



Minireviews

Mini-review: Wild laughs: Ontogenesis and phylogenesis of humour

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ABSTRACT

This mini-review discusses the existing evidence on various forms of humour and humour-like behaviour in non-human animals, combining ontogenetic and phylogenetic perspectives. The first section describes humour-like behaviours, from the simplest to the most complex form (from laughing, tickling, joking, and chasing to ToM humour). In the second section, we propose the SPeCies (Social, Physiological, and Cognitive) Perspective, which frames the various types of humour based on Social motivation, Physiological state, and Cognitive skills. Finally, in the third section, we discuss future directions for further development.

1. Introduction

Humour characterises many of our daily experiences. It can occur when we are alone, observing, or thinking something funny, but especially when interacting with someone else or within a group. Humour is, therefore, a central aspect of human (social) life.

However, do we also share the subjective experience of amusement in the humorous context with other non-human animals? The present work aims to provide insights into humour and humour-like behaviours in humans and other animals, identifying points of divergence or convergence, and combining an ontogenetic and a phylogenetic perspective. We cautiously start the discussion by highlighting three significant intellectual traps. The first trap is to adopt an anthropomorphising view, which makes artificial parallels between species that do not account for each species' behavioural characteristics. This might lead to attributing unique and special skills to human beings (see also the "killjoy explanations" wittily discussed by Shettleworth [1]). The second trap is pure reductionism, which struggles to study non-human animals outside of manifest behaviour. The third trap is agnosticism, which argues the impossibility of studying the phenomenon objectively [2,3]. Overall, anthropomorphising, reductionist, and agnostic positions might prevent us from delving into an important psychological construct that deserves more attention.

Taking these traps into account, we develop our perspective through three sections. First, we describe and discuss the characteristics of

humour expression and humour-like behaviour in humans and other animals. Second, we introduce the SPeCies Perspective to provide an interpretative framework for humour that considers different levels of complexity. Third, we discuss criticisms and future developments in humour research in human and non-human species.

2. The sound of Humour: Laughter and vocalisations

Laughter is probably the most overt and well-known behavioural expression of humour. It is a ritualised and largely stereotyped vocal act that serves as a communication signal [4]. Laughter emerges in infants as early as four months of age and is crucial for strengthening the child's bond with their caregivers [5]. Infants' laughter increases in frequency in the first year of life and remains relatively stable during the second year [6]. However, by the second year, the frequency and duration of laughter are significantly correlated between mothers and children.

Over the last decades, studies have confirmed that human laughter has ancient roots, predating the development of the verbal skills that led us to articulate the "hahaha" [7]. In addition, it has been suggested that the neurofunctional correlates of laughter reside in areas and networks of our brain we share with other non-human animals. These include motor, premotor, supplementary motor areas, the frontal operculum, and emotion-related areas, such as the amygdala and insula [8].

But then, do animals laugh, too? If they do, we might not notice. When naive college students listened to recordings of chimpanzee

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laughter and were asked to guess what kind of sounds they were, only 2 out of 119 students correctly identified the vocalisations as laughter [9]. The most frequent responses included different behaviours such as panting, sexual vocalisations, asthma attacks, and some sounds from non-natural sources, such as work tools. This finding suggests that when we talk about laughter in the animal kingdom, we should not think of something too similar to human laughter but rather a series of vocalisations that some animals (mainly mammals, but also some birds) produce in a playful context. Thus, it is more a matter of identifying parallels that consider laughter's functional role in different species. Recently, Palagi et al. [10] proposed a unified evolutionary explanation of laughter and defined laughter as a "social behaviour aimed at regulating social relationships, easing social tensions and establishing social bonds" (p. 1). For these reasons, it is important to consider laughter within a broader framework and valorise it *per se*, as a social activity with its own status.

3. Play behaviours in human and non-human animals

A species is defined as social when its members constantly interact with other individuals of the same species outside the mating season or the family circle [11]. Living in herds, in constant interaction with others, makes developing sophisticated communication and social skills necessary. Some of these skills find expression in behaviours that vary in form and complexity. Such behaviours could, at least concerning the human species, be considered humour-like behaviours or precursors of humour. In the following paragraphs, we present these behaviours in a comparative perspective.

3.1. Play and play-fighting behaviours

Children's laughter is mainly expressed during social play behaviours. Early literature has already highlighted how, during play, children laugh much more when another person is involved than when there is only a toy that disappears and reappears. For example, the sudden disappearance and reappearance of a familiar face during the peek-a-boo game causes a pleasant surprise effect, which is particularly effective during object permanence acquisition, thus generating laughter [12]. One-year-olds enjoy this play more when interacting with caregivers than with strangers, suggesting the importance of play in a familiar and trusting environment [13].

