Intentional Use of Laughter in Bonobos and Chimpanzees?

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Although laughter is generally associated with humor and was long thought to be uniquely human, growing evidence highlights its existence in other species like primates or rats. Research on nonhuman primates' laughter emphasizes its emotionality and context-specificity as it mostly occurs during play or when tickled, whereas human voluntary laughter presents such functional flexibility that no classification system seems to exhaust its meaning. Although laughter is identified as a tool to coordinate joint actions by easing transitions between topics and by managing social relationships in humans, these patterns have not yet been investigated in other primates.

Focusing on dyadic social play in two species of great apes, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), we explore the interaction of coordination (transition between moments of an interaction) and social relationships (rank differences and social bond strength) in predicting laughter presence (1/0) and type (contact/non-contact).

We show not only that laughter is used to reengage play in apes, but also that non-contact laughter seems to be a specialized coordination tool used to intentionally reengage play-activity in apes, almost absent at other moments of the interaction, be it during the Main Body or at other transition points. Rank differences and social bond strength did not however appear significant predictors neither of laughter presence nor of type. Although the same patterns were observed between species and although laughter quantity was not directly assessed, bonobos showed a higher propensity to laugh during the Main Body of the interaction and when reengaging play than chimpanzees.

Key words: laughter, bonobo, chimpanzee, social play, joint-action, rank differences, social bond strength, shared intentionality, coordination

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INTRODUCTION

Classifying laughter

Darwin (1872) observed that laughter, conceived as a voiced extension of a smile, indicates a state of happiness. Yet, he further argued that human laughter was not a mere reflexive and automatic action, as tickling could not reliably induce happiness and as laughter could be used strategically to deceive or to mask other emotions such as anger. This definition highlights two fundamental yet paradoxical aspects of laughter: it can both be spontaneous and reflect complex social intents (Gervais and Wilson, 2005). Long thought to be uniquely human, growing evidence suggests that other species possess this ability like rats or primates (Panksepp et al., 2003; Winkler et al., 2021). However, the difference between human and other species' laughter appears to revolve around the potentially intentional aspect of laughter (Wild et al., 2003). Unlike other animals, humans appear to use laughter for diametrically opposed functions, such as easing or damaging social relationships by expressing as varied emotions as politeness, embarrassment, or *shadenfreude* i.e., the pleasure derived by someone from another person's misfortune (Gervais and Wilson, 2005; Feather, 2014; Mauersberger et al., 2022).

Gervais and Wilson (2005) propose the existence of two different types of human laughter. The first, the "Duchenne" laughter, is ancient and evolved from primates' play faces. Thus, being purely involuntary, spontaneous and emotional (Keltner and Gross, 1999; Van Kleef, 2010), it reflects authentic positive affect. In humans, it is considered a hard to fake emotional signal as it is under relatively weak voluntary control (Provine, 2000), and thus tends to be interpreted as an honest signal of affiliation reflecting positive qualities such as honesty or transparency, as well as to be produced partly beyond conscious self-report, thus indicating authentic positive affect between participants (Brosy et al., 2020). The second, "non-Duchenne" laughter evolved more recently and is specific to humans. According to them, this second type of laughter is the one responsible for the functional flexibility observed in humans and apparently not in other species, at least to this extent.

Biological basis of laughter

Anatomical and neural structures

The behavioral cues linked with the Duchenne display, i.e. the authentic emotional expression of laughter absent from non-Duchenne smiles and laughter, refers to the simultaneous contraction of the zygomatic major and orbicularis oculi muscles, pulling the lips back- and upwards and causing the eyes to narrow (Ekman et al., 1990; Shiota et al., 2003; Drack et al., 2009).

The literature on laughter's neural correlates evidences two partially independent neuronal pathways for involuntary (Duchenne) and voluntary (non-Duchenne) human laughter, which are coordinated in the dorsal upper pons (Wild et al., 2003). The first system for involuntary or emotion-driven laughter, shared with other primates, involves the amygdala, thalamic, hypo- and subthalamic areas as well as in the dorsal/tegmental brainstem and is associated with the Duchenne display.

Following behavioral accounts of nonhuman primates' laughter led through brain stimulation experiments (Weinstein et al., 1943), Jürgens (1986, 2002) proposed an emotion-based system accounting for those similarities between species : i) voluntary vocalizations stem from the anterior cingulum; ii) the hypothalamus, amygdala and medial thalamus process the emotional state and its impact on intonation; iii) the PAG works as a relay station, coupling the emotional state with the call, iv) the medulla and the lateral pontine reticular formation (RF) are responsible for their motor coordination. The second one, for human-specific non-Duchenne laughter is under voluntary control as it originates in neortical areas, calling upon the premotor and frontal opercular areas, then leading through the motor cortex and pyramidal tract to the ventral brainstem (Wild et al., 2003; Ackermann et al., 2014). Furthering this hypothesis, Belyk et al., (2022) gathered evidence of two distinct vocal tract combinations during spontaneous and volitional human laughter.

Acoustic features

Broadly defined as a sequence of acoustic bursts, human laughter is characterized by the combination of laryngeal activity and rhythmic respiration (Yanagisawa et al., 1996; Provine, 2000; Bachorowski et al., 2001; Filipelli et al., 2001). This nonverbal vocalization is produced by the air forcing through the glottis and vocal folds, as intercostal and abdominal muscles contract periodically, with more energy in the initial burst, then decreasing over the bout (Titze et al., 2008). These rapid opening and closing of the vocal folds are characteristic of human laughter, resulting in alternated tonal and nontonal components (Bryant, 2020).

Evolution of laughter: a comparative approach

Literature in comparative cognition highlights the acoustic (Darwin, 1872; van Lawick-Goodall, 1968; Gervais and Wilson, 2005; Leavens, 2009) and contextual (Darwin, 1872; Andrew, 1963; Chevalier-Skolnikoff, 1973; Redican, 1982; Preuschoft, 1992) similarities between humans' and other primates' laugh vocalizations. Although nonhuman primates' laughter had previously been described as pant-like vocalizations accompanying their relaxed, open-mouth play-face (Darwin, 1872; Fry, 1994; Provine, 2000; Gamble, 2001; Caron, 2002), further evidence gathered by Davila-Ross et al. (2009, 2010) of two acoustic evolutionary changes in laughter production in Hominidae enabled to establish human and apes' laughter as the same type of vocalization and to bring forward evidence of direct phylogenetic continuity between them, suggesting that human laughter evolved from ancestral apes within the context of play at least 10–16 million years ago.

The main acoustic differences between human and other primates' laughter can be summed-up by three factors: voicing (vocal-fold vibration), pitch intensity (vibration regimes, i.e. patterns of energy distribution over time) and airflow intensity (Davila-Ross et al., 2009, 2010). Human laughter is more voiced, has a more intense pitch and is more strongly vocalized while exhaling than that of nonhuman primates. This shift is further marked by the evolution of discernable exhalation-inhalation sequences in nonhuman primates into exhalation-only bouts in humans (Filippelli et al., 2001).

Analog vocalizations are also found in at least 65 species across taxa (Winkler et al., 2021). It has been mainly studied during social play in great apes (Chimpanzee (*Pan troglodytes*): Van Lawick-Goodall, 1968); Marler and Tenaza, 1977; Van Hooff and Preuschoft, 2003; Matsusaka, 2004; Bonobo (*Pan paniscus*): de Waal, 1988; Förderreuther and Zimmermann, 2003; Gorillas (*Gorilla gorilla gorilla* and *Gorilla beringei beringei*) : Salmi et al., 2013; Schaller, 1963; Fossey, 1972; orangutans (*Pongo abelii and Pongo pygmaeus*), but also in other primates (see Winkler et al., 2021) for a complete review); rats (Panksepp et al., 2003; Burgdorf et al., 2005, 2008), canines (Simmonet, 2004), birds like magpies (Pellis, 1981) and parrots (Diamonds and Bond, 2003; Schwing et al., 2017), as well as in dolphins (Blomqvist et al., 2005).

Social play: mechanisms underlying laughter

In great apes, laughter occurs naturally and mainly during social play (Black, 1984; Davila-Ross et al., 2009, 2010; Vettin et al., 2005; Panksepp, 2012, 2014). Highly versatile and unpredictable (Palagi et al., 2016; Spinka et al., 2001), social play enables to develop the neural connections in the prefrontal cortex responsible for executive functions, which plays a key role in regulating emotions, making plans and solving problems, hence participating in building pro-social brains, able to interact optimally and flexibly with others (Pellis et al., 2014; Palagi, 2018). It has thus been proposed that laughing bares important fitness-relevant benefits like participating to the development of fundamental cognitive and socio-emotional skills (Fredrickson, 2001; Gervais and Wilson, 2005). Laughter has hence been theorized as a way to make manifest their playful mood and shared intention to pursue play activity (Flack et al., 2004; Matsusaka et al., 2004, Cordoni and Palagi, 2011; Bekoff, 1995).

