PHILOSOPHICAL
TRANSACTIONS B

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Opinion piece

Cite this article: Palagi E, Caruana F, de Waal FBM. 2022 The naturalistic approach to laughter in humans and other animals: towards a unified theory. *Phil. Trans. R. Soc. B* **377**: 20210175.
https://doi.org/10.1098/rstb.2021.0175

Received: 6 April 2022
Accepted: 15 June 2022

One contribution of 17 to a theme issue 'Cracking the laugh code: laughter through the lens of biology, psychology and neuroscience'.

Subject Areas:
behaviour, cognition, evolution

Keywords:
evolutionary basis of laughter, neural basis of laughter, facial expressions, vocalizations, social play, facial mimicry

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THE ROYAL SOCIETY
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The naturalistic approach to laughter in humans and other animals: towards a unified theory

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This opinion piece aims to tackle the biological, psychological, neural and cultural underpinnings of laughter from a naturalistic and evolutionary perspective. A naturalistic account of laughter requires the revaluation of two dogmas of a longstanding philosophical tradition, that is, the quintessential link between laughter and humour, and the uniquely human nature of this behaviour. In the spirit of Provine's and Panksepp's seminal studies, who firstly argued against the anti-naturalistic dogmas, here we review compelling evidence that (i) laughter is first and foremost a social behaviour aimed at regulating social relationships, easing social tensions and establishing social bonds, and that (ii) homologue and homoplasic behaviours of laughter exist in primates and rodents, who also share with humans the same underpinning neural circuitry. We make a case for the hypothesis that the contagiousness of laughter and its pervasive social infectiousness in everyday social interactions is mediated by a specific mirror mechanism. Finally, we argue that a naturalistic account of laughter should not be intended as an outright rejection of classic theories; rather, in the last part of the piece we argue that our perspective is potentially able to integrate previous viewpoints—including classic philosophical theories—ultimately providing a unified evolutionary explanation of laughter.

This article is part of the theme issue 'Cracking the laugh code: laughter through the lens of biology, psychology and neuroscience'.

1. Introduction

Laughter is a multifaceted social behaviour that has aroused great interest in many major Western thinkers. Over the years, the enigma of laughter gained the interest of philosophers [1,2], psychologists [3,4], neuroscientists [5,6], neurologists [7,8], anthropologists [9], ethologists [10] and even historians [11,12].

Classic philosophical theories of laughter suggested that laughter can be explained as the outcome of a feeling of dominance (Superiority Theory), the appreciation of something that violates our expectations (Incongruity Theory), or the release of nervous energy (Relief Theory; see [1]). However, none of these theories can fully explain the phenomenon of laughter, and even if these theories are taken together, what remains outside of them is much more than what is explained. Most importantly, these theories are theories of humour—not theories of laughter, with its acoustic and visual components—and, despite the obvious relationship between humour and laughter, the two phenomena are not always associated.

A second problem concerning the classical philosophical approach to laughter is the assumption that laughter is a uniquely human feature, an idea shared by all relevant scholars since the time of Aristotle [1], and most unambiguously expressed by the German philosopher and sociologist Helmut Plessner: 'the principle according to which only man disposes of laughter and crying, and not the animal, is not a hypothesis that could one day be refuted, but a certainty' [13, p. 25].

Starting in the ninteenth century, the humour- and homocentric accounts of laughter started to creak, and the suspicion began to spread that—albeit targeting some interesting aspects of how we use laughter—classic explanations of laughter were probably scratching the surface of a wider phenomenon, missing the opportunity to develop a naturalistic, evolutionary, account of laughter. Coherently with Darwin's view that 'we may confidently believe that laughter […] was practiced by our progenitors long before they deserved to be called humans' [14, p. 361]—emerging research in the field of psychology, ethology and neuroscience provided compelling evidence for animal homologues or analogues of laughter, highlighting the primarily communicative function of this behaviour.

Two names that, more than others, contributed to the emergence of such a new view are the late Estonian-American neuroscientist Jaak Panksepp, and the late American psychologist Robert Provine. Panksepp firstly discovered a homoplasic behaviour in rats, paving the way for a comparative approach to laughter focused on the affiliative and playful nature of this behaviour. Provine, in contrast, focused more on primate laughter, including human laughter, revealing its communicative role, and its independence from humour. The aim of the present opinion piece opening the special issue on laughter is not only to recognize the seminal contribution of these two authors but also to flesh out the direction indicated by them. Thanks to the legacy they started, classic theories of laughter advanced by philosophers over the centuries can now be flanked by an additional naturalistic hypothesis, which argues that the primary function of human laughter—and homologue or analogue behaviour in other species—is to affiliate, boost social bonding and signal positive intentions during playful interactions.