Play-fighting behaviours are prevalent in preschool children. It is similar to actual fighting but can be differentiated because of the following reasons: The facial expression is usually neutral or smiling, while during real fighting, children often show staring, frowning, or red faces [14]; Children usually laugh, whereas during actual fighting, they more often cry; The participants are generally more than two, while during actual fighting they are just two in most cases. Thus, play-fighting behaviour functions as social bonding and cohesion and serves as an exercise for specific social skills, such as defining social roles [15].

Similar activities have been observed in non-human animals. In some species, the actions during play-fighting behaviours are accompanied by specific vocalisations similar to laughter in humans. From a phylogenetic point of view, these vocalisations seem to have evolved from laboured breathing forms before being ritualised into a communicative exchange [9,16]. They might serve as a facilitatory/regulatory tool to communicate benevolent intentions [16] and prevent aggressive escalations [17]. Play-related vocalisations have been studied in mammals, mainly within primate species [18], but also in rats [19], dogs [20], dolphins [21], and birds, including parrots and magpies [22].

3.2. Tickling

Starting from the first year of life, tickling is an activity that greatly amuses young humans [23]. Like other humorous situations, tickling

can be considered the product of benign violation [24] or, according to the Incongruity Theory [25], the perception of something incongruous that violates our mental patterns and expectations. One perceives a physical threat (violation) as playful (benign) at the same time.

During tickling play with the caregiver, children seem to appreciate the reciprocal social interaction rather than the physical sensation of tickling [26]. In healthy adults [27], the phase preceding tickling is characterised by an increased activity of the anterior insula, hypothalamus, nucleus accumbens, and ventral tegmental area. This circuit is responsible for different emotion-related processing. Moreover, actual tickling is associated with a more extensive activation pattern, including the anterior cingulate cortex, which is responsible for the volitional control of the affective components of vocalisation and social awareness [28]. The recruitment of areas involved in emotional and social processing would support the hypothesis that emotions have a primary role during tickle play. This could account for children's preference for reciprocal social interaction rather than the physical sensation *per se*.

Tickling might seem to be an exclusively human activity. Yet, other species are also ticklish. For example, the idea of tickling animals (Heterospecific Hand Play [19]) found open doors in Jaak Panksepp's laboratory [7,29], where researchers found that rats' 50 kHz ultrasonic vocalizations (USVs), usually associated with positive affective states, were significantly increased during tickling [19]. Confirming this, Rygula and colleagues [30] found that neural substrates associated with USV in rats during tickling are consistent with those generated by positive affective states in humans and include reward-associated brain areas such as mesolimbic dopamine circuits and opioid systems [31,32]. In addition, it has been observed that induction of USV in rats strengthens bonding, both between rats and with experimenters [33].

A phylogenetic analysis of tickle-related vocalizations in humans and great apes revealed similarities and differences between orangutans, gorillas, chimpanzees, bonobos, and human infants. The research results supported the idea of phylogenetic continuity between non-human and human expressions and a common evolutionary origin despite differences in acoustic characteristics.

3.3. Pranking and Chasing

Pranking and chasing behaviours can be considered play-related behaviours. However, they may represent the following step, requiring more complex social and cognitive skills. Similarly to being tickled, from the age of one year, most children are entertained by chasing activities [23], which include a variety of games, including hide-and-seek.

Behaviours related to spitefulness (playful teasing, [34]) have also been observed in other species, such as elephants and primates [35]. For example, elephants enact anti-predation-like behaviours, which happen not only with species that may pose a danger to them but also with harmless species. In addition, baboons have been observed grabbing and pulling the tails of cows. However, this behaviour was not always present: It occurred only when the cows were harmless, that is, when they were confined inside a pen. Eckert and colleagues [34] also reported that the same teasing patterns of preverbal human infants are also found in great apes, including teasing with offer and withdrawal, provocative noncompliance, and interruption of others' activities.

Turning to more anecdotal insights, similar behaviours have also been observed outside the mammalian class. For example, Horgan [36] describes several interesting episodes involving his two children and George, an orphaned crow who trapped the children in a cage.

Given the purely anecdotal nature of these behaviours, such evidence should be rigorously verified to understand their adaptive nature and significance.

4. The Theory of Mind in Humour: An essential Ingredient?

The play behaviours just described have led to the hypothesis that, at least for some of them (i.e., pranking), the involvement of skills related

to Theory of Mind (ToM) is necessary [37,38]. For example, it has been observed that the fun side of pursuit only occurs when one realizes what the other person is experiencing.

