggressive intent (de Waal, 1988), more explicit facial expressions of anger may be tied to corresponding vocalisations, such as threat barks. Still, facial expressions resulting from vocalisations may be distinctive. More conserved features are found in bodily expression, such as making the body appear larger, and also vocal expressions show similar patterns. This apparent difference in the use of facial expression may be important in the evolution of human facial features.

Fifth, humans have a facial expression of surprise. In apes, no such facial expression, and also no bodily postures or vocalizations, are yet found for this emotion. This should be scrutinized further.

Altogether, our review suggests many conserved features in facial, bodily and vocal emotional expressions in humans and our great ape relatives. This does not preclude species-specific elements or elaboration of certain aspects of such expressions, particularly in the case of humans.

4.2. Intentionality of emotion expressions

One key question we aimed to address in this review is ‘To what extent do apes/humans have control over their expressions?’ Although the control humans possess over their emotion expression production is unparalleled in the animal kingdom, there are some indications that great apes may have some control over their facial, vocal and bodily expressions, which implicates a certain level of social intention. While more systematic research is needed, one further way to gain insight into this question is to study the delay of the emotional expression as measured from the onset of the triggering event. Play-wrestling chimpanzees can show both rapid facial mimicry (of the play face, response within 1 s from the triggering play face) and delayed facial mimicry (response from 1 to 5 s from the triggering stimulus) suggestive of some intentionality (Palagi et al., 2018). In gorillas, only rapid facial mimicry was observed. Rapid and delayed facial mimicry may thus differ in intentionality and vary across great ape species (see also Davila Ross et al., 2011). Complementary findings gave also been shown for delayed vocal reference in the alarm calls of wild orangutans (Lameira and Call, 2018). Given that cultural learning may influence expressions which is possibly related to intentionality, the literature would also be helped with the analysis of expressions of human children, who may be less influenced by social conventions regarding expressions in their first three years of life.

Intentionality is difficult to recognize and underlying emotional states difficult to detect. An expression may look alike from the outside, but reflect different underlying mechanisms. For these purposes, the use of methods yielding physiological measures such as thermal heat cameras and pupillometry may be particularly useful. The main advantage of these measures is that such methods rely on the autonomic nervous system, which is dependent on limbic neural circuits that are a) evolutionary preserved - therefore common to all mammalian species and b) difficult to control. We propose that a combination of facial expressions, body posture and movements, vocalizations in concert with autonomic measures may provide a holistic window into the emotional links between human and non-human primates.

Some emotional expressions are expressed in a certain specific way as it provides direct benefits for the expressor, but it is well known that some expressions become ritualised into clearer into clear signals meant for conspecifics. The human smile is perhaps the clearest example. Although there is currently little literature discussing *why* expressions are expressed in a certain configuration (why do the corners of the mouth go up in a smile and not down?), some studies are starting to tackle this question. In one study, authors demonstrated that enlarging the expressor's eyes has visual perceptual benefits for that person (Lee et al., 2013). Better being able to take in visual information has great benefits when it comes to fearful or surprising situations. The disgust expression also may have direct benefits for the expressor where closing the nostrils prevents poisonous material from entering the body and the tongue protrusion is a derivate from spitting these out (Chapman et al., 2009). This argues for an intrinsic connection between emotions and specific facial muscle actions. As described earlier, the acoustic properties of alarm calls and screams - high-amplitude and frequency, sharp onsets, dramatic acoustic contours, and non-linear noisy features; are aversive to receivers and difficult to habituate to (Hammerschmidt et al., 1994; Owren and Rendall, 2001; Rendall et al., 2009). In other words, emotions and their expressions contain adaptive properties that apply across emotions and phylogeny (Darwin, 1872; Anderson and Adolphs, 2014). Apart from preliminary work on the face, advantages of expressions from the bodily or vocal domain have never been experimentally tested directly, neither in humans, nor apes.

5. Conclusion

In sum, while progress has been made, many more studies of emotion production are needed to enhance our understanding of the mechanism of emotion expression in humans and our closest relatives. Recent technological advances including thermography or pupillometry can improve insight into the underlying mechanisms, invisible to the naked eye. In addition, systematic study of the context in which such expressions are conveyed is lacking in most species, with chimpanzees being the exception (van Hooff, 1971). In chimpanzees and bonobos, facial and vocal displays may be more narrowly context-bound than gestures (Pollick and de Waal, 2007), but whether this extends to bodily expressions of emotion, and how that compares with humans, is not known. Detailed comparisons of naturalistic production, and the intentional basis of emotional expressions from humans and great apes in social interactions are needed to inform theories of emotion perception and attribution.

Acknowledgements

This paper emerged from discussions during the Lorenz Workshop on Comparative Affective Science (2017). We would like to thank Eliza Bliss-Moreau and Jorg Massen for co-organising with Mariska Kret and to colleagues who attended for many stimulating discussions. We would like to thank the Editor and two anonymous reviewers for their constructive contributions to previous versions of this manuscript. This research was supported by the European Research Council (Starting grant #804582) and the Templeton World Charity Foundation (the Diverse Intelligences Possibilities Fund #TWCF0267) to Mariska E. Kret and by the European Research Council (Starting Grant #802979), the Royal Society Research Grant (RG170270) to Zanna Clay and the ESRC-ORA Research grant ES/S015612/1 co-awarded to Zanna Clay and Mariska E. Kret and a Talent Grant #406-15-026 from Nederlandse Organisatie voor Wetenschappelijk Onderzoek (to MEK and EP).

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