Laughter, bonding and biological evolution

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Abstract

This paper combines perspectives from evolutionary biology and linguistics to discuss the early evolution of laughter and the possible role of laughter-like vocalisation as a bonding mechanism in hominins and early human species. From the perspective of evolutionary biology, we here emphasise several things: the role of exaptation, the typically very slow pace of evolutionary change, and the danger of projecting backwards from the current utilities of laughter to infer its earlier function, hundreds of thousands, or even millions, of years ago. From the perspective of linguistics, we examine both the semantics of the word 'laugh' and the vocal mechanics of human laughter production, arguing that greater terminological care is needed in talking about the precursors of laughter in the ancient evolutionary past. Finally, we turn to hypotheses about how laughter-like vocalisations may have arisen, long before articulate language as we know it today. We focus in particular on Robin Dunbar's hypothesis that laughter-like vocalisation, which stimulated endorphin production, might have functioned as a bonding mechanism (a kind of "vocal grooming") among hominins and early human species.
 The paper contributes to the special issue theme (Humour and Belonging) by casting a long look backwards in time to laughter-like vocalisation as a distant evolutionary precursor of humour, and to bonding as an evolutionary precursor to cognitively and socially modern forms of "belonging". At the same time, it cautions against casual theorising about the evolutionary origins of laughter.

Keywords: laughter, biological evolution, natural selection, vocal grooming, bonding.

1. Introduction

This paper combines perspectives from evolutionary biology and linguistics to focus on the evolution of laughter and its possible role as a bonding mechanism deep in the evolutionary past of the human lineage. Section 2 comes mostly from evolutionary biology. It provides a tutorial on changing understandings about natural selection and why it does not make necessary sense

to say that laughter evolved "for" its current range of social functions or assumed functions. It introduces and explains the key concept of exaptation. It gives an approximate timeline for human evolution.

Section 3 comes mostly from linguistics, looking into the lexical semantics of the word 'laugh' and also examining the acoustic phonetics and vocal mechanics of (non-conversational) laughter. On both semantic and phonetic considerations, we argue that in discussions of laughter evolution, the term 'laughter' is often used in a loose and potentially confusing fashion. For conceptual clarity it is necessary, we argue, to distinguish between "play-vocalisations", "laughter-like vocalisations" and "modern human laughter". Laughter-like vocalisations likely existed for millions of years in pre-human hominins and early human species, whereas modern human laughter (laughter as we know it) is a recent phenomenon.

In section 4, we consider how laughter-like vocalisations could have arisen under natural selection, and we summarise Robin Dunbar's hypothesis that laughter-like vocalisation may have played an important role for bonding in hominins and in early, pre-linguistic, humans. This section is necessarily inconclusive, but (we hope) it is instructive. Section 5 presents concluding remarks, cautioning against casual theorising about the evolutionary origins of laughter.

This paper is in part an exercise in cross-disciplinary communication. We attempt to construct a bridge between evolutionary biology, linguistics, and humour studies, at the same time integrating a number of ideas from comparative primatology, palaeoarchaeology, and cognitive psychology. This means we will need to pay special attention to the terminology and jargon of different disciplines and sub-disciplines. As an expository strategy, the presentation is layered rather than strictly linear, and we often give simplified explanations. Our use of sources and quotations is eclectic and selective, including "trade books" by reputable researchers, as well as publications in scientific journals.

2. Perspectives from evolutionary biology

2.1. What is biological evolution? (or: what does it mean to say this or that evolves for the purpose of X or Y?)

Much thinking about evolution is unfortunately dominated by mechanistic thinking; specifically, by the idea that what a thing is good for at any particular time – its current utility – is its "reason for existence". Even to non-biologists, this means that it has been "built" by natural selection (i.e., it has been directly selected for) on account of it favouring the survival of individuals and the species. Putting it another way, the idea is that features (or characters) of a species have typically evolved on account of them having an adaptive function or purpose. In reality, natural selection (thought by many to be the driver of biological evolution) seldom works this way and this has been understood (and misunderstood) since the time of Charles Darwin. To a large extent, the misunderstanding comes about on account of differing uses and senses of words like 'adaptation' and 'function'.

It was not till 100 years after Darwin that Gould and Vrba (1982) argued, in a landmark publication in evolutionary biology, that conceptual and terminological reform was needed.

> "Adaptation" has been defined and recognized by two different criteria: historical genesis (features built by natural selection for their present role) and "current utility" (features now enhancing fitness no matter how they arose). Biologists have often failed to recognize the potential confusion between these two different definitions. (Gould and Vrba 1982: 4)

Most features, they argued, are better understood not as adaptations, but as what they termed at the time 'exaptations', i.e., features whose origins are not to be explained in terms of their current functions (current utility), but as incidental consequences of something else.