However, the development of higher-order social and cognitive skills in animals, such as ToM, is still debated in the scientific community. ToM is a multidimensional construct, even if it is usually treated as a monolithic ability. This is important because it allows the systematic study of the various components [39], including imitation, understanding others' mental states, goals, intentions, knowledge, desires, and beliefs. Although this distinction seems subtle, it is meaningful because, for example, apes seem capable of tracking the goals, perceptions, and knowledge that motivate others' actions. Still, in some cases, they fail to use this information to represent what others believe [39,40]. In other cases [41], however, evidence suggests they are capable of belief attribution.

The idea of fragmenting different components within ToM-related competencies makes the study of this phenomenon more inclusive and comprehensive. In their review, Krupenye and Call [42] collected the latest evidence on ToM in animals, highlighting meaningful issues for future research. The authors discussed the possibility of a more blurred boundary between humans and non-human animals. They leaned towards the presence of "a non-egocentric view of the world" ([42], p.4) in various animal species. Their analysis highlighted the presence of at least some ToM sub-components in primates, corvids, and dogs. For example, some birds display a sensitivity to the desires of others, and great apes manage to solve the classic tasks of false belief.

5. Humour in Animals?

Let us now try to go a step further and address the issue of humour in animals. When discussing humour, we must introduce some cognitive skills fundamental to understanding puns. So, let us start with humans and, more specifically, with children to answer how we develop the capacity to get a joke.

McGhee's cognitive-stage theory [43] is the most recognised reference for understanding humour development, reflecting specific development phases. During the first year, children laugh more at adults' strange and abnormal behaviours. Later, their humour becomes more complex due to the acquisition of symbolic play and the mental representation of familiar objects. Therefore, their humour usually consists of assimilating objects into wrong patterns (e.g., using a shoe as a telephone). As language skills become more refined (around the third year), humour consists of deliberately mislabelling actions or objects. Around age five, children begin to laugh and repeat jokes they have heard without really understanding them (the "pre-riddle period"). Finally, at six or seven, children recognise the different forms of ambiguity in language (phonological, semantic, syntactic, etc.) and begin to understand and appreciate the concept of double meaning. They also develop various cognitive skills, such as manipulating mental representations, imagining the effects of actions on objects, and better recognising the perspective of others. These skills contribute to the ability to appreciate more sophisticated forms of humour.

A similar form of humour was studied in a gorilla named Koko, who, through training, had learned to practise some sign language, which, according to her trainers, she used to create jokes and wordplay. Gamble [44] described many examples of Koko's humour-like behaviour referring to children's stages. As an example of Stage 1, Koko seemed able to generate humour by misusing objects, such as the ruler, as earrings or barrette. An example of Stage 2, humour is depicted in an amusing exchange between Koko and Barbara Hiller, a docent at the zoo, philanthropist, and integral part of Project Koko, the first-ever project about the linguistic capabilities of gorillas through sign language. This exchange is reported in Gamble [44], which we quote verbatim here for a better appreciation:

"B: What does Penny use to clean your teeth? K: Foot.

B: That's silly. She uses a toothbrush. K: Toothbrush.
B: What does Penny put on your toothbrush? K: Nose.
(Then she puts her foot up to her nose and laughs.).
B: You're a goof. Koko laughs". ([45], 1986:5).

The use of incongruous features (Stage 3) is attested by Koko's capacity to identify incongruities in pictures (e.g., bikes with square wheels), to make up insults ("You dirty toilet" was her favourite), and to invent witty poems ("Flower pink, fruit stink. Fruit pink stink"; [46] 1986: 10).

Finally, the most indicative example of Stage 4 of Koko's supposed humour is summarised in the answers she gave when she was asked: "What can you think of that's hard?" that was "rock" and "work" ([47], 1986:3), as well as other puns about double meanings or assonances [44]. Through these examples, it is possible to conjecture that Koko liked to make people laugh, in line with the idea of humour as a form of social exchange, suggesting the presence of a social intention. Future controlled studies must challenge this hypothesis about the interpersonal mechanisms of humour in non-human animals. At present, the available evidence is still sparse. Some claim that although some apes possess a sense of humour, there is no evidence that they respond with laughter to the humorous behaviours of others [9].

It is important to note that the interpretation of these behaviours is still controversial. There are alternative and less fascinating interpretations for these cases. For example, most of the data were collected and interpreted by Koko's caregivers, running the risk of no objective interpretations and overinterpretation and anthropomorphism [34]. Moreover, it is unclear whether any particular training preceded these episodes.