Since playful behavior is borrowed from more serious contexts like mating, agonistic or anti-predatory behavior (Bekoff and Byers, 1981; Fagen, 1993; Pellis, 1988; Pellis and Pellis, 2009), it is all the more crucial for interactants to ensure that their playful session does not escalate into aggression (Cordoni et al., 2023, Palagi et al., 2007; Bekoff 1974, 1995; Bekoff and Allen, 2002, Flack et al., 2004). When playing, laughter seems to be mainly emitted when being tickled or chased, and not the contrary, as well as to increase in frequency with the perceived aggressiveness of their partners actions to avoid the misinterpretation of their reaction as defensiveness, thus encouraging and leading to an increase in the duration of play activity (Matsusaka et al., 2004).

Although the same play faces are produced when laughing and when silent (Davila-Ross et al., 2015), full play faces (upper teeth exposed) appear more salient than the regular play face (upper teeth covered), and laughter more than a play face alone (Parr, 2003; Waller and Cherry, 2012). Like play faces (Palagi, 2008; Palagi and Paoli, 2007), laughter is more frequent during rough-and-tumble (RT) than in any other type of play (Winkler et al., 2021; Palagi et al., 2016). Although no quantitative differences have been reported between the play signals used in contact, rough or gentle play, less facial expressions and gestures are however used during locomotor play, suggesting that contact may be a key factor for apes when assessing risks of escalation into aggression and the need for fine tuning of each other’s playful intentions (Demuru et al., 2015; Davila-Ross et al., 2015).

Some differences in social play have been reported between chimpanzees and bonobos (Palagi, 2006; Palagi and Cordoni, 2012). Bonobos’ neotenic tendencies (Palagi, 2006; Palagi and Cordoni, 2012; Wobber et al., 2010a, b) lead them to engage more in play and to display more full play faces (Palagi, 2006; Palagi and Cordoni, 2012), even as adults (Palagi and Paoli, 2007; Palagi and Cordoni, 2012; Demuru et al., 2015). During ontogeny, if solitary play is performed similarly between species, social play differs when individuals transition from infants to juveniles (Palagi and Cordoni, 2012). Bonobos display longer play sessions, less overt aggressions and continuous use play fighting as they age, contrarily to chimpanzees (Palagi and Cordoni, 2012; Palagi, 2006). They present less formal submission displays and more undecided conflicts than chimpanzees but play in a rougher manner, possibly for social assessment purposes as it is not automatically driven by rank differences (Palagi, 2006). The fact that roughness yields more play faces in bonobos but not in chimpanzees further hints in this direction, reflecting their respectively more egalitarian and more hierarchical social systems (Palagi, 2006). More social play is furthermore observed among females in bonobos, whereas no sex combination appears significant in chimpanzees, which forwards the idea that it presents specific advantages for them in increasing symmetrical relationships and behavioral flexibility (Palagi, 2006; Palagi and Cordoni, 2012).

As such, this study will aim at further exploring the link between physical contact and laughter, as well as at assessing potential interspecific differences in laughter production by weighing in different variables representing laughter's possible functions. The relevance of these measures is developed here under.

Functions of laughter

Emotional regulation: building bonds by sharing laughter

Laughter has high functional flexibility in humans: the case of schadenfreude highlights how much context and in- and outgroup dynamics impact its derived meaning. Indeed, laughter and laughter mimicry are significantly more present when individuals are presented with scenes dubbed "funny" – hence socially accepted as such - than in "*schadenfreude*" scenes, and even less in "disgust" scenes (Mauersberger et al., 2022). The driving factor behind laughter in response to *schadenfreude* scenes appeared to be the perceived deservedness to be hurt of the actors, thus rendering laughter more socially acceptable (Feather, 2014; Mauersberger et al., 2022). In such cases, laughter mimicry means bonding and affiliating with others who laugh about someone else's bad luck, and at the same time, signals the intention to exclude the target of the laughter and sanction their behavior (Elison, 2019).

Shared laughter may thus serve an important purpose in shaping social membership, as it is positively correlated with trust and with a shared understanding of the situation (Martin and Ford, 2018; Smoski and Bachorowski, 2003; Owren and Bacharowski, 2003). It enables to co-construct affiliation (O'Donnell-Trujillo and Adams, 1983; Schenkein, 1972) and is often the result of successful laugh-invitations, which are in themselves cooperative activities within conversations that heighten positive emotion, perceived familiarity and liking (Kurtz and Algoe, 2017). It may hence be particularly helpful in ambiguous or threatening situations, like interactions between strangers, to reduce uncertainty about the feelings and intentions they can attribute each other (Glenn, 2010; West, 1984). Indeed, in interactions inducing positions of vulnerabilities and where trust is not fully established like between strangers, a signal that is difficult to fake emotionally and under relatively weak voluntary control (Provine, 2016), though costly for the sender (Zahavi and Zahavi, 1999), may be especially useful to facilitate and build affiliation (Grønnerød, 2004; Scott et al., 2022).

Although no study has focused yet on whether nonhuman primates take into account the strength of their mutual bonds when laughing, it seems to be a driving factor into their choice of signals while playing or, more broadly, when interacting. Bonobos for instance tend to respond more conspecifics with whom they share a close bond (Levréro et al., 2019). They furthermore use different methods with familiar and with unknown individuals when communication fails, respectively repeating previously successful signals versus elaborating with new ones (Genty et al., 2015). Such results suggest that great apes may be able to distinguish shared from private knowledge by taking into account information from previous interactions with an individual (Genty et al., 2015).

In nonhuman primates, laughter mimicry may also play a key component in fostering interpersonal bonds. As non-Duchenne laughter seems to be unique to humans, laughter in other primates tends to be described as an affective signal beyond their volitional control (e.g. Flack et al., 2004; Matsusaka et al., 2004). However, some studies highlight some of its more strategic and learned aspects. Davila-Ross et al. (2011) reported more use of spontaneous laughter in juveniles than in adults, but an increase of shared laughter during ontogeny as well as inter-colonies differences in its usage rate. They further demonstrated significant acoustic differences between those two types of laughter, with fewer calls per laugh series identified in laugh replications than in spontaneous laughter, and observed the same delay between their shared laughter and humans replicating positive expressions. Such results indicate that the use of this second type of laughter may be learned during ontogeny in other primates as well and may consist in a blend of affective and nonautomatic traits, embodying the evolutionary transition between Duchenne and non-Duchenne laughter. Although only one study focuses on the use of shared laughter in nonhuman primates to this day (Davila-Ross et al., 2011), mimicry seems to be a good predictor of social bond strength (Davila-Ross and Palagi, 2022; Preston and de Waal, 2002, 2017). This trait indeed presents strong evolutionary advantages for social groups to foster affective and behavioral synchronization (de Waal and Preston, 2017; Couzin, 2007).

In this study, we thus attempt to assess the use of unilateral and shared laughter in the colonies studied and to explore the weight of the social bond strength between interactants in predicting them.

Aggression avoidance: preserving the hierarchy

Human laughter can furthermore convey other important social relationships cues. Depending on the way they are voiced (“disinhibited”-“inhibited”), laughs can be perceived as reflecting more or less dominant or submissive social statuses (Oveis et al., 2016). Individuals in less dominant positions tend to laugh more. For instance, during job interviews, applicants laugh more than recruiters (Adelswärd, 1989; Glenn, 2010; Brosy et al., 2020). Brosy et al (2020) further showed that, while laughter wasn’t consciously used as an impression management tactic (Roulin et al., 2014), recruiters perceived negatively unilateral laughter initiated by applicants, but when their invitation to laugh was shared by applicants, they contrarily attributed them with transparency or honesty characteristics. In medical settings, patients laugh more than their doctor, who tend to avoid reciprocating laughter (West, 1984, Haakana, 2001). In the same way, gender asymmetries are also reflected in laughter with women laughing significantly more than men (Smoski and Bachorowski, 2003; Brosy et al., 2020) and engaging more in shared laughter (Adelswärd, 1989; Smoski and Bachorowski, 2003). They also use laughter in different manners: men tend to invite laughter with jokes without laughing themselves (Jefferson, 1979) and to use it for differentiation purposes (Robinson and Smith-Lovin, 2001; McLachlan, 2022), while women tend to accept the invitation to laugh first, thus furthering an invitation to reciprocate laughter (Jefferson, 1979; McLachlan 2022), and use it to mitigate interactional risks towards cohesion (Adelswärd, 1989; Robinson and Smith-Lovin, 2001; McLachlan, 2022).