This hypothesis should not be intended as an outright rejection of classic theories of laughter; rather, the aim of this contribution is to reach a new inclusive perspective, potentially able to integrate previous viewpoints, ultimately providing a unified evolutionary explanation of laughter. This naturalistic approach will be articulated by integrating insights from ethology, psychology and neuroscience.

2. Towards a naturalistic account of laughter

The hallmark of contemporary research on laughter is the continuity between play vocalizations in animals and human laughter. All research on laughter in humans and other animals risks the traditional criticism of unjustified anthropomorphism. Why not call the laughter of apes something neutral, such as vocalized panting? To avoid confusion between humans and animals, some other scholars have spoken of 'laugh-like' behaviour. The problem with such linguistic censorship is that it obscures homologies, whereas language should respect them. In the same way that we do not, or should not, call the arms and hands of chimpanzees 'front legs,' or call their faces 'snouts,' our language needs to respect the evolutionary connection at the root of similarities. 'Homology' is the term used for cross-species similarities that derive from shared ancestry, which concept is as applicable to anatomy as to behaviour, such as laughter [15]. From a Darwinian perspective, the simplest assumption is that if related species show similar behaviour under similar circumstances, the underlying psychology must be similar, too. This principle, known as evolutionary parsimony [16], urges us to apply a unified language to humans and their closest relatives.

Laughter is one of humanity's most 'animalistic' expressions. We go crazy. We become limp, lean on each other, turn red and shed tears to the point that the line with crying vanishes. We literally pee in our pants! After an evening of laughter, we may be totally exhausted. This is partly because intense laughter is marked by more exhalations (producing sound) than inhalations (needed for oxygen), making us end up gasping for air. Laughter is one of the great joys of being human, with well-known health benefits, such as stress reduction, stimulation of heart and lungs, and release of endorphins [17,18]. Laughter brings body and mind together, fusing them into a single whole [13]. We may experience this as a loss of control. As one theatre critic put it 'To watch inspired laughter register with an audience is to be present at a great and violent mystery. Faces convulse, tears stream, bodies collapse, not in agony but in rapture' [19, p. 206].

Other hominids do not laugh as loudly and as often as humans and use this expression under a more limited range of circumstances. They do share its repetitive sound, though, which derives from rhythmic panting. Laughter during play starts with audible panting, which grows more and more vocal the more intense the encounter becomes. Rapid panting by itself, outside the play context, expresses friendly intentions and a desire for contact [10]. For example, a female chimpanzee walks up to her best friend while uttering audible pants before kissing her. This audible panting, which signals good intentions, has been turned by evolution into a play vocalization, the main function of which is again to signal benign intentions. Since play interactions (e.g. play fighting) often resemble contests, it is crucial to set the two apart. Play signals serve as *metacommunication* (i.e. communication that refers to communication) to clarify the meaning of fight-like behaviour shown for fun [20].

The facial expression of laughter is remarkably similar across hominids, with the main variation being whether the upper teeth show or not, which occurs in humans and bonobos, but less so in other hominids [10,21]. The laugh expression is set apart from teeth-baring, such as in the grin or smile, which activates the zygomaticus major and minor muscles, and remains silent. This expression is closer to an appeasement signal, usually shown outside a relaxed, playful context. In most primates, it is typical of tense encounters. For this reason, van Hooff [10], who described the laugh as a 'relaxed open-mouth face' and the grin or smile as the 'silent bared-teeth face,' viewed their phylogenetic origins as quite separate, although recent findings suggest a less clear-cut operational and functional separation between the two different facial expressions (see [22]).

In psychological studies on humans, on the other hand, the laugh and smile are still often conflated, as if they concern the same signal of different intensities. But whereas the smile is often presented as a sign of happiness (e.g. [23]), this expression's background seems much richer with many meanings other than cheerfulness. Dependent on the circumstances, human teeth-baring indicates nervousness, a need to please, reassurance of anxious others, a welcoming attitude, amusement, attraction to others, embarrassment and so on [24].