In conclusion, this fascinating case of humorous behaviours in a gorilla will need to be further confirmed and verified by more rigorous and controlled empirical research.

6. The SPeCies perspective

To explain the phenomenon of humour across different species, we propose a theoretical model integrating social, physiological, and cognitive aspects of humour, the SPeCies Perspective, see Fig. 1. Like other theoretical frameworks [48,49], SPeCies integrates different dimensions to understand complex human and animal behaviour. For example, Tinbergen [48] proposed that animal behaviour can be described and defined by answering four fundamental questions. Different from this model, SPeCies narrows down the field of analysis by identifying three specific dimensions that, depending on their levels of complexity and their interaction with each other, can explain an animal's and human's complex behaviour.

In particular, we consider that the expression of a specific behaviour (and its degree of complexity) is modulated by ethology, the presence (or absence) of specific cognitive abilities, and the physiological state of an organism (stress or homeostasis). Thus, we propose a multi-component framework in which we hypothesise that humour behaviour is explained by the inter-relation of these three different aspects.

In the present work, we apply this approach to the complex phenomenon of humour. In this context, we use SPeCies to explain the variety and complexity of this phenomenon through a non-hierarchical perspective: The higher levels described in the perspective do not replace the previous ones. Indeed, despite possessing a plethora of cognitive capacities to produce and enjoy complex and sophisticated jokes, humans maintain and continue to play and laugh with simpler and more physical behaviours, mainly related to an immediate release of energy and tension, such as fighting games and tickling.

6.1. Ethology (I)

It can be inferred from the human and animal behaviours described above that humour, in its various forms, emerges directly from social

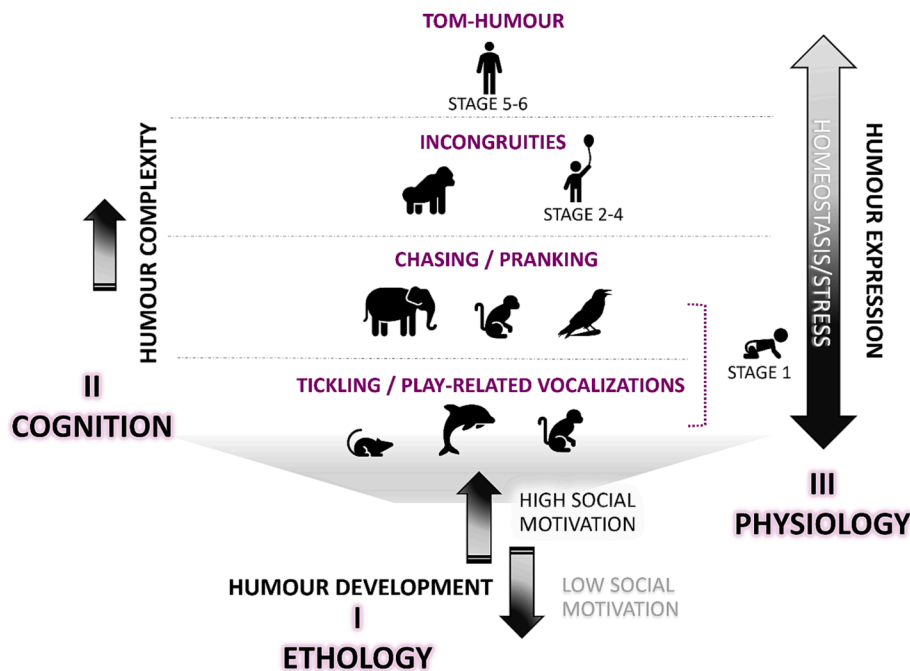


Fig. 1. A graphic representation of the SPeCies Perspective on humour with I Ethology (bottom), II Cognition (left), and III Physiology (right) components.

interaction. In humans, although solitary forms of laughter and amusement exist, they still seem to have social roots and are enhanced by social interactions [50]. For example, it has been observed that laughter is 30 times more frequent in social situations than in solitary ones [9].

However, although humour and humour-like behaviours emerge from social communication, this does not imply that they are expressed similarly for all species. This model hypothesises that Species-specific social motivation influences the level of development of communication skills, which in turn influences the complexity and expression of humour or humour-like behaviour in different species.