We will come back to exaptations shortly, but before that we want to illustrate with a now classic example that shows how easy it is to mistakenly infer a feature's original function (i.e., its hypothesised adaptive function) from its current utility. The example concerns feathers, birds, and dinosaurs. As many people now know, birds are the direct descendants of dinosaurs; more specifically, of a group of feathered, carnivorous dinosaurs which, along with true birds, are referred to as paravians. A paravian fossil is shown in Figure 1.

Observing the primitive feather-forms in Figure 1, it would seem to be obvious that we are looking at an ancestral flying dinosaur – but this would be mistaken. In fact, a range of evidence indicates that *Anchiornis* could not fly (Pan et al. 2019). And, moreover, although there were flying reptiles (pterosaurs, such as Pterodactyl and Pteranodon) at roughly the same time period, these groups flew without feathers. Hence, feathers did not evolve for the function of flight. The current utility of feathers in assisting avian flight is a later development, an exaptation. Their original adaptive function is unknown but is commonly suggested (without evidence) to be temperature regulation. [1]

Figure 1: Anchiornis huxleyi fossil (BMNHC PH828). The feathers around the body of Anchiornis (a paravian species) revealed a newly-described feather-like character. Photo from Wikipedia, Creative Commons licence (CC-BY-SA-2.0). Photographer credit: Kumiko

At this point it may be useful to note that evolutionary biologists often use the term 'function' to mean that the character evolved for that purpose. For example, in another classic work G.C. Williams (1966) argued that adaptation is "a special and onerous concept that should not be used unnecessarily". He wrote that something should not be assigned a function (in the evolutionary sense) unless there is very strong evidence that it is the result of "design", rather than simply chance or an incidental consequence of something else.

To anticipate, the relevance of this example is that although laughter currently plays an important role in human communication (e.g., in the myriad forms of humour, and in conversational laughter), the evolutionary origins of laughter may well have nothing to do with communication. Before we can commence the discussion of laughter, however, we need some additional background.

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[1] Pan et al. (2019) provide evidence that *Anchiornis* feathers were 'pennaceous', i.e. superficially like those of most modern birds, but that they lacked key ultrastructural and molecular characteristics of extant feathers and were unlikely to have been used for powered flight. It has been plausibly suggested, however, that *Anchiornis* was or became tree-climbing and that its feather-like structures allowed a gliding downward flight.

2.2. Natural selection and exaptation

Gould and Vrba (1982) suggested that when features of organisms are non-adapted but are available for useful cooptation in descendants, such features should be called exaptations. The term adaptation should be restricted to features built by natural selection for their current role. Essentially, to say that something is an exaptation is to say that it has arisen as a by-product of other factors.

Figure 2 shows schematically how evolutionary biologists see evolution as series of cascading effects which result in the development of a trait or a character. In the diagram the term 'function' designates an adaptive, evolutionary function, meaning that it is the direct product of natural selection for that reason or purpose. Each function gives rise to multiple effects which are in real sense the material basis of evolution; cf. Goldschmidt (1982) which includes a relevant introduction by Stephen Jay Gould.

A key principle for understanding biological evolution is to recognise that a single function may result in many effects and that these in turn may set up an "evolutionary cascade". Hence characters – roughly, formal features – are not necessarily for anything since they can be incidental consequences of natural selection and random drift. Indeed, some now argue, in the light of recent developments in genomics and population-genetic theory, that the default suggestion or null hypothesis should be that characters are exaptations (Koonin 2016).
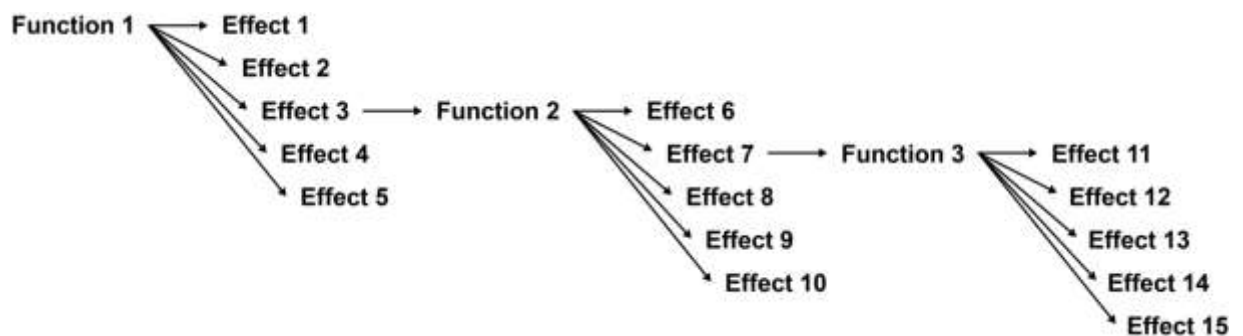
Figure 2: Adaptive functions and cascading effects ("one function, many effects").