The hominid laugh is most easily aroused in a context of physical stimulation, such as during play fighting. As described by de Waal [25, p. 47]: 'Tickling a juvenile chimpanzee is a lot like tickling a child. The ape has the same sensitive spots: under the armpits, on the side, in the belly. He opens his mouth wide, lips relaxed, panting audibly in the same familiar 'huh-huh-huh' rhythm of inhalation and exhalation as human laughter.' This context of physical stimulation must have a long evolutionary history because the connection between tickling and laugh-like sounds has also been reported by Panksepp in his pioneering work on rats, which made animal emotions an acceptable topic of discussion.

(a) Panksepp and the comparative and neuroscientific study of laughter

A pioneer who more than any other has made laughter an acceptable research field in neuroscience and animal behaviour is Panksepp [26–28]. Panksepp's contribution to laughter is based on the discovery of vocal patterns in rats that may have evolutionary relationships to primates' laughter and joyful social interaction. In a 1997 seminal paper—that never saw the light of day in its original form and which was re-published as a book chapter two years later—Panksepp & Burgdorf [29] described ultrasonic vocalization patterns (50-kHz chirps) that—similarly to human laughter—are regularly emitted during juvenile play [30] and rapid manual stimulation (i.e. tickling). Similarly to human laughter, such high-frequency, ultrasonic, laughter-type chirping responses occurred during positive, playful social situations, they were more evident in younger animals, modulated as a function of previous social experience and reduced during stressful conditions (bright light or cat smell). Importantly, laughter-type chirping responses were distinctly different from a much slower vocalization pattern (22 kHz) elicited by negative emotional arousal induced by fear and social defeat. Given the many similarities between 50 kHz chirps and human laughter, Panksepp & Burgdorf [29, p. 366] concluded that the former 'may be homologous to, or at least functionally akin' to the latter, hypothesizing that the discovery of a primal form of laughter in rats provided a new way to study the neural sources of positive social-emotional processes (i.e. joyful affect) in other mammals [31]. This research represents a milestone for both ethological and neuroscientific studies on laughter.

On the ethological side, it supports an evolutionary interpretation according to which the common ancestral roots of human and animal laughter are primarily related to playful social joy and affiliation, and possibly mediated by common mechanisms based on the recruitment of the dopaminergic and the opioid systems [31,32]. It can be objected that the evolutionary distance between rodents and primates, and the less noticeable facial expressions in the former, should invite caution, and to consider rat chirps as a homoplasic behaviour (i.e. deriving from an evolutionary convergent mechanism), rather than a homologous one (i.e. having the same evolutionary origin). Although recent findings suggest that during playful tickling rats perform facial expressions in association with 50 kHz vocalizations [33].

It must be noticed that Panksepp's account of laughter in rats converges with Dunbar's hypothesis [34] that, in humans, laughter evolved as an alternative mechanism to social touching, for reinforcing social bonds in groups beyond those that can be maintained by grooming in primates, and that this mechanism is mediated by the activation of the opioid system ([9,35]; see also [36,37]). The hypothesis of laughter as a means to connect subjects 'at distance' holds on for non-human primates too. An elucidating example describing the role of the play face in the communication at distance comes from gorillas [38]. After being repeatedly invited to play by a juvenile, a gorilla female was observed to conceal her play face with her hand, apparently to avoid the possibility of the juvenile seeing it. The gesture of hiding the laughing face suggests that the subject is 'aware' of the message that the facial expression can convey (e.g. expressing motivation to play). This anecdotic observation also underlines that laugh faces are spontaneously produced, unstoppable and, for this reason, difficult to inhibit.

On the neuroscientific side, a primal form of laughter in rats points at deep homologies in the neurological mechanisms underpinning play behaviour and playful vocalizations in rodents and primates, including humans. His neuroscientific study of rats' laughter was focused on the role of the subcortical reward system, and in particular on the nucleus accumbens (NAcc), where microinjections of amphetamine, a dopamine agonist, increase 50 kHz chirps [39]. More recent studies confirmed the contribution of the NAcc to 50 kHz chirps [40,41] and—in line with the hypothesis of a continuity between rats and human laughter—there is now evidence that, in humans, the NAcc is activated by tickling anticipation [42] and that its electrical stimulation induces mirthful laughter and mood elevation [43,44].