In addition, humour has a communicative function that allows for the experience of positive valence behaviours, such as making faces, which reinforce interpersonal closeness, or negative valence behaviours. The latter include specific behaviours, including the practice of conflict, competition, and prevarication (see also Superiority Theory, [49]) using, for example, sarcasm and irony. However, joy and anger are typically regarded as emotions related to rapprochement, reflecting the motivational tendency to maintain contact rather than avoidance [50].

From this point of view, the ethological structure suggests that the different expressions of humour depend on the species' different social communication capacities and communicative functions.

6.2. Cognition (II)

The presence or absence of specific cognitive abilities can influence humour complexity. In species that possess some ToM skills, we can appreciate more sophisticated playful behaviours, such as chasing and teasing, which are fun only if you can imagine the others' point of view. According to contemporary perspectives [35,36], even if these behaviours help improve social skills, they are probably produced without any other reason than pure pleasure and fun.

In humans, high-level cognitive skills such as ToM and language allow for sophisticated forms, such as ToM humour and verbal jokes. According to current knowledge [51], this type of humour develops in children around six or seven (Stages 5–6) and is unique to our species. However, even without high-level cognitive skills and partial or absent development of ToM and perspective-taking skills, it is possible to observe forms of humour, such as play-fighting behaviours and tickling,

along with their typical vocalisations.

6.3. Physiological state (III)

Human and non-human animals usually display behaviours associated with amusement (e.g., play, laughter, laughter-vocalizations) in the absence of immediate danger. For example, when children feel uncomfortable or insecure, they do not indulge in play-related activities with strangers, but trigger stress-related control mechanisms such as avoidance [52]. The same phenomenon has been hypothesized to occur in rats: Tickling studies have shown that play-related vocalizations do not occur (or occur much more rarely) in labs that also house cats [18]. However, when interpreting this phenomenon, it is important to point out that rats generally do not vocalise in the immediate presence of predators, likely to avoid attracting their attention. Once hidden in their burrows, they emit 22-kHz vocalizations related to avoidance behaviours, probably inducing conspecifics to freeze or seek shelter [53].

In safe contexts, humorous and playful behaviours can be interpreted as a release of excitement and a form of positive social interaction and bonding occasion, as already discussed in the previous paragraphs (see also [52]). This applies both to simple (play) and to complex (ToM humour, puns, verbal jokes) behaviours (see Fig. 1).

Nonetheless, as already highlighted by the Relief Theory [54,55], it is well known that people can also display humour as a coping mechanism in high-stress situations [56,57]. This type of humour has been observed especially in studies on survivors of extreme adversity, such as concentration camps. In these contexts, the use of humour through jokes about oppressors and the difficulties suffered is a valuable tool to maintain cohesion among the group and to maintain high self-respect, individual well-being, and hope, enabling individuals to survive in extreme circumstances [58–60]. This is a complex kind of humour, which, by involving incongruity and multiple interpretations, provides a way for the individual to change perspective on a stressful situation, reevaluating it from a less threatening point of view by allowing the person to think more broadly and creatively about problem-solving [61]. In addition, this positive emotion may have the physiological benefit of preserving psychophysiological well-being by accelerating recovery from the cardiovascular effects of stress-related negative emotions [62,63].

This evidence suggests that humour for coping with stress usually occurs in a social context and requires higher-order cognitive skills. Therefore, it is hypothesized that this type of humour is present in adults with high cognitive abilities. So, according to our model, the expression of humour can occur either in a homeostatic or a stressful physiological condition, depending on the individual's situation and cognitive resources.

7. Future perspectives

Analysis of the literature has made it increasingly evident that, for both human and non-human species, humour is a complex social, cognitive, and affective construct that deserves to be analysed for a deeper understanding of animal and human cognition [44]. In this regard, we quote the words of Richard W. Byrne [35]: “Yet precisely what animals find fun has seldom been examined for what it can reveal about how they represent and think about the world” [14, p. R2]. “In the future, the analysis of the specific content of animal fun, in addition to its distribution and functionality, may have the power to help us understand much more about how animals see their world” [14, p. R4]. To avoid anthropomorphising attributions, future research should shed light on what animals find enjoyable, with the aim of understanding if, how, and why they find something funny or entertaining. The SPeCies perspective will be useful in integrating these aspects and targeting this critical issue, starting from the contribution of ToM components.

8. Conclusions

In conclusion, this brief review aimed to explore the development of humour and humour-like behaviours in humans and other animals, trying to follow the idea of a common evolutionary root with a functional meaning and highlight the importance of addressing some debates that still represent open questions.

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CRediT authorship contribution statement

Maria Elide Vanutelli: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Moritz M. Daum:** Resources, Validation, Writing – review & editing. **Mirella Manfredi:** Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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