Coming now to "laughter" (the double inverted commas indicate that we will later question whether it represents a single character), for an evolutionary biologist the first question must be: Does it have an adaptive function? Is it 'for something' or even 'for anything at all', i.e., can we exclude the possibility that it is an epiphenomenon from the point of view of biological evolution?

The critical thing to be avoided is the tendency to project backwards from current utility (roughly, what something is useful for now) to hypothesised adaptive function.

As we will see, there is evidence to suggest that the biological origins of laughter (tickle-induced vocalisations, play-vocalisations, laughter-like vocalisations) probably existed in ancestral species millions of years ago. The current utilities of laughter, on the other hand, are very much tied up with recently-evolved cognitive abilities (including intersubjectivity and a human-like 'theory of mind') and with recently-evolved modes of communication, i.e., speech.

2.3.   A quick look at the timeline of human evolution

For ease of reference, some terms and approximate dates are listed below. [2] Abbreviations: mya = million years ago, kya = thousand years ago.

– Last Common Ancestor, ancestral apes, bipedal apes: 7-6mya
– hominins, e.g., *Australopithecus* species ('Australopiths'): 5-3mya
– early *Homo,* early human species, e.g., *Homo ergaster/erectus*: 3-1mya
– archaic humans, e.g., *Homo heidelbergensis*: 1mya-500kya
– anatomically modern humans, *Homo sapiens*: 200kya (cognitively modern: 70-60kya)

Note that more than half the entire timeline above is occupied by ancestral apes, bipedal apes, and hominins, followed by a very long period of early *Homo* and archaic humans, prior to the eventual late emergence of anatomically modern humans some 200,000 years ago. Many behaviours that would commonly be thought of as characteristically "human", such as use of composite tools (i.e., tools with two or more parts made of different materials), eating together, cooking and sleeping around fires, and building large shelters, are not in evidence until relatively recently on the 6-7 million-year timeline. As for 'cognitively modern' humans, this term does not designate a species but refers to the expanded cognitive and communicative abilities connected with fully developed languages, complex symbolic thinking, cultural change and diversity, ritual/religion and symbolic art. For scholars in the humanities, in particular, two points that must be emphasised are the typically very slow pace of evolutionary change and the enormous difficulty of imagining the mental and social life of ancestral pre-human species.

As discussed earlier, biological evolution under natural selection relies heavily on emergent exaptations of features which were originally selected for an earlier adaptive function or which arose as a matter of chance. As a corollary, there can be complex and hidden interdependencies (feedback loops, constraints) between apparently unrelated developments, as well as with changes in the physical environment. For example, the gradual transition from living mainly in the trees to mainly on the ground was likely prompted by climatic changes. This made ancestral apes and hominins more vulnerable to predators which increased the value of a more upright stance (for better visual scanning) and made it more advantageous to live in larger groups (Maslin 2017; see section 4.2 below).

To pave the way for discussion of how laughter-like vocalisation might have evolved early in hominin-human history, we now summarise some developments in anatomy, social organisation, communication and cognitive capacities over evolutionary time.

Bipedalism, breath control. Bipedalism developed early (7-5mya), well before the expansion of brain size began (c.3-2mya) (Dunbar and Schultz 2017). Bipedalism enabled the development of the dextrous human hand. It also freed the thorax of its supporting role during quadrupedal locomotion, which permitted flexibility in the coordination of breathing, running and vocalisation. (This is a good example of an incidental effect that was not originally selected for.)

Larger group sizes, less intragroup aggression, social cognition. From about 3mya, expansion of brain size began and at the same time hominins and early *Homo* began to live in ever larger groups, which implies reduced intragroup aggression. Many researchers accept that living with others provided an environment that selected for problem-solving ability and social cognition: the 'social brain' hypothesis (Dunbar 2014; Gowlett et al. 2014; Shilton et al. 2020).

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[2] There are many other genera and species in the family tree of which the human lineage is part. We list here only those used in this paper. It should also be noted that some dates and date ranges are contested.

Communication, cooperation, cognitive development, speech. Cognitive capacity developed very gradually, with long intervening periods without apparent change. Remarkably, there is little evidence of symbolic expression until 150-100kya, but early human and archaic human communication (presumably mimetic) must have been effective in order to support increasing cooperation and coordination of activities, e.g., in tool-making, maintaining fire, and living together in fixed sites over long time periods. Estimates differ widely, but language (speech) as we know it may have developed only in the past 150-100kya (Donald 2001; Christiansen and Kirby 2003; Tattersall 2012; Tomasello 2014; Goddard et al. 2014).