Of note, Panksepp was famously inspired by Paul MacLean's theory that subcortical regions of the mammalian brain contain a variety of emotional systems that are phylogenetically preserved across mammals. Recently, however, it has been demonstrated that laughter is not a uniquely subcortical phenomenon and much work is being done to discover the cortical control of laughter. In rats, it has been shown that the somatosensory cortex shows intense tickling-evoked activity and that its electrical stimulation evokes vocalizations [45]. In humans, electrical stimulation studies conducted on surgical patients revealed that laughter can be elicited by stimulating a limited number of emotional regions—such as the pregenual anterior cingulate cortex (pACC) [46–52] and the temporal pole [49,53–55]—and motor regions—such as the pre-supplementary motor area (pre-SMA) [56–58] and the frontal/Rolandic operculum [49,59,60].

In line with the classic neurological observation that emotional and voluntary laughter are dissociated in the human brain [5,6,8,61,62], the regions from which laughter can be elicited by stimulation are arranged along two partially segregated networks [63]. A first network is constituted by pACC, temporal pole and NAcc, and it is probably involved in the production of emotional laughter and positive affect. A second network is anchored to the frontal/Rolandic operculum—adjacent to the Broca's region—and the primary motor cortex, and it is involved in volitional and non-emotional laughter and in the connection between laughter and speech. The pre-SMA is connected to both pACC and frontal/Rolandic operculum, connecting the two networks.

These two networks may be differently represented in humans and nonhuman primates. A comparison between human and monkey connectivity reveals that the emotional network—constituted by pACC, temporal pole and NAcc—is preserved in both species, thus supporting the hypothesis that it serves an evolutionarily conserved affiliative function [63]. Considering that the NAcc was one of the regions originally described by Panksepp as crucial for rats' 50 kHz chirps and that he predicted the possible involvement of the anterior cingulate cortex based on its role in emotional vocalizations [31], one could argue that current neuroscientific research on the emotional network for human laughter production follows in the footsteps of Panksepp. The voluntary network, in contrast, might be a peculiar human circuit, based on connections that are not described in monkeys [63]. Given its proximity to the Broca's region, it possibly contributes to the strategic use of laughter in conversation, that is, what Robert Provine [64, p. 46] dubbed 'laughspeak': 'a kind of laugh/speech hybrid that is under more conscious control […] and is often used by people to defuse a sensitive point'.

(b) Provine and the communicative and contagious nature of laughter

Panksepp's hypothesis that laughter is primarily related to social interaction and affiliation, rather than simply humour appreciation, was an assumption also shared by the American psychologist Robert Provine, who argued that the philosophical literature on laughter 'is long on casual theorizing and short of empirical data, a fatal flaw that has impeded progress for more than 2000 years […] The most readily apparent feature of all this theorizing is that most of it is really about humour or comedy, not laughter in itself. This laughterless study of laughter continues to the present day […] Philosophical inquiries also fail because they are too far removed from the phenomenal world they seek to explain' [3, pp. 12–18].

Provine's seminal studies, conducted both through ethological observations in public places and through self-annotations from college students, demonstrated that only 10–20% of statements eliciting laughter are related to humour, that laughter is 30 times more frequent in social than solitary situations, and that it is more frequently produced by the speaker than the listener [65,66]. This evidence led Provine to develop an innovative interpretation of laughter as a social tool shaping verbal and nonverbal conversations.

Provine's forays into laughter range from the report of a 'punctuation effect'—which describes the placement of laughter in conversation and indicates the dominance of speech over laughter [67]—to the demonstration of a similar effect in deaf individuals [68]. His contribution to cracking the laugh code also includes a detailed description of the social grammar that regulates laughter production based on social hierarchies and gender [3]. All these insights have paved the way for a rich series of investigations based on conversation analysis in the ethnomethodological tradition, investigating laughter in interaction and turn-taking in a variety of contexts including broadcast news interviews, employment interviews, medical examinations and everyday talks (see [69]).

Coherently with his naturalistic approach, Provine studied the evolutionary trajectory of laughter in primates, comparing the acoustic structure of laughter in humans and great apes [70], and he capitalized on these results to develop a 'bipedal theory' of speech evolution, i.e. the theory that bipedal locomotion freed the respiration system of its support function during running, permitting greater breath control—as revealed by human-type laughter (a parsed exhalation) compared to the characteristic panting chimpanzee laugh (one sound per inward or outward breath; [70]).