Laughter in nonhuman primates may transmit information other than purely affective as well. Indeed, apes seem to take into account the social relationships and rank differences of their partner when playing. They for instance produce more play faces when they match in age and size (Palagi, 2008; Palagi and Paoli, 2007). When playing in front of their partner’s mother, younger chimpanzees increase play signaling to avoid the mother interrupting, whereas older partners tend to play more roughly (Flack et al., 2004). Results on shared laughter in chimpanzees (Davila-Ross et al., 2011) further highlights that submissive individuals like orphans of newly established groups tend to replicate more laughter than others, which potentially indicates its use in making playful intentions more manifest when unpredictability and the need risk mitigation are high. The fact that more play faces and laughter are observed in RT or contact play than in other types of play further hints in this direction (Palagi, 2008; Palagi and Paoli, 2007, Winkler et al., 2021; Palagi et al., 2016, Demuru et al., 2015; Davila-Ross et al., 2015). Although no studies have yet been conducted on the matter for laughter, play faces use in relation to rank differences seems to vary between species. Indeed, more relaxed play faces are observed from submissive to dominant individuals in species described as despotic like chimpanzees, whereas the difference does not appear significant in more pacific species (Preuschoft and Van Hoof, 1995; Kim et al., 2022, Petit and Thierry, 1992; Demaria and Thierry, 2001).

The role of rank differences between interactants is thus also evaluated in this study, as a second measure of social relationships.

A coordination tool

To sum up laughter's general functions, conversational, non-Duchenne laughter appears spontaneously and seems to serve the general function of helping to signal intentions in ambiguous situations (Glenn and Holt, 2013; Provine, 1996; Vettin and Todt, 2004) by promoting positive affiliative feelings (Devereux and Ginsburg; 2001; Vettin and Todt, 2004) and mitigating situations of stress (Keltner and Bonanno, 1997) to further cooperation (Mehu and Dunbar, 2008). Contrarily to the stereotype that human laughter mainly occurs in reaction to humor, around 95% of laughter occurs in natural conversation (Martin and Kuiper, 1999), and the speaker produces up to 46% more laughter than their listeners (Provine 1993; La-Greca et al., 1996; Vettin and Todt, 2004). As such, it has also been proposed that laughter's cooperative effects extend to its place and structure in conversation, as a coordinating tool. Strong evidence supports the hypothesis that laughter facilitates potentially delicate transitions between topics, with 99% of laughter occurring during pauses, at phrase boundaries, and at the beginning or end of statements and questions, punctuating speech rather than randomly interrupting it (Provine, 1993, 2000; Brosy et al., 2020). This phenomenon is also present in deaf signers, for whom laughter does not have to compete with speech for priority over the vocal apparatus (Provine and Emmorey, 2006). Laughter can also help solving conversational dilemmas such as the introduction of a new topic (Holt, 2010), or work as a sign of consensus to change between topics (Bonin et al., 2012; Holt, 2010). This coordinating function seems to be preserved in written text messages mimicking everyday conversation (Petitjean and Morel, 2017). It has been described as a way to mitigate feelings of seriousness and to facilitate transitions between serious or less serious topics (Guo, 2023; Myers et al., 2015). Laughter hence appears to be profoundly engrained in human cognition for optimal cooperation and coordination, signaling the participants' engagement and willingness to pursue the joint action that conversation is, when it is at delicate transition point.

Laughter in nonhuman primates also appears to be predominantly social, as it emerged and remains observable only in the context of play (Davila-Ross and Dezecache, 2021; Palagi et al., 2018). However, if laughter has been described as a tool to mitigate ambiguous and potentially dangerous situations (Cordoni et al., 2023; Matsusaka et al., 2004) and as a way to maintain play activity (Enomoto, 1990; Palagi, 2008), it has not yet been specifically investigated as a coordination tool used to manage transition points in nonhuman primates. However, great apes appear to be attentive to the other's attentional state. Though some interspecies differences were reported, they show a strong preference for gesturing in front of an experimenter even when it requires them to move, rather than to use signals to attract their attention before begging for food (Call and Tomasello, 1994; Hostetter et al., 2001; Liebal et al., 2004). Similarly, while playing, play faces appear more frequently during contact interactions than when in movement (Palagi and Paoli, 2007; Demuru et al., 2015; Davila-Ross et al., 2015), suggesting that they are attentive to their recipient's attentional state before using this signal.

Furthermore, flexibly monitoring their partner's attentional state and adapting their behavior to it, they exchange multimodal signals to coordinate their mutual actions. There are records on their ability to participate in joint actions like grooming or social play, and thus to discriminate between shared and private information to achieve joint attention (interactants are willing to share in a joint action) and joint commitment (they share the same goals and intentions towards the joint effort) (Heesen et al., 2017, 2020; Genty et al., 2015, 2020; Pika and Zuberbüehler, 2008, Bangerter et al., 2022).

Heesen et al., (2017) showed that the structure of their play interactions broadly matched that of human conversations (Clark, 1996, 2006; Tomasello and Moll, 2010; Goffman, 1981), identifying macro-phases of Opening, Main Body and Closing, coordinated by micro-phases each made manifest by their own behavioral markers of shared intentionality (Bangerter et al., 2010; Bratman, 1992; Gräfenhainet al., 2009; Levinson, 2016; Schegloff and Sacks, 1973; Tomasello and Moll, 2010). They brought forward evidence of the opening phase serving the purpose of establishing joint attention and joint commitment (pre-entry, entry), of the coordination of play continuation with role-reversal, play type-change, suspension and reengagement after an interruption in the main body, as well as of leave-taking communication signals in the closing phase (pre-exit, exit). As moments of transition embody the uncertainty and vulnerability bound with the (re-)negotiation of the interaction and contain markers of intentionality (Heesen et al., 2017), vocal or gestural signals observed within these short timeframes can reliably be identified as intentional. They indeed signals fulfill the necessary criteria for first-order intentionality, namely (i) a signaler acts with a goal when communicating to a recipient; (ii) the signaler exhibits volitional control over recipient-directed signal production to obtain their communicative goal; and (iii) that the recipient alters their behavior in a way that is in line with the signaler's goal (Townsend et al., 2017; Dennet, 1990).

This framework present strong advantages to measure the use of laughter as a coordination tool in nonhuman primates, as it enables high level of comparability with human behavior and reliably identifies economical markers of shared intentionality. Such research on ape cooperation in a context like social play that demands considerable improvisation and mutual attunement (Bekoff and Allen, 1998, 2002; Palagi, 2006) hence appears to be a particularly good candidate to study laughter in relation to specific moments of the interaction. By applying the framework of Heesen et al. (2017), the present study further attempts to evaluate primates' laughter coordinative purposes.

RESEARCH QUESTIONS AND HYPOTHESES

The present paper aims at investigating the finer details of the evolutionary advantages of laughter by studying the role of coordination and of social relationships in predicting it. We addressed this issue by formulating two distinct research questions summarized in Figure 1 in Appendix, which correspond to our two statistical models: (1) Do moments of transition (subphases only), social relationships and species affect laughter presence? (Model 1); (2) When there is laughter, do moments of the interaction (subphases + main body), social relationships and species affect laughter type (contact (C) /non-nontact (NC))? (Model 2).

We hypothesize that both bonobos and chimpanzees use laughter as a coordination tool to negotiate the start or continuation of play activity at moments of transition. Since laughter in humans is used to manage transition points (Provine, 1993, 2000; Brosy et al., 2020) and is in nonhuman primates linked with play continuation (Davila-Ross et al., 2011), we expect non-human primates to use laughter as a coordination mechanism by producing laughter when play is started or continued, but not when play is disrupted or ended, that is to say as a way to participate in the organization of the joint activity in an orderly manner, sharing in the efforts to achieve group goals. We hence expect laughter to be significantly more present in the subphases pre-entry, entry, reengagement and type change bouts than in suspension, interruption, pre-exit and exit bouts.

Since signals produced at transition points can reliably be identified as intentional (Heesen et al., 2017; Townsend et al., 2017), we further hypothesize that laughter is used differently at transition points and during the main body of an interaction. As physical contact appears to yield more laughter, than non-contact play in nonhuman primates (Demuru et al., 2015; Davila-Ross et al., 2015), we propose the absence of physical contact as a new proxy for identifying potential intentionality in laughter. We indeed expect to observe more laughter not caused by contact at transition points where the nature and continuation of the interaction needs to be negotiated, whereas we expect to witness more automatic, contact-driven laughter during the main body of the interaction.

As chimpanzees exhibit more authoritarian and competitive tendencies than bonobos (Palagi, 2006; Palagi & Cordoni, 2012), we can expect a higher drive of rank differences on laughter production in this species. On the contrary, in line with their neotenic tendencies and thus higher propensity to play and to use it to form close symmetrical social bonds (Palagi, 2006; Palagi & Cordoni, 2012), we can expect social bond strength to be more significant than rank differences in predicting laughter in bonobos, as well as expect to find more (sub)phases containing laughter in bonobos than in chimpanzees.

If our hypotheses are supported and laughter in nonhuman primates exhibits some volitional properties, distinguishing different levels of analysis of its cooperative and prosocial compounds may help untangle and weigh which evolutionary advantages drove the transition between Duchenne and non-Duchenne laughter in humans. Although we do not expect non-Duchenne laughter in nonhuman primates, we can however fathom the expectation of its first-degree use in both primate species studied, with no significant differences in the patterns they may exhibit, hence the use of laughter to communicate about beliefs and desires, but not to convey beliefs and desires about beliefs and desires (Townsend et al., 2017; Dennet, 1990).