3. Perspectives from linguistics

3.1. Semantic traps to be avoided

Linguistic findings indicate, first, that in its basic meaning the word 'laugh' is likely to be a lexical universal, and second, that this meaning incorporates cognitive-social assumptions that are inapplicable to the precursors of laughter in the deep past.

Lexical semantics, the branch of linguistics concerned with word meanings, is challenging both on account of the inherent difficulty of pinning down meanings and methodological problems which can broadly be termed 'metalanguage issues'. Chief among these is the danger of getting "tangled up in words" by way of excessively abstract, obscure or implicitly circular definitions. Undue reliance on Anglocentric terminology is another hazard (Wierzbicka 2015; Goddard 2020). The most direct attempt to overcome metalanguage issues comes from the NSM (Natural Semantic Metalanguage) approach to meaning description. Like conventional dictionaries, the NSM approach represents meanings using paraphrases based on how people use the word in everyday discourse. Unlike dictionaries, however, NSM paraphrases (also termed explications) are composed of simple, cross-translatable words (Goddard and Wierzbicka 2014). NSM researchers have proposed that all languages have a word for 'laughing' (Goddard and Wierzbicka 2016), a claim which is consistent with the common agreement that laughing is a universal human trait.

For present purposes, we do not need to consider the proposed explication for 'laughing' in full detail, but it will be useful to consider one section of it, shown below. This presents a prototypical scenario which, it is claimed, forms part of common human understanding of 'laughing', embedded in the lexicon. [3]

> people often do this when they feel something good for a short time
>   because they think like this:
>   "something is happening here now, something like this doesn't happen very often
>   people here can feel something good because of it"

The scenario depicts 'laughing' as typically triggered by a person experiencing a brief good feeling occasioned by the thought that, roughly put, something "unusual" is happening and that 'people here can feel something good because of it'. One need not agree with every detail of the phrasing to see that the scenario assumes a well-developed 'theory of mind' and the capacity for something like social empathy. The question then arises: How appropriate is it to use the word

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[3] It is important to take durative uses, e.g. 'She is laughing', as the starting point. A separate but closely-related explication is needed for "punctual" uses, e.g. 'She laughed nervously/scornfully', which do not necessarily imply the same prototypical scenario.

'laughter' to designate behaviours of early ancestral species whose cognitive abilities, and capacity for social cognition in particular, were much more limited than our own?

We will return to this question after considering another aspect of modern human laughter: the nature and production of laughter sounds.

3.2. Acoustics phonetics and physiology of laughter production

The mechanics of human laughing is more complicated than many people would think, and significantly different from homologous behaviours in other primates. Human laughing involves a predominantly egressive (outward) airflow, which requires considerable breath control. As well, it is typically accompanied by "voicing", i.e., vibration in the larynx, which makes the sound louder than it otherwise would be, and it is punctuated into syllable-like bursts. (Modern human laughter can be, and often is, integrated into the speech flow but this is not relevant to its evolutionary origins.)

Because chimpanzees and bonobos are our closest living relatives, they are often used as comparison points for modern humans. As mentioned, it is generally believed that the last common ancestor dates back 6-7 million years. It is therefore significant that in rough-and-tumble play and when tickled, chimpanzees typically make an "in-and-out" panting sound which many have seen as an indication of the precursor to human laughter (Vettin and Todt 2005; Provine 2000, 2012). It is equally pertinent, however, that chimpanzee vocalisation is different from human laughing in terms of its acoustics and vocal production. It is not predominantly egressive, but ingressive-egressive, it is not voiced, and it does not have the punctuated, syllable-like quality of human laughter. All these aspects reflect the fact that chimpanzees do not have the necessary physiology (respiratory and laryngeal musculature, neuromuscular circuitry) to produce sounds comparable to human laughter.

Importantly, we are not referring here to the physiological specialisations necessary for speech, which go far beyond what is needed for laughter vocalisations. For example, speech production requires specialised fine-motor control over tongue, lips and other supralaryngeal articulators (cf. Bryant and Aktipis 2014).

3.3. "Play-vocalisations", "laughter-like vocalisations", "modern human laughter"

In view of the preceding discussion, we suggest that an orderly discussion is best served by using the following terminology. [4]

• Play-vocalisations: for chimpanzees and hominins, linked with social play and ticking.
• Laughter-like vocalisations: for vocalisations closer in form to modern human laughter, presumed to exist in late hominins and early *Homo*, but with significantly different functions.
• Modern human laughter: for laughter as we know it in cognitively modern humans; laughter with a wide range of forms and functions (current utilities).