What is probably the major contribution of Provine to the study of laughter is the emphasis on its pervasive social infectiousness in everyday social interactions, and the focus on the idea that the most effective stimulus for inducing laughter is another person laughing ([64,71] see also [72]). Provine predicted that 'the efficacy of laughter to elicit laughter suggests that humans may have a 'feature detector' for laughter, a neural circuit that responds exclusively to this vocalization and triggers the motor pattern of laughter in listeners', complaining that 'contagious laughter […] has obvious mirror-like properties, but are seldom mentioned in the literature about mirror neurons'. ([67, p. 1537]; see also [71]) This issue has been tackled by neuroscientists only recently.

Perceiving others' laughter activates a wide network of occipito-temporal (middle occipital gyrus, basal temporal, and auditory regions of the supratemporal plane), parietal (supramarginal gyrus), limbic (insula, amygdala) and frontal (pACC, pre-SMA, anterior medial prefrontal cortex (amPFC), orbitofrontal cortex (OFC) and inferior frontal gyrus) regions ([49,73–79], see also [80]). Such a distributed processing—encompassing sensory, motor, and cognitive areas—is telling of the complexity and richness of information conveyed by this stimulus.

More closely in line with the hypothesis advanced by Provine, some of these regions are directly involved in the control of the emotional and motor aspects of laughter production, such as the pACC [49,78,81] and the pre-SMA [58,77,82]—suggesting the existence of a mirror mechanism specific for laughter of the kind foreseen by Provine [83,84]. According to the perception-action model [85–87], such a mechanism could be part of the neural machinery implementing laughter contagion. Considering the complexity of emotional contagion and its context-based modulation, however, it is likely that such a mechanism is controlled by a variety of systems operating both upstream—at the level of the high-order visual and auditory systems—and downstream—top-down modulated by prefrontal regions involved in the cognitive and affective evaluation of others' laughter, as the amPFC; [73–76]) and the OFC [88,89].

3. Bridging the naturalistic and classic theories

In the Introduction, we argued that classic philosophical theories of laughter, such as the Superiority Theory or Incongruity Theory, were typically associated with two problematic key predictions, namely, the quintessential link between laughter and humour, and the putative uniqueness of human laughter. In the previous sections, we demonstrated the intrinsic weakness of both assumptions, and the heuristic power of an alternative, naturalistic, approach to laughter. Here we argue that such a naturalistic account is in the position to integrate previous viewpoints within an evolutionary framework. Indeed, while studies on the sense of humour in animals are still lacking, in the present section we argue that some core elements of the Superiority and Incongruence theories can already be traced in some ethological findings related to animal laughter and social bonding.

(a) From the Social Bonding to the Superiority Theory

Although most instances of laughter can be classified as affiliative social signals, a philosophical tradition started by Plato thought that the joy conveyed by laughter is always because of a feeling of superiority over other people, or over our own former position and that ultimately laughter is always related to scorn and aggression. The Superiority

Theory, which made laughter ethically suspect, has been predominant for nearly two thousand years and supported by thinkers such as Plato, Aristotle, [90] and Hobbes [1]. Since Hobbes notably suggested that humans are in constant struggle with each other, it follows that the failure of other individuals is equivalent to our success, and recognizing others' failure induces in us a sudden glory exemplified by a burst of laughter. While Descartes firstly recognized that there are other causes of laughter besides hatred, only from Kant onwards philosophers started to consider alternative accounts of laughter and humour.

A strong argument against the Superiority Theory is that laughter arises first in a context where superiority does not matter. Laughter is common in the early mother–infant playful interactions in both human [91] and non-human primates [90]. Mother-infant play is an everyday occurrence not related to scorn and aggression but rather to teasing and tickling. Later, the laugh expression is most reliably seen and heard in relaxed play among juveniles. These situations are far removed from the expression of strife and hostility postulated by Hobbes and others. In other words, the Superiority Theory is out of touch with the way laugh expressions arise during ontogeny.