METHODS & INTERNSHIP

Sampling

We conducted our observations on bonobos (*Pan paniscus*, N = 12; Age between 2-24, F= 7, M=5) and chimpanzees (*Pan troglodytes*, N = 11; Age between 4-44, F= 5, M=6) using 100 videos of dyadic social play for each species (see Table 1 in Appendix for detailed group composition). We determined our sample size using an online sample calculator from Easy Calculation (Ver. 2022). For a confidence interval of 95%, a margin of error of 5% and a population of 66 possible bonobo dyads and 27 possible chimpanzee dyads, our minimal sample size is of 56 observations for bonobos and 25 for chimpanzees.

Participants were recorded at two different zoological parks in France, La Vallée des Singes for both species, and Sigean for additional data on chimpanzees. Videos were recorded from April to September 2017 by Raphaela Heesen and a trained assistant in La Vallée des Singes and from June to August 2018 by Aude Pajot in Sigean.

La Vallée's site is composed of large enclosures with an outdoor island encompassing a spacious forest and climbing structures in grassy areas (8000 m^2 bonobo, 7500 m^2 chimpanzees) as well as an indoor enclosure with various enrichments and climbing structures (600 m^2 bonobo, 220 m^2 chimpanzees). In stable weather conditions (>13°C), the group is locked in their outdoor enclosure. Water is always available from a fresh water source at the building and a stream surrounding the island.

Bonobos and chimpanzees hosted in La Vallée receive food five to six times a day, including daily rations of primate pellets, fruits, and vegetables. Occasionally, they also receive rice, nuts, meat, and eggs. Individuals can additionally forage for wild berries and herbaceous vegetation in their outdoor enclosure. In stable weather conditions (>13°C), the group is locked in their outdoor enclosure.

Sigean's site consist in a 200 m^2 indoor and a 1.3 ha outdoor island compound. During the day, they are kept on the outdoor island that features natural vegetation, bushes, trees, sand, a surrounding water pond, climbing structures, bridges and shelters. The group is provided with food six times a day, including vegetables, fruits, primate pellets and nuts, and chicken and eggs once a week.

Fresh water for all groups is always provided and all groups can also drink from water sources in their outdoor enclosures.

During our pilot study and pre-tests, we also used data from two additional sites, Basel Zoo (CH) and Lola ya Bonobo (RDC), which were excluded from subsequent analyses as they did not match our observational requirements.

Data collection

Videos were recorded using two Panasonic HC-V770 Camcorders on tripods with externally attached directional microphones (Sennheiser MKE 400) placed at the two different locations. R.H. was standing in the public area and filmed the dyads of interest as well as the whole group. Play bouts were recorded from the beginning (both partners start to play with one another) until the end (partners have stopped playing for at least two minutes), including interruption periods. R.H. timed the interaction from its onset to the predetermined interruption time.

Due to COVID-19 restrictions at the time of my internship, we were not able to create our own video corpus, specifically tailored to the requirements of recording and analyzing nonhuman primate laughter.

Pilot study and pre-tests

To realize this study, I followed a year-long internship with E. Genty, who supervised the procedural steps necessary for a reliable and replicable data collection process.

Pilot study on apes

We first conducted a pilot study on chimpanzees and bonobos to assess whether laughter was clearly identifiable in our video corpus, using 100 different videos than the ones used in the final experiment for each species. We dedicated three weeks to training to get acquainted with the open-source software ELAN to be able to annotate video recordings, and with nonhuman primate behavior to be able to distinguish laughter from other actions such as trying to bite, sex, or vocalizations like Pant-Hoots. Based on this first training session, we noted the relatively low audio quality of our recordings and decided to first annotate laughter when heard as well as when identifiable through behavioral proxies such as the full play face or repetitive jerking belly movements.

However, our interrater reliability, realized with A. Doerr who annotated the totality of our chimpanzee sample, was low (file missing, approximately 30%) which led us to realize three subsequent pre-tests to better define our variables operationally.

Based on Davila-Ross et al. (2011), we assessed shared laughter presence as laughter produced by both participants within a five-seconds timeframe, but did not find any occurrence in our corpus, which is in line with previous research evidencing that this behavior was not consistent across populations (Davila-Ross et al., 2011; van Ljzendoorn et al., 2009). This outcome was hence excluded from future analyses.

Subsequent pre-tests

Do we need to hear laughter to reliably code it?

The first implication of our low interrater agreement rate is that identifying laughter without conditioning it to its characteristic vocalization may not be a sufficiently restrictive nor reliable method. Although we expected some laugh instances to be missed due to movements and to the low audio quality of our recordings, this more problematically lead us to count as laughter behaviors that could have been something else. For instance, we manually observed cases where we could not distinguish when a play face was with or without laughter in the absence of reliable sound, even with belly movements as an additional proxy.

As such, we compared our annotations on N=20 videos, coded twice, once with sound and once without for both coders (E.G. and L.V.M.). To avoid biases linked to the audio-visual quality of our recordings, we used videos from another corpora, collected by E. Genty in 2021 at the Lola ya Bonobo sanctuary specifically to observe laughter. Since they did not contain full interactions analyzable in phases, they were not usable for the purpose of our research. However, their high audio-visual quality enabled us to precisely sample interactions which did (N=10) or did not (N=10) contain laughter, before randomizing them for this double annotation process.

Results show 40% (N=16/40) of agreement, indicating that sound is indeed a necessary condition for a reliable identification of laughter. Among the instances of disagreement, we find that 50% (N=12/40) correspond to missed instances, and the other 50% (N=12/40) to misinterpretation of behavior as laughter. These results signal both that visual cues are not sufficient to reliably identify instances of laughter, and that they lead to identifying laughter when there is none.

Sound-quality test: Do we have enough videos available to achieve an optimal sample size?

Consequently, we needed to exclude from our sample videos that did not match our new audio requirements and to assess whether we had enough exploitable videos in our corpus to match our optimal sample size. We first excluded all interactions that did not contain an audio file or which were filmed indoors, where vocalizations can hardly be heard due to glass barriers. In order not to bias the selection of the remaining videos by including only those where laughter could be heard, thus arbitrarily discarding interactions devoid of laughter, we established other criteria for sampling. Namely, we included videos in which we could hear apes walk, as well as insects chirping or leaves rustling. On the contrary, we excluded videos where the wind or other background noise like tourists were too strong and saturating our audio recordings. However, some recordings containing comments from zookeepers were retained when they matched our inclusion criteria. Other factors irreducible to our corpus such as the distance between the experimenter filming and the apes may also have affected our capacity to detect laughter.

We first assessed the N=87 videos fully pre-annotated for phases by E.G., out of which N=50 met these new inclusion criteria. We then assessed a total of N=470 videos, out of which we retained N=199 exploitable ones. Among those, we randomly selected N=100 chimpanzee videos and N=50 bonobo videos.

Is there an age bias for who tends to laugh more (juveniles v.s. adults)?

We further used this sampling process to assess potential age biases in our corpus. Although the literature highlights a higher propensity to play in bonobos than in chimpanzees due to their neotenic tendencies (Palagi, 2006; Palagi and Cordoni 2012), we wanted to further play partners diversity between species and to try to assess the extent of the generalization we could potentially formulate on laughter in apes.

Out of the N=60 videos assessed for chimpanzees using videos sampled in La Vallée that were not included in further analyses, we identified 37% (N=22) of interactions among juveniles, 26% (N=16) among adults and 37% (N=22) mixed, among which the adult laughed in 41% (N=9) interactions and the juvenile in 59% (N=13) interactions.

Out of the N=60 videos assessed for bonobos using videos sampled in Lola ya Bonobo to avoid depleting our usable set of bonobos videos, we identified 20% (N=12) of interactions among juveniles, 46% (N=28) among adults and 33% (N=20) mixed, among which the adult laughed in 30% (N=6) interactions and the juvenile in 70% (N=14) interactions.

Except for expected neotenic effects in bonobos, this test enabled us to determine that no significant age biases in laughter production should stem from differences in partner diversity between species.

Pilot study on human children

Since one of the advantages of the framework of Heesen et al. (2017) is its high inter-specific comparability, our initial project entailed a direct comparison between human and non-human primate's laughter in dyadic social play. However, annotation tests on two available corpora on human children showed poor exploitability for the purpose of our research and were hence excluded from the final project.

Additional work realized during my internship with E. Genty

In order to annotate for phases the videos remaining for bonobos (N=50), I was trained during 4 weeks by E.G. to apply the framework used in Heesen et al. (2017).

During my internship, I also had the opportunity to participate in the interrater agreement of Sebastien Quigley's study on ape's gesture amplitude as part of his MS Thesis. As such, I was thoroughly trained in the recognition of gestures and of their amplitude by E. Genty during six weeks, before annotating N=156 videos. I also participated in writing the R code for the power analysis necessary to compute the inter-observer agreement rate.