As readers of this journal well know, modern human laughter can be differentiated into multiple forms and functions. Most of these are tangential to the main concerns of the present study, but it may be helpful to mention the distinction between so-called 'Duchenne laughter' (spontaneous involuntary laughing, including children's spontaneous play laughter, and laughter

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[4] Some authors (Gervais and Wilson 2005; Vettin and Todt 2005; Byrant and Aktipis 2014) have used these or similar terms. Davila Ross et al. (2010) say that because the roots of human laughing go back millions of years it is not anthropomorphic to use 'laughter' to designate pre-human vocalisations or phylogenetically allied vocalisations in apes. To be clear, we are not concerned about whether such usage is or isn't anthropomorphic. Our recommendations are made in the interests of avoiding conceptual confusion and interdisciplinary cross-talk.

elicited by tickling) and 'non-Duchenne' laughter (Gervais and Wilson 2005; cf. Wild, et al. 2003). [5] Only the former is relevant to the present study. Non-Duchenne laughter includes not only volitional laughter, but also conversational laughter, i.e., laughing while speaking (cf. Trouvain 2014; Trouvain and Campbell 2019). The latter requires great precision of breath control and articulatory precision and was obviously only possible after the evolution of speech. Additionally, conversational laughter often involves coordinated laughing between several speakers, which requires precise anticipation of the intentions of one's interlocutors.

4. Hypotheses about laughter evolution and social bonding

In *The Expression of Emotion in Man and Animals*, Darwin (1872) was already very interested in laughter, along with smiling, blushing, and other physical behaviours which exist in other mammalian species. His observations included the fact that laughter provides pleasure, that in apes and humans it is related to social relationships (as can be seen from the fact that self-tickling does not elicit laughter), and that amongst children at play one hears laughter all the time. Darwin did not note the significant fact that laughter is highly "contagious", in the sense that hearing and/or seeing others laugh is often a sufficient stimulus to elicit laughter (Provine 2000, 2012).

Though Darwin did not doubt that human laughter has an ancient evolutionary ancestry (no-one does, really), he had little to say about the mechanics of how it could have evolved under natural selection. In this section we review several studies we consider to be useful contributions to the debate about the biological mechanisms underlying the evolution of laughter – highlighting the possibility that laughter-like vocalisation played a role in enabling hominins and early *Homo* to "bond" more effectively.

4.1. The long timeline to laughter as we know it

Davila Ross and colleagues (2009, 2010) undertook an acoustic analysis of tickle-induced vocalisations in infants and juveniles of several species of great apes (orangutans, gorillas, chimpanzees, bonobos), as well as tickle-induced laughter in human infants. A suite of acoustic measures was examined and compared, such as airflow, voicing (vocal fold vibration) and the number and length of individual 'bursts' per bout. Variation between individuals was taken into account.

The authors reconstructed the likely sequence of phylogenetic emergence, noting that it is consistent with well-established trees based on comparative genetics. The comparative acoustic analysis indicates that primordial laughter-like vocalisation dates far back to the last common ancestor of humans and great apes (including orangutans and gorillas), around 16-10 mya. Davila Ross et al. further inferred that primordial laughter-like vocalisations included a mix of alternating ingressive-egressive and more consistently egressive airflow, along with mixed voicing regimes. They suggested that selection pressures on these pre-existing variations gave rise to the different patterns found in present-day humans and chimpanzees (i.e., egressive airflow and consistent voicing for humans, alternating airflow and little voicing for chimpanzees) after the hominin-human line diverged from the common ancestor of chimpanzees and bonobos. The general picture is summarised in Figure 3 (next page). Needless to say, these findings reinforce the point that laughter-like vocalisations were in place in the human lineage

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[5] Named after 19th century French neurologist Guillaume Duchenne, a 'Duchenne smile' designates a 'stimulus-driven' smile associated with good feeling, produced by involuntary contraction of muscles around the corners of mouth and the eyes. The term 'Duchenne laughter' appears to have been coined by analogy.

when cognitive abilities were much less advanced (e.g., without a modern 'theory of mind'), and much earlier than speech (cf. Byrant and Aktipis 2014).