A possible link between the Superiority Theory and the use of laughter as a tool for social bonding can be traced back to the work of the French philosopher Henri Bergson, who recognized the intrinsically social nature of laughter. Bergson [92] argued that laughter always occurs exclusively in social contexts, as a form of punishment for out-group members that are unable to conform to social standards. Starting from the observation that we rarely mock someone in the absence of an audience we want approval from, it has been suggested that the emphasis on the individual's inadequacy to social norms can be interpreted as a strategy to reinforce fellowship and cohesiveness in the group, at the expense of the out-group member [93–95]. According to this approach, scorn laughter turns into a specific case of affiliative laughter: the typical dyadic interaction of laughter turns into a triadic one, but the third element—the out-group member to be laughed at—is functional to reinforce cohesiveness with the in-group members. This hypothesis would lead to the prediction that scorn laughter does not differ from affiliative laughter, either from the bioacoustic point of view or from that of neural control—since the difference between scorn laughter and affiliative laughter would rather be in the eyes of those who perceives it, and mainly derived from the social context in which it is produced. However, considering that listeners are able to appraise different types of laughter sounds (joy, tickling, taunting, Schadenfreude) from the acoustical laughter sounds [96,97], an alternative hypothesis is that the switch from a dyadic to a triadic interaction may also affect the motor pattern of laughter production.

Albeit theoretically sound, this hypothesis remains largely speculative. However, there is evidence that primates use affiliative behaviours such as grooming to establish social bonding *with* an individual *against* a third one [98], suggesting that, at least in some cases, affiliative behaviours can be used to mark closeness towards specific subjects and distance towards others, once the dyadic interaction is turned into a triadic one. An example comes from the two sister species of the *Pan* genus. Chimpanzees (*Pan troglodytes*), which are notably less tolerant and more neophobic than bonobos (*Pan paniscus*), engage in more dyadic than polyadic grooming compared to the sister species [99].

(b) From the Social Bonding to the Incongruence Theory

At first sight, to link the Social Bonding Theory with the Incongruence Theory—a theory of humour arguing that laughter emerges when something violates our expectations—seems to be an even more challenging endeavour. In 1998, however, Ramachandran theorized that laughter can be a means through which humans respond to a false alarm. When an individual suddenly ('in a flash of insight', [100, p. 351]) understands that a potentially dangerous situation shifts into a trivial one, the subject reacts with laughter. The higher the latency of this shifting, the higher the motivation to laugh. This is because the high latency between the *spannung* (a figure of speech indicating the climax of the narrative tension) and the final punch line intensifies in the subject the expectation mood.

At a first glance, the False Alarm Theory seems to be formulated to explain the proximate factors at the basis of laughter in a typically human context. Instead, if we take a step back, we can easily realize that the theory can be interpreted from a more naturalistic perspective, with the consequence of a much larger application. During free social play, children and nonhuman animals engage in a large variety of actions of multiple nature. Offensive, defensive and surprising behavioural patterns (e.g. peek-a-boo, ambush) are all recruited in a completely random way to create unexpected situations that seem to be highly pleasurable and rewarding for the subject.

Hence, free social play is an activity specifically built by natural selection to increase unpredictability providing motor and cognitive challenges to the players that experience positive emotions [101]. The linkage between the spontaneity of laugh faces and playful social reward is evident from the data coming both from primates and social carnivores. There is empirical evidence on non-human animals demonstrating that the duration of a playful session is affected by the presence of laugh faces performed by the players [102–104]: the longer the session, the higher the number of laugh faces. Although these studies are correlational and it is, therefore, difficult to establish the cause-effect relationships between the two variables, what appears clear is that laugh faces increase the reciprocity of the playful patterns performed by the players, thus suggesting they are experiencing a relaxed and positive mood [105,106].

However, owing to its physical involvement, social play can also imply a certain degree of risk that seems to be managed by children and animals thanks to different tactics, including the so-called play face often accompanied by play-specific vocalizations [107,108]. This multimodal signal can function not only at a dyadic (between the interacting subjects) but also at a triadic level (between playing subjects and potential bystander). There is evidence that silent play faces are frequently produced when the playmate is in front of the emitter to increase the probability to detect the signal (wild spotted hyenas, *Crocuta crocuta*, and bonobos, *P. paniscus* [109,110]). Moreover, during the play fighting sessions involving juvenile and infant chimpanzees, the older subject tends to perform play faces more often when the mother of the infant is in proximity and can easily follow the entire scene [111]. Such play faces performed by the exuberant youngsters inform the mother of the infant that everything is under control and that it is only play. This finding shows that play faces and laughter in chimpanzees convey a 'false alarm' message highly similar to that suggested for the evolution of laughter in humans. As a matter of fact, we could hypothesize that the False Alarm Theory proposed by Ramachandran has its biological roots in the free physical play during which offensive and surprising behavioural elements are recruited to increase the surprise effect that can flow into a burst of laughter in the end.