Final procedure & video annotation

We dedicated eight months to annotating our video corpora using the software ELAN (See file in Appendix "Joint-Action Protocol for ELAN (Heesen et al., 2017)"). We created a tier, i.e. a variable line in ELAN, for each player (ID1, ID2), where ID1 is the initiator of the interaction. The tier Activity-type represents the activity performed together by participants, which enables not only to distinguish between chase (running) and contact play (still or walking with body contact) but also to exclude sex or grooming bouts from our analysis since laughter is not expected in the absence of social play.

Phase annotation

Macro-phases, delineating the opening, the main body and the closing, and micro-phases, representing moments of transition i.e. Subphases, were annotated in two different tiers as they embody different levels of the interaction. Concerning macro-phases, we excluded from our analysis bouts overlapping with subphases, as we needed the moments of transition and the main body of the interaction to be mutually exclusive. Joint attention and joint commitment, alongside partner, location, and activity choice, are established in the opening phase. The main body phase, which designates where the main business of the interaction unravels, as partners maintain joint commitment to the activity and show mutual responsiveness. In the closing phase, they establish mutual agreement to stop interacting and disengage from their joint activity.

Within subphases, in the opening, the pre-entry corresponds to the moment when partners are selected and when joint attention (mutual gaze) and joint commitment (mutual conviction that both partners are willing and ready to interact) are established. It starts at the onset of the initiator's approach toward their partners and stops when mutual gaze is achieved. When partners reach joint attention starts the entry, which relates to the choice of content, nature and location of the interaction. It stops at the onset of the first movement typical of the joint activity (e.g. First body contact or running movements), when the main body starts. When ID1 initiates play without joint attention, only a pre-entry is annotated.

In the main body phase, we annotate subphases embodying moments of play negotiation. When the interaction and joint attention are interrupted by one or both partners, we annotate an interruption, which starts when partners cease all characteristic movement of the activity and ends when they resume said movements. Interruptions need to last at least 3 seconds and maximum 2 minutes. To better capture these transition points, we surround interruptions bouts by 3 seconds-long suspension and reengagement segments, where signals respectively linked with the breaking off from play (e.g. "Push") and with its recommencement (e.g. "Grab", "Touch") are used (see Byrne et al.,2017). When the nature of the activity or partners' roles are re-negotiated as play continues, we respectively identify 200ms type-change and role-reversal subphases. As those transition points are swift, we added 1500ms segments before and after to better account for potential laughter linked with these moments of negotiation. However, due to too few occurrences (n= 8), role-reversal bouts were discarded from final results.

We observe in the closing, subphases linked with final play disruption. Symmetrically to the opening phase, it can be composed of a pre-exit, where one signals their will to stop playing without reaching agreement, and of an exit, where this mutual conviction is reached and all characteristic movements of play cease. The exit bout stops the instant joint attention is disrupted, either with the first gaze back after play interruption if they don't reengage in an activity within 2 minutes, or when they engage in another activity.

Laughter annotation

To be reliably identified in our video corpus, we assessed that laughter necessarily needed to be heard as rapid voiced or unvoiced inhalation-exhalation bouts, with at least one inhalation-exhalation sequence. It was coded as two different laugh occurrences when more than three seconds separated heard bouts. Other cues correlated with but not sufficient to identify laughter are the full play face/open-mouth display and belly movements linked to the specific respiratory pattern of this vocalization (Yanagisawa et al., 1996; Bryant, 2020; Provine, 2000; Bachorowski et al., 2001).

We first created a laughter tier for each ID for a primary delineation of laughter bouts. Although this method implies some information about quantity, laughter quantity was not directly assessed in our study, as too many confounds regarding the audiovisual quality of our recordings could not be eliminated. However, this tier later enables us to assess not only whether a (sub)phase contains laughter or not, but also whether we find one or both type.s of laughter in it (contact/non-contact).

A laughter presence tier was added for each player, containing 200ms segments under each subphase and at the end of the main body, which indicate “1” if laughter is initiated there and “0” if it isn't. When laughter was heard, it was coded as present only in the bout in which it was initiated, discarding overlaps between phases to create the least possible bias due to laughter bouts delineation. Laughter was coded only when produced between our interactants.

We defined contact laughter as laugh occurrences produced by the partner's contact, while tickling, biting or while using tactile gestures like “Grab” or “Touch “(See Byrne et al., 2017). On the contrary, we describe non-contact laughter as laughter not primed or driven by contact. In more practical terms, this does not exclude the possibility of a physical contact between partners, but it excludes from NC laughter occurrences produced within one second after tactile gestures, tickling or biting the vocalizer. This information is coded in the two first Laughter tiers, as “C” or “NC” within primarily delineated laughter bouts.

Interrater agreement

After a two weeks training at reliably recognizing laughter, a third party (Luca De Giorgi), ignorant of our hypotheses and predictions, annotated 20% (N=40 videos) of our data with an equal proportion of chimpanzee and bonobo videos.

We calculated the intraclass correlation coefficients (ICCs) between our laughter annotations, both for presence and type, to assess the reliability of our measurements. The analysis used a two-way mixed-effects model with absolute agreement for single and average measures.

For single raters, the ICC values indicated moderate reliability: absolute agreement (ICC1) = 0.56, random raters (ICC2) = 0.56, and fixed raters (ICC3) = 0.57. The F-values for these measures were 3.6, with degrees of freedom df1 = 2392 and df2 = 2393 or 2392. All p-values were less than .001, indicating that the results were statistically significant. The 95% confidence intervals for these measures ranged from 0.54 to 0.59.

For average raters, the ICC values reported good reliability: absolute agreement (ICC1k) = 0.72, random raters (ICC2k) = 0.72, and fixed raters (ICC3k) = 0.72. The F-values for these measures were also 3.6, with degrees of freedom df1 = 2392 and df2 = 2393 or 2392. All p-values were less than .001, indicating statistical significance. The 95% confidence intervals for these measures ranged from 0.70 to 0.74.

These results suggest that the measurements have moderate to good reliability, both for individual raters and when averaging across raters. The ICC values, combined with the narrow confidence intervals and significant p-values, indicate a fair to high degree of consistency in the measurements across the subjects.

Rank differences and social bond strength measures

We used rank differences and social bond strength measures reported in Heesen et al. (2021), who used the same population and corpus as the ones used in this research. To compute rank differences, Elo-ratings were established (Neumannn et al., 2011; Albers et al., 2001) for individuals of each site using the ‘EloRating’ package in R (Neumannn et al., 2014), which rely on the outcomes of agonistic interactions between partners and depend on the sequence in which interactions take place over time.

To compute the social bond between partners, we used an inverse proxy referring to the social affinity or social bond strength between partners, the dyadic composite sociality index (DSI) (Silk et al., 2006, 2013) using the ‘socialindices’ package in R (Neumannn et al., 2016). The values of the DSI scale can range from 0 to 1. Lower DSI values indicate weaker bonds, and higher DSI values indicate stronger bonds. Our DSI computation included the measures of partners’ duration of grooming and play, their proximity rates (i.e. having been in arm reach distance) and their approach rates (i.e. focal having approached the partner or the partner having approached the focal).

Ethical Agreements

We received ethical agreement to collect and use data from the Commission d’Ethique de la Recherche of the University of Neuchâtel (based on agreement number: 01-FS-2017), the internal ethical committee of La Vallée des Singes, the UCSD Human Research Protections Program (Project number: 161452S), the IACUC committee of San Diego Zoo Global (Project number #17-007), the internal ethical committee of the Réserve Africaine de Sigean, and the Kantonales Veterinäramt BS at Basel Zoo.

RESULTS

We carried out our statistical analyses with the R software package (v. 2023.03.1+446). We created two subsets for each studied outcome, laughter presence (1/0) and laughter type (C/NC). As our design presents hierarchical dependencies and binary outcomes, we built a logistic regression model for each outcome using the glmer function in R with dyad as a random factor with random intercept but fixed slope for both our models. Due to too few occurrences, the subphases role-reversal (N= 8) and pre-exit (N=10) were excluded from our dataset. Missing values were also removed prior to analyses.

Model 1:

A Generalized Linear Mixed Model (GLMM) was fitted using the Laplace approximation with a binomial distribution and a logit link function to predict the presence of laughter based on the subphases, rank differences, social bond strength, and species, with random intercepts for dyad. The model's AIC was 443.5, BIC was 476.0, and the log-likelihood was -215.7. The model deviance was 431.5 with 1652 residual degrees of freedom. The variance for the random intercept dyads was 0.3698, with a standard deviation of 0.6081, indicating moderate variability in the intercepts across dyads.

The effect of subphases was significant ($\beta = 1.6936$, SE = 0.2951, $z = 5.740$, $p < .001$), suggesting that reengagement is a subphase associated with the highest likelihood of laughter. The effect of species was also significant ($\beta = -1.4867$, SE = 0.4181, $z = -3.556$, $p < .001$), indicating that chimpanzees were less likely to exhibit laughter compared to bonobos. Social bond strength ($\beta = 0.0428$, SE = 0.1147, $z = 0.373$, $p = .709$) and Rank differences ($\beta = -0.0447$, SE = 0.1589, $z = -0.282$, $p = .778$) were however not significant predictors of laughter presence.