In its earliest forms, Davila Ross et al. (2009, 2010) suggested, laughter-like play vocalisations were "limited in usage and effect". It was only after the separation of hominins from the common ancestor with chimpanzees and bonobos that there was a dramatic expansion beyond its origins in tickling and social play: "This dramatic expansion of laughter [= laughter-like vocalisation – CG/DL] production most likely occurred in an intermediate hominin species, suggesting that selection could have been acting directly on these sounds. Notably, human infants also produce whoops, pleasure cries and hics when tickled, vocalizations that seem to be absent in the apes" (Davila Ross et al. 2010: 192).
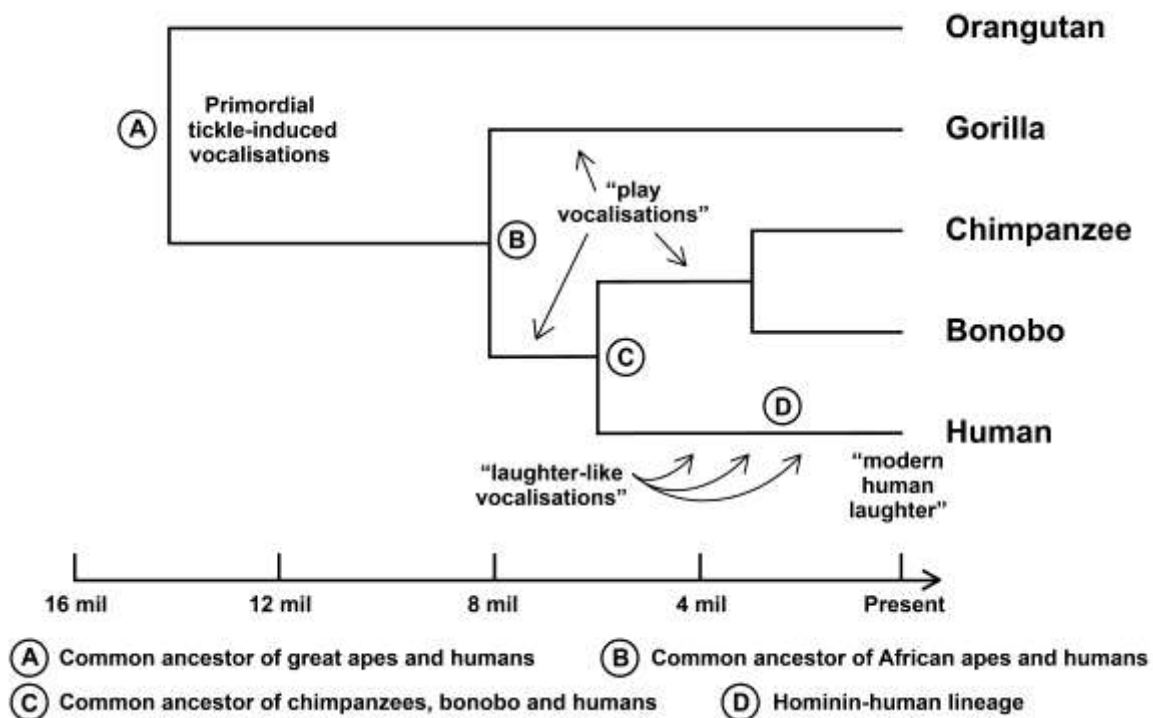

Figure 3. Phylogenetic model of laughter evolution based on acoustic analysis of tickling-induced vocalisations by the Hominidae (after Davila Ross et al. 2009; modified text), Illustration by Lauren Sadow

Before leaving this section, we need to note that the discussion has been about relative timeframes and sequencing. "The question left unaddressed is of course why those particular acoustic properties emerged, and what functions they may have served as laughter became a pervasive and characteristic component of human social communication" (Davila Ross et al. 2009: 1109).

4.2. Dunbar's "Bridging the bonding gap" hypothesis

We now present a well-developed hypothesis, due to Robin Dunbar (2012, 2014, 2017), about a selective mechanism for laughter-like vocalisation in the late hominin-early *Homo* period (roughly 3-1mya). Dunbar and colleagues have long been interested in the selective advantages and costs of varying group sizes and living patterns in species of primates and other social

animals. Multiple studies indicate that larger group size is advantageous in providing better defences against predation and hence better survival (recall that ground-dwelling bipedal apes and hominins were extremely exposed to predation). Any increase in group size is constrained by several factors, however. These include greater time demands on extracting food from the surroundings and the stresses of living in close proximity, especially the demands of intragroup aggression.

In extant great apes, group sizes of up to about 50 individuals are possible due to a distinctive form of 'bonded' primate sociality that relies on (i) coalitions between mutually-supportive pairs or small groups, and (ii) well developed capacities for social cognition, including the ability to understand and anticipate others' intentions and likely future actions. A crucial mediating factor, it is argued, is so-called 'social grooming' which involves pairs of individuals stroking, picking and cleaning each other's bodies. Dunbar (2012, 2017) and others argue that social grooming, which is common among primates but rare in other mammals, triggers release of the opioid brain chemical endorphin, thereby creating pleasurable feelings, calming tensions, and promoting bonding between pairs of individuals who groom one another. Obviously, social grooming can only occur when individuals are together, at rest, and safe. But while social grooming enables larger group size, it also puts an upper limit on group size. This is because grooming takes time. More time spent on social interactions mediated by touch means less time available for food search. As mentioned, a typical upper limit in extant apes is about 50 individuals per group.

Modern human hunter-gatherers, however, typically live in much larger groups (~150) and there is evidence from the fossil record that late hominins and early *Homo* broke through the glass ceiling of 50 individuals 1.5 million years ago or earlier. See Figure 4, paying attention to the timeline. [6] The exponential increases in group size at the top of the Figure are too recent to be the result of biological evolution, but the increased group sizes in the bottom part of the figure – that took place over millions of years – are presumably underpinned by biological evolution. But how?