Similarly to the False Alarm Theory, the Darwin-Hecker hypothesis—albeit speculative—is worth mentioning because it represents an intriguing attempt to explain humour from a naturalistic and evolutionarily sound perspective, rather than as a uniquely human cognitive trait. Here we argue that this theory also applies to non-human animals. This theory, originally proposed by Darwin [14] and elaborated one year later by Hecker ([112]; see also [113]), predicts the presence of a connection between humorous laughter and tickling, and affirms that two different kinds of tickling can evoke a laughing response in humans. The first one is the direct solicitation operated intermittently on the body of the playmate and the second one is the psychological titillation of the mind owing to a comical idea. In summary, according to the Darwin–Hecker hypothesis, human laughter finds its original point in tickling.

Can this theory also apply to non-human animals or does it remain a prerogative of our species? Tickling is an important part of physical social play, extremely frequent during rough and tumble play, both in human and non-human animals. When tickling is provided by a playmate, is soft and concentrated in areas known to be sensitive to the subject, it often induces a reflex laughter in the receiver. However, in many cases both children and great apes start laughing well before the hands or the mouth of the tickler can reach the body target. Coherently with the Darwin-Hecker hypothesis, in children, the first year of life is characterized by a development of the elicitors of laughter, with intrusive tactile stimulation characterizing the first months, followed by a trend in the second half-year towards laughter at social and subtler visual stimulus situations, including provocative social events, visual incongruities and in anticipation of physical contact [114,115]. Altogether, these observations can be explained by what Darwin [14, p. 201] defined as 'tickling of the mind'. Both humans and great apes can anticipate what is going to happen and their laughing response in absence of any type of body contact suggests they can 'mentally' experience the tickling sensation without being physically tickled. If these anecdotic observations are confirmed in great apes by more rigorous and quantitative approaches, we would have the possibility to understand if the neural circuitry responsible for laughter during physical tickling is the same at the basis of laughter induced by a mental representation of pleasurable situations.

4. Conclusion

Laughter has puzzled philosophers for more than two millennia, but only today we are in a position to unravel its psychological, ethological and neural mechanisms in humans and other animals. There is a growing consensus, emerging from different fields of research, that laughter is a multifaceted behaviour not exclusively related to the expression of humour or happiness. Whereas the philosophical tradition links laughter to the sense of humour, not all laughter is about jokes, and we should not overlook this behaviour's social functions in relation to bonding and play. A new naturalistic account of laughter places less emphasis on humour, and more on the social context of this communicative behaviour. A further conceptual element breaking with the philosophical inheritance concerns the evolutionary continuity of laughter in human and non-human primates, as well as the existence of homoplasic (if not homologue) behavioural traits in rodents. This more naturalistic vision is not an alternative to philosophical accounts. Rather, it can provide the biological scaffold to understand the cultural vision of the phenomenon. We hope that the naturalistic account of laughter sketched in the present opinion piece will boost new research on the multiple contexts in which laughter emerges, the diverse social functions laughter can perform, and the variety of taxa other than primates and rats showing a homologue/homoplasic play signal. Moreover, our attempt to interpret classic theories of humour through the lens of a naturalistic and social account of laughter wants to raise awareness on an understudied phenomenon, that is, the sense of humour of non-human animals, as animals do seem to like and generate surprises, and to show play faces or signals under incongruent situations. Finally, such a 'unity in diversity' framework places laughter in an ideal position to investigate multiple social and cognitive phenomena such as emotional contagion, motor mirroring, facial mimicry, and empathy.

Data accessibility. This article has no additional data.

Authors' contributions. E.P.: conceptualization, supervision, writing—original draft, writing—review and editing; F.C.: conceptualization, supervision, writing—original draft, writing—review and editing; F.B.M.d.W.: conceptualization, supervision, writing—original draft, writing—review and editing.

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

Conflict of interest declaration. We declare we have no competing interests.

Funding. We received no funding for this study.

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