A further Analysis of Variance (ANOVA) confirmed a significant effect of subphases on laughter presence ($\chi^2(1) = 32.94$, $p < .001$) and of species on laughter presence ($\chi^2(1) = 12.64$, $p < .001$). However, the effects of Rank differences ($\chi^2(1) = 0.079$, $p = .778$) and of social bond strength ($\chi^2(1) = 0.139$, $p = .709$) were not significant.

As shown in Figures 2 and 3, among subphases, Reengagement was the category where laughter was significantly the most present, which supports our hypothesis that both bonobos and chimpanzees, although to a significantly lesser extent than bonobos, use laughter as a coordination tool to negotiate the start or continuation of play activity at moments of transition. Further pointing in this direction, other subphases linked with the negotiation of how and if play continues also contained laughter, whereas those linked with play disruption (except for suspension, which will be further examined in the Discussion section of this paper) contained none.

Model 2:

A generalized linear mixed model (GLMM) was used to examine the relationship between the predictors subphases, rank differences, social bond strength, and species and the response laughter type (C/NC), while accounting for the random effect of dyads. Employing a binomial family with a logit link function, the model showed a reasonable fit with an AIC of 102.5, a BIC of 121.0, a log-likelihood of -44.2, and a deviance of 88.5 with 97 residual degrees of freedom. The scaled residuals ranged from -1.6769 to 4.5832. The variance for the random intercept of dyad was 0.804, with a standard deviation of 0.8967. This suggests a moderate level of variability in the intercepts across dyads.

The intercept was highly significant ($\beta = -4.5313$, SE = 1.3726, $z = -3.301$, $p < .001$), indicating that, when all predictors are at their reference levels, the log-odds of NC laughter are significantly negative. This suggests a low probability of non-contact laughter occurring independently from our predictors, contrarily to contact Laughter. Subphases was also significant ($\beta = 5.0972$, SE = 1.4016, $z = 3.637$, $p < .001$), indicating a strong positive association between non-contact laughter and transition points. If social bond strength does not appear overall significant ($\beta = 0.8646$, SE = 0.4495, $z = 1.923$, $p = .054$), it however presents an interaction with subphases ($\beta = -1.0803$, SE = 0.4837, $z = -2.233$, $p = .026$), suggesting that if it may not be a good predictor of non-contact laughter at transition points, it has a positive effect on contact laughter during the main body. The effect of rank differences showed however no significance ($\beta = 0.1980$, SE = 0.3202, $z = 0.618$, $p = .536$), indicating that it did not significantly influence the observed outcome. Species was also non-significant ($\beta = 0.3412$, SE = 0.8837, $z = 0.386$, $p = .699$), suggesting low variability between species in the patterns they exhibit.

A further Analysis of Variance (ANOVA) confirmed the significance of the predictor subphases ($\chi^2(1) = 8.688$, $p = .003$) and of the interaction between subphases and social bond strength ($\chi^2(1) = 4.988$, $p = .026$), as well as the non-significance of species ($\chi^2(1) = 0.149$, $p = .699$), rank differences ($\chi^2(1) = 0.383$, $p = .536$) and of social bond strength ($\chi^2(1) = 0.0005$, $p = .981$) on laughter type.

As shown in Figures 4 and 5, subphases thus appeared a significant predictor of laughter type, supporting our second hypothesis that contact laughter occurs predominantly during the main body (and more anecdotally in the entry, which will be further examined in our Discussion & Conclusion section) whereas non-contact laughter occurs mainly at transition points (predominantly reengagement) and can hence be used intentionally. Furthering this hypothesis are the significant intercept indicating an important effect of our predictors on non-contact laughter, but not on contact laughter, as well as the unexpected interaction between social bond strength and subphases represented in figure 6 suggesting that social bond strength is a significant predictor of laughter type only in the main body but not at transition points. Contact and non-contact laughter may thus serve distinct functions and depend on different drives. Our results suggest that non-contact laughter may work as a specialized tool to negotiate transitions, whereas contact laughter may be used more automatically to show positive affiliative feelings.

DISCUSSION & CONCLUSION

The aim of this paper was to investigate the evolutionary advantages of laughter by studying the effects of coordination as joint-action (macro-phases and subphases), social relationships (social bond strength and rank differences) and species (bonobos and chimpanzees) in predicting laughter presence and type (C/NC). Our results supported our hypothesis that both bonobos and chimpanzees (although to a lesser extent than bonobos) use laughter as a coordination tool to negotiate the start or continuation of play activity at moments of transition by producing laughter when play is started or continued, but not when play is disrupted or ended. They further supported our hypothesis that the absence of physical contact may be a good candidate as a new proxy for identifying potential intentionality in laughter, as both species exhibit a differential use of contact and of non-contact laughter, with NC laughter occurring almost only at transition points, where the nature and continuation of the interaction needs to be negotiated between participants, and C laughter during the Main Body, where play activity is ongoing and stable. Our results further suggest that non-contact laughter may have evolved for coordinative purposes as a specialized tool to make manifest the caller's intention to reengage play. Our hypotheses concerning social relations were however not supported, with no overall effect of either social bond strength nor rank differences on either laughter presence nor type and no differential patterns between species. However, the unsuspected interaction between social bond strength and subphases revealed further evidence in support of our hypotheses, suggesting that social bond strength is a significant predictor of laughter type only in the Main Body but not at transition points, and hence that contact laughter may be used in a more automatic way to show positive affiliative feelings when the negotiation of the interaction is not at stake.

Such results appear to validate the framework developed by Heesen et al. (2017) to use the coordination of interactional phases to identify first degree intentionality. Considering the differential observation that non-contact laughter serves as a specialized tool used to reengage play activity whereas contact laughter is used more automatically during the main body implies not only that apes are context sensitive, but also that they volitionally and flexibly use laughter to signal their will to pursue play activity at specific transitions points when play continuation is mutually unsure. As such, and although this study does not directly assess the three commonly accepted criteria for first order intentionality in prelinguistic humans and nonhuman animals, namely that a signaler i) acts towards a goal, ii) to change their recipient's actions to obtain this communicative goal, and iii) that the recipient does so

(Townsend et al, 2016; Kirsty et al, 2019), using the framework of Heesen et al. (2017) dedicated to do so enables to reliably control for these variables. Our findings, which appear to support the almost unprecedented hypothesis (Davila-Ross et al., 2011) that laughter can be used as an intentional signal of first order both by chimpanzees and bonobos (Byrne et al., 2017; Townsend et al., 2016), should encourage to further replicate it in future research. Adding other multimodal signals compatible with this framework such as the gaze or facial expressions used between interactants could further help in validating the reliability of our results.

Fitting emotions within cognitive accounts of intentionality thus appears to be an enduring challenge in both human and nonhuman apes' studies. Mimicry, and in our case, shared laughter, has been the main proxy in past studies to study this issue through the prism of emotional contagion (Davila-Ross et al, 2011, Demuru et al, 2015). However, our differential results on laughter type suggest that the intentional use of emotional signals used for emotional contagion such as laughter when used to influence one's disposition to play can also be studied through the prism of coordination (Heesen et al, 2017; Brosy et al, 2020). The highly significant proportion of non-contact laughter found specifically when reengaging play seems to hint in this direction. Future research could be focused on replicating our findings on other emotional signals by using the framework of Heesen et al. (2017). It could also focus on shared laughter absent in our dataset, which further seems to replicate previous findings that the use of shared laughter may or may not be learned through ontogeny between non-human ape colonies (Davila-Ross et al, 2011).

Some slight differences were observed between our predictions and our observations, and, although not significant, need to be addressed. In particular, the presence of contact laughter in the entry and of non-contact laughter in suspension bouts are contrary to our predictions. We indeed predicted the use of non-contact laughter in subphases linked with the negotiation of the play activity's nature and continuation, but did not predict its use when persuasion fails, which is the case of suspension bouts. This effect however brings further support to our use of the absence of contact in laughter as a new proxy for identifying intentionality in apes, as the presence of non-contact laughter in suspension bouts supports its coordinative purpose towards play continuation. Similarly, as entry bouts are linked with play start, we predicted that they would mainly present non-contact laughter. This subphase however does not serve the purpose of establishing interactants' mutual will to play (i.e. their joint commitment) as this function is fulfilled in the pre-entry. These differences could have been avoided by refocusing the operationalization of our predictions regarding subphases specifically around play continuation attempts, i.e. the negotiation of joint commitment, and not of the nature, content and location of the play activity.