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[6] Dunbar's estimates of group/community size in fossil populations are derived from the size and structure of fossil skulls. The inferences depend on well-established correlations between cranial volume and group/community size in many extant species, consistent with the social brain hypothesis.
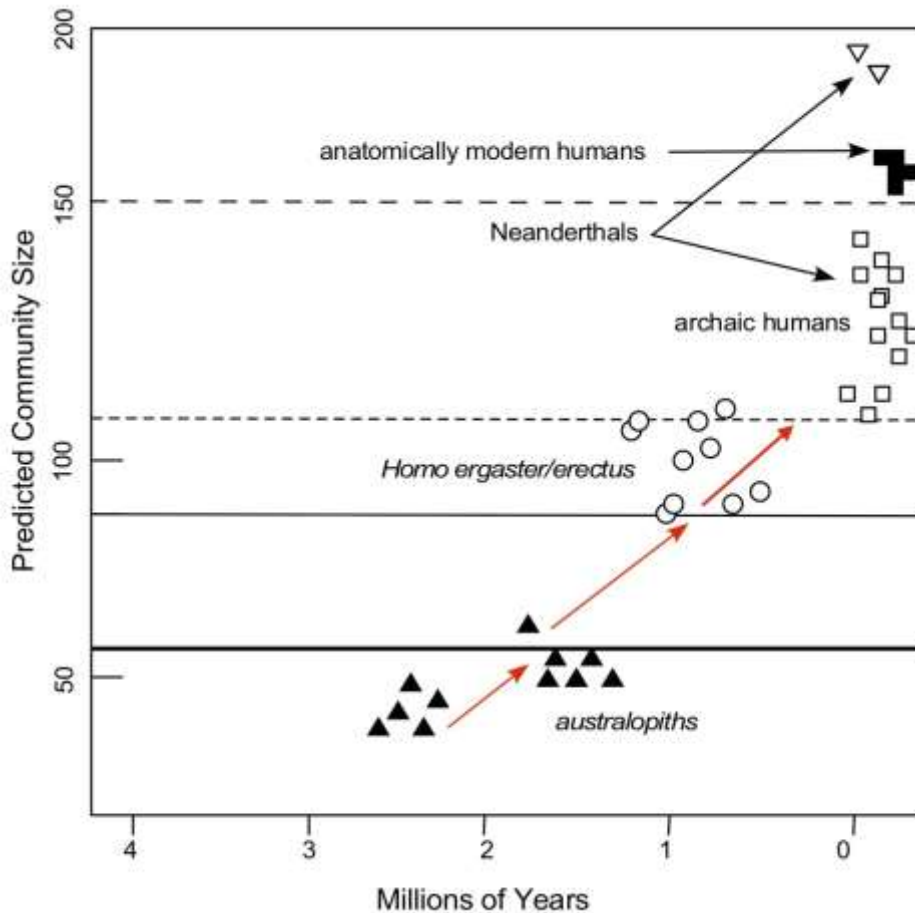
Figure 4: Changes in estimated group (= community) size for hominin and *Homo* fossil populations (after Dunbar 2012, red arrows added).

For Dunbar (2012, 2017), the question comes down to this: How could individuals have triggered endorphin release in others in a more time-efficient fashion than physical grooming? His answer is that laughter (laughter-like vocalisation) provided such a mechanism. The argument depends on two premises: first, that laughter-like vocalisations were already in place; second, that like physical grooming, laughter (laughter-like vocalisation) triggers endorphin activation (cf. Keverne et al. 1989; Manninen et al. 2017). [7] In short, Dunbar proposes that laughter (laughter-like vocalisation) was available to provide "vocal grooming" which could operate at a distance and with several individuals at once.

As previously noted, modern human laughter is highly contagious in the sense that seeing and/or hearing others laugh is often a sufficient stimulus to elicit laughter. Dunbar's proposition is that this tendency likely also existed, variably, in late hominin and early *Homo* populations (i.e. *Homo ergaster/erectus*) and that it became adaptively functional and was therefore selected early in the *Homo* lineage. Dunbar (2012: 1843) also suggests that face-to-face visual contact (eye contact) was likely a factor. He envisages shared laughing (laughter-like vocalisation) as a form of pleasurable "wordless chorusing" between 3 or 4 individuals that reduced stress and promoted bonding between them. With laughter chorusing as a more efficient bonding

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[7] That endorphin release is triggered by laughing as such, as opposed to being in pleasant social situations, is actually difficult to establish and has been disputed.

mechanism, calculations suggest that resulting viable community size would go up to about 108 individuals, which corresponds to the dashed line in Figure 4. [8]