As such, considering the validity of our novel contact proxy for intentionality in laughter with respect to the use of the framework of Heesen et al. (2017), it could be argued that contact can be expected in the midst of playing (i.e. in the main body), but not as play is being negotiated (i.e. at transition points). However, reengagement and entry bouts are for instance both operationally defined as ending with the onset of the first movement typical of the joint activity, which often consists in tactile gestures in play. The fact that reengagement bouts contained significantly more non-contact laughter than entry bouts suggests that this assumption is not confounding, as it indicates that apes are able to reliably distinguish between moments that require the negotiation of joint commitment for play continuation (like suspension and reengagement bouts) from those that do not (like entry or type-change) by laughing without tactile priming. This evidence further implies the validity of our proxy, but also the need to refocus the operationalization of non-contact laughter as a specialized tool for joint-commitment negotiation to indicate the ape's will to pursue the play activity. As no evidence of the coordinative purposes of laughter in nonhuman apes had been unveiled prior to this study, future research should investigate these effects further to see if our results are replicable.

Although very encouraging, our study presents several other limitations, the main one being that our video samples were not directly collected for the purpose of this research, and thus not optimally tailored towards studying laughter. However, our interrater agreement rate (ICC) seems to validate the reliability and reproducibility of our annotation of laughter, with more laughter instances missed than misheard by second rater. Anecdotal evidence from our first and third pre-tests using a sample from Lola ya Bonobo tailored for laughter but not for phases further hints in this direction. Laughter quantity was thus not directly assessed in our study, which could have affected the significance of our social indices, rank differences and social bond strength. Further studies in this direction would be needed to confirm the effect found in our study, as it is rather surprising considering their role in both our ape species social systems (Palagi, 2006; Palagi & Cordoni, 2012).

Even though they are converging and running smoothly, our statistical models could have been improved. Indeed, we could have ideally performed a sequential analysis to further weigh in the nature of phases and subphases as a process in interaction but were constrained by time and personal knowledge. The collection of our dataset could have also been improved by better experience in the statistical field to avoid large reshaping and subsetting operations on our data, as well as a more balanced handling of dyadic representation in our sample. This may have had an effect on the large proportion of variance not explained by our fixed effects, but by our random effect dyad. An investigative analysis not included in our final results (see R code) because it slightly weighted down our models (e.g. AIC = 447.0, BIC = 484.9, log-likelihood = -216.5, and deviance = 433.0 with 1651 degrees of freedom for our first model) further assessed the effect of play initiator as a random effect, which had a relatively high variance of 0.1447 and a standard deviation of 0.3804. Further studies would be needed to investigate the role of these random effects and how they might interplay with our results on rank differences and social bond strength.

Studying laughter in nonhuman primates as a potentially intentional signal through the prism of coordination thus appears to yield many cues towards its cognitive and communicative role as an emotional signal. Although not presenting evidence of non-Duchenne laughter in apes, this study should contribute to a better understanding and operationalization of its potential intentional uses, as well as a finer-grained and nuanced vision both of intentionality and of the evolution between Duchenne and non-Duchenne laughter.

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APPENDIX

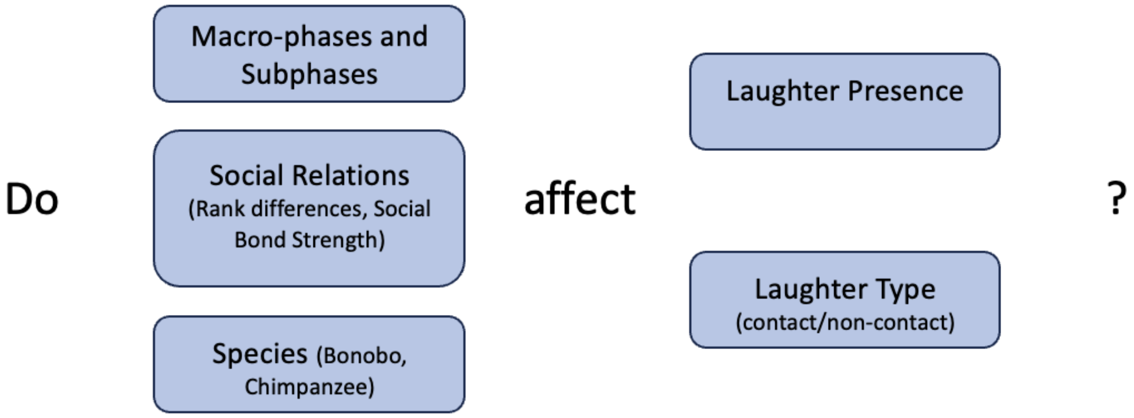
Key Resources

- **Dataset in Excel and CSV files**
- **R script for Models 1 & 2**
- **Dataset for Interrater Agreement**
- **R script for Interrater Agreement**
- **Joint-Action Protocol for ELAN (Heesen et al., 2017)**

Figures and Tables

Figure 1

Overview of Research Questions



Note: Summary of our predictor (left) and response (right) variables.

Table 1

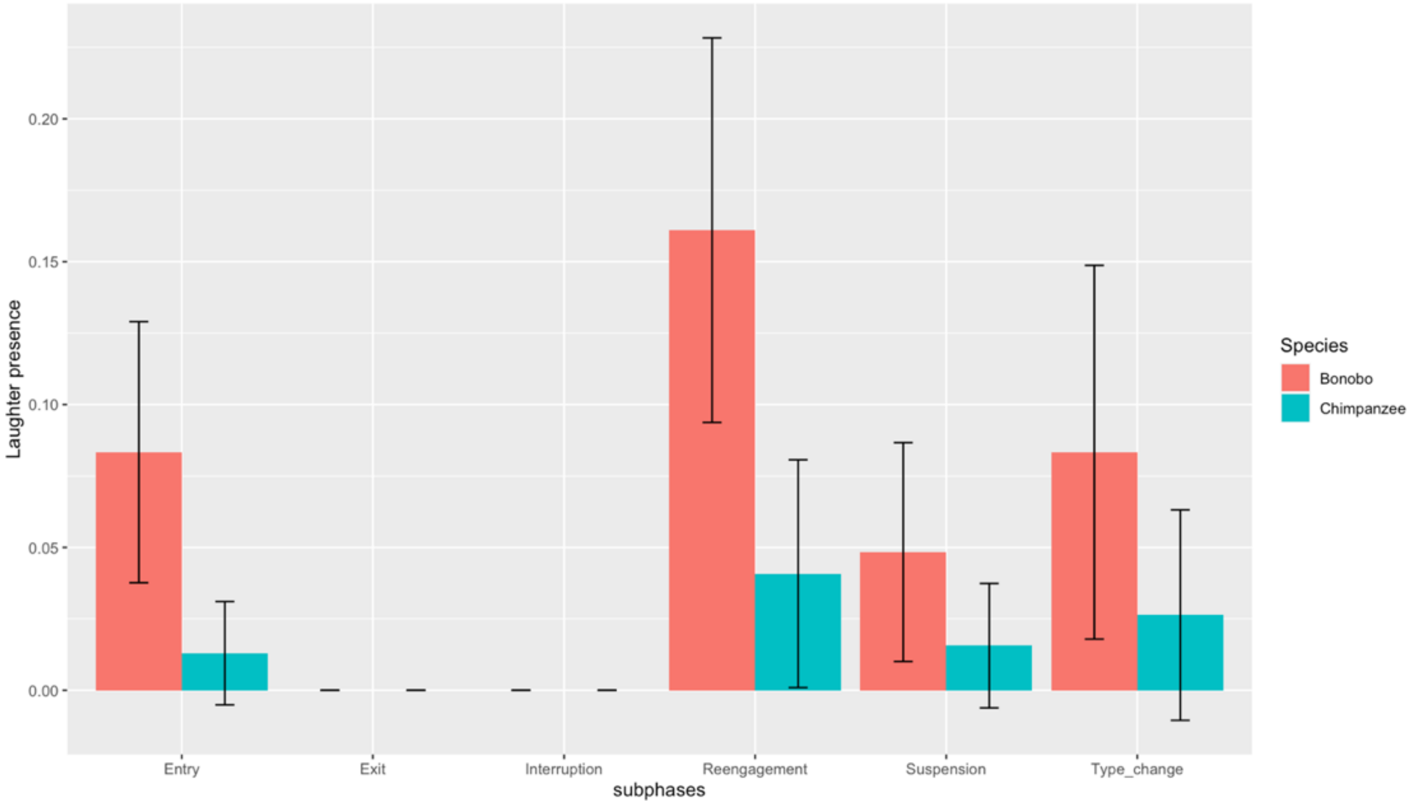
Index of bonobo and chimpanzee individuals

Site	Species	Focal ID	Birthdate	Sex	Hours observation
La Vallée des Singes, France	Bonobo	David	27/07/2001	M	20.25
		Kelele	22/07/2004	M	22
		Khalessi	12/12/2012	F	20.25
		Khaya	19/10/2001	F	20.5
		Lokoro	22/05/2015	M	21.25
		Loto	02/09/2009	M	20.5
		Lucy	01/12/2003	F	20.25
		Moko	04/08/2012	M	20
		Swahili	21/09/2014	F	20.75
		Ulindi	10/10/1993	F	21
		Yahimba	07/08/2009	F	21
		Yuli	14/07/2014	F	20.25
		n = 12			330.25
	Chimpanzee	Cauna	05/05/2007	F	37.1
		Conan	20/03/1996	M	37.4
		Jorg	01/01/1995	M	37.1
		Lila	20/06/2009	F	37.4
		Panya	14/07/2008	F	36.1
		Roy	27/09/1997	M	37.2
		Wonder	19/03/1997	M	36.8
		n = 7			259.1
La Réserve Africaine de Sigean, France	Chimpanzee	Ann	21/07/2002	F	18.9
		Goldie	29/08/1989	F	19
		Inongo	19/06/2009	M	18.8
		Jessica	1973	F	18.8
		Macourie	12/12/1999	F	18.6
		Madingo	02/09/2013	M	17.8
		Pablo	12/11/1999	M	19.3
		Penny	1989	F	19.3
		Poppy	13/04/2013	F	18.7
		n=4			169.2
Grand total		n= 23			37308

Note: Index of bonobo and chimpanzee individuals represented in our sample, comprising their location sites, names, birthdate, sex and amounts of recorded observation.