Before leaving this section, we want to draw attention to three things. First, Dunbar's hypothesis – that chorusing laughter (i.e., laughter-like vocalisation) was a crucial mechanism in bridging the "bonding gap" – is just that: a hypothesis. Second, the posited ancestral behaviour, i.e., laughter-like chorusing in small groups, was strikingly different to social laughter among modern humans, in being involuntary and not subject to strategic manipulation.[9] Third, the posited bonding effect was also very different from modern forms of sociality and quite remote from anything that could be meaningfully called a 'sense of belonging'. For example, at the time period in question (prior to 1mya), it is likely that pair bonding between males and females had yet to develop, let alone anything resembling kinship in the modern sense (cf. Chapais 2013; Layton 2020; Planer 2020). Cultural and linguistic diversity as we know it today was still hundreds of thousands of years in the future.

5. Discussion

In this study we have considered only the very early origins of laughter-like vocalisation. Our discussion leaves off before many of the distinctively human characteristics connected with humour and belonging were in existence, including advanced social cognition and language (speech) as we know it. Just to remind the reader (see section 2.3), our species *Homo sapiens* did not appear until 200,000 years ago, and many argue that cognitively modern, as opposed to anatomically modern, *Homo sapiens* are not in evidence till 60-70,000 years ago. In this brief concluding section, we touch on some possible developments on the way to modern human laughter.

5.1. Modern language, laughter and humour

The evolution of language is one of the most contested topics in evolutionary science (Christensen and Kirby 2011). Yet whenever, and however, it came into existence, one thing is certain: "The evolution of language changed the nature of laughter forever" (Dunbar 2014: 269). Previously laughter (or as we would prefer to say, laughter-like vocalisation) had been "a form of chorusing in which – most likely – spontaneous bursts of laughter were triggered by some event (perhaps play, perhaps another's misfortune)". But "[l]anguage changed all that by enabling us to manage laughter much more effectively: we could trigger choruses of laughter" by "telling jokes" (which require high order cognitive skills) and/or by "telling stories" (p270). Dunbar's terminology here is a little simplistic (e.g. 'joking' would have been a better choice of words than 'telling jokes'), but the essential point is surely sound: that language and associated higher-order cognition enabled strategic manipulation of laughter and that this in turn opened opportunities (via exaptation) for laughter to support new forms of social inclusion and exclusion. These matters are beyond the purview of the present paper.

It would be remiss to close without mentioning several proposals about the development of modern laughter, some of which may be plausible as adaptations, or, more likely, as exaptations

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[8] Dunbar's (2017) calculations differ somewhat from those presented in his 2012 study, but the general point remains. As for the steep boost in group/community size from about 500kya, this must be due to other factors. It was still too early for modern language/speech. Intriguingly, Dunbar (2014, 2017) suggests that singing (musical chorusing) may have been the next step in ratchetting up the endorphin-bonding feedback loop.

[9] Incidentally, it is notable that evidence from both evolutionary biology and comparative primatology indicates that laughter and smiling developed along separate evolutionary trajectories; see Provine (2000: 45-46) and Apte (1985: Ch. 8) for an early discussion.

in evolutionarily recent times. Owren and Bachorowski (2003) advocate the 'affect induction' theory, i.e., that laughter allows individuals to induce a positive affect in the perceiver and thereby create a more favourable stance towards the laugher (cf. Owren and Amoss 2014). Miller (2000) proposed that humour evolved as a fitness indicator through sexual selection (cf. Li et al. 2009). Gervais and Wilson (2005) propose that laughter is a reaction to "nonserious social incongruity" and has an adaptive function because it signals a nonthreatening environment and/or "a playful and cooperative intent". Byrant and Aktipis (2014), among others, have proposed that laughter, and especially, co-laughter, reinforces affiliative relationships; while, conversely, Billig (2005) and others have highlighted the role of laughter in social exclusion and ridicule (cf. Viana 2017: 8-12).

5.2. Concluding remark

It should be clear at this point that modern human laughter, i.e., laughter as we know it today, is not a unitary phenomenon in an evolutionary sense. Rather, it is the end product of multiple adaptations and exaptations, some going back eons into evolutionary time, others much more recent. Despite the existence of some plausible hypotheses, the nature, sequence and interplay of these adaptions and exaptations is presently unknown and, in view of the difficulty of obtaining direct evidence, may never be known with full certainty.

Unsatisfying as this may seem, the main implication is that scholars should avoid casual theorising about the evolutionary origins of laughter. It may sometimes be tempting to do so for rhetorical effect (for example, in support of one's preferred theory or hypothesis about humour or conversational laughter) and it might seem to make intuitive sense to do so; but any argument that relies on projecting backwards from the current utilities of laughter to earlier assumed functions is almost certain to be invalid.

Acknowledgements

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