Figure 2

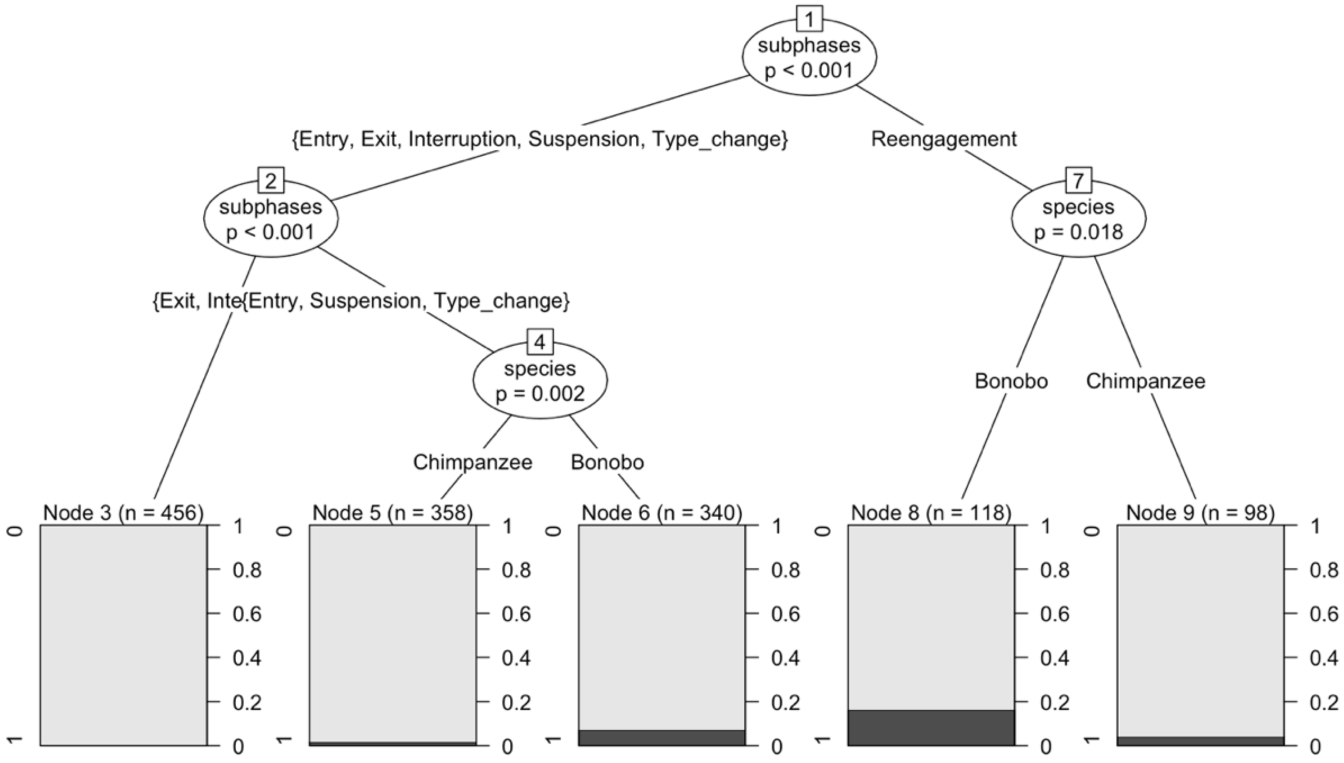
Laughter Presence per Species across Subphases



Note: The y axis represents the mean number of phases in which laughter was present per species in each subphase, which are noted on the x axis.

Figure 3

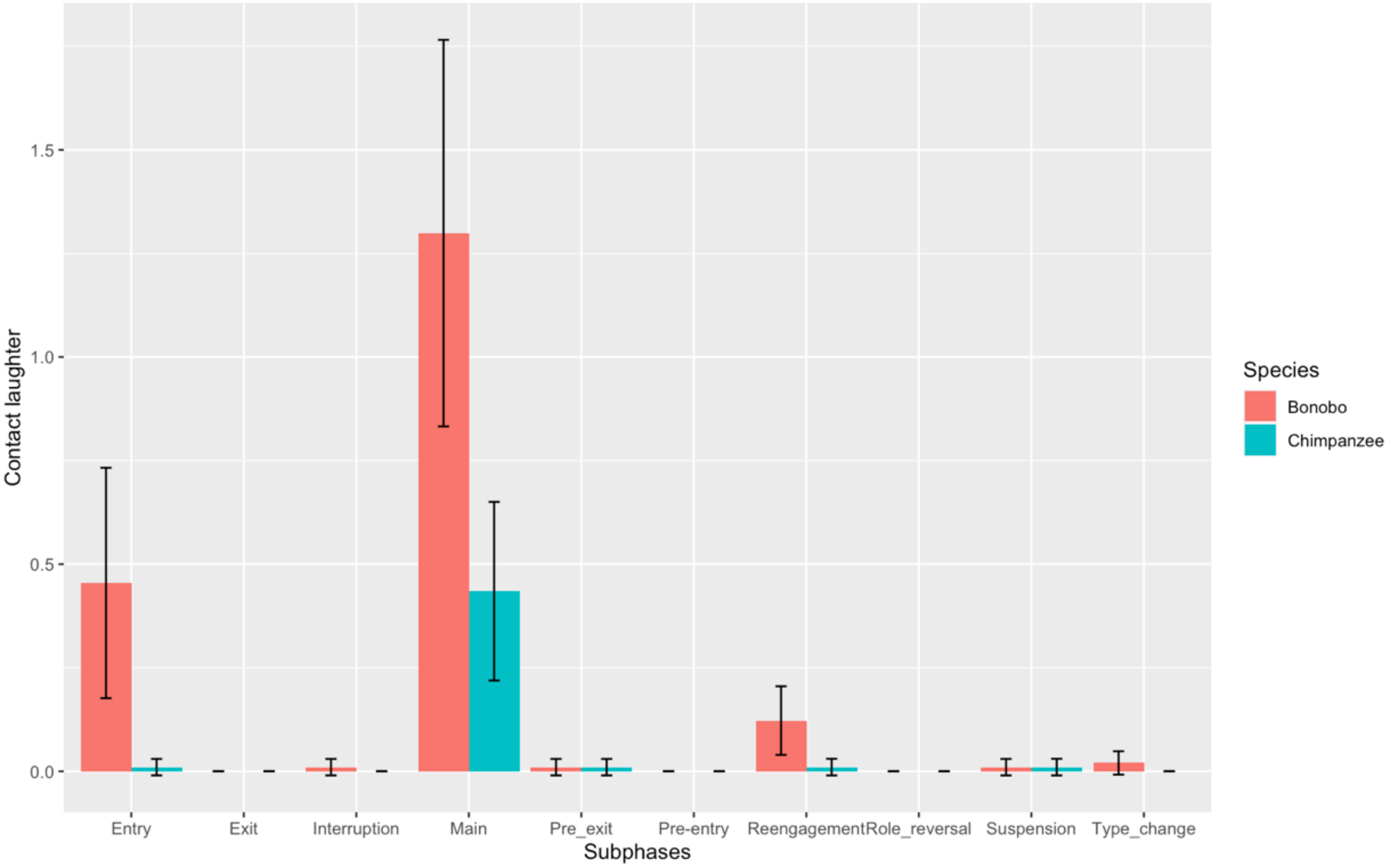
Conditional Inference Tree Showing the Differential Effect of Species and of Subphases on Laughter Presence



Note: Reengagement is positively linked with laughter presence in both species, but more strongly in bonobos than in chimpanzees. This tree was computed using the ctree function in R, which operationally differs significantly from the statistical tests used in our final models. As such, the p-values indicated are unreliable and do not necessarily coincide with those officially reported in our results section.

Figure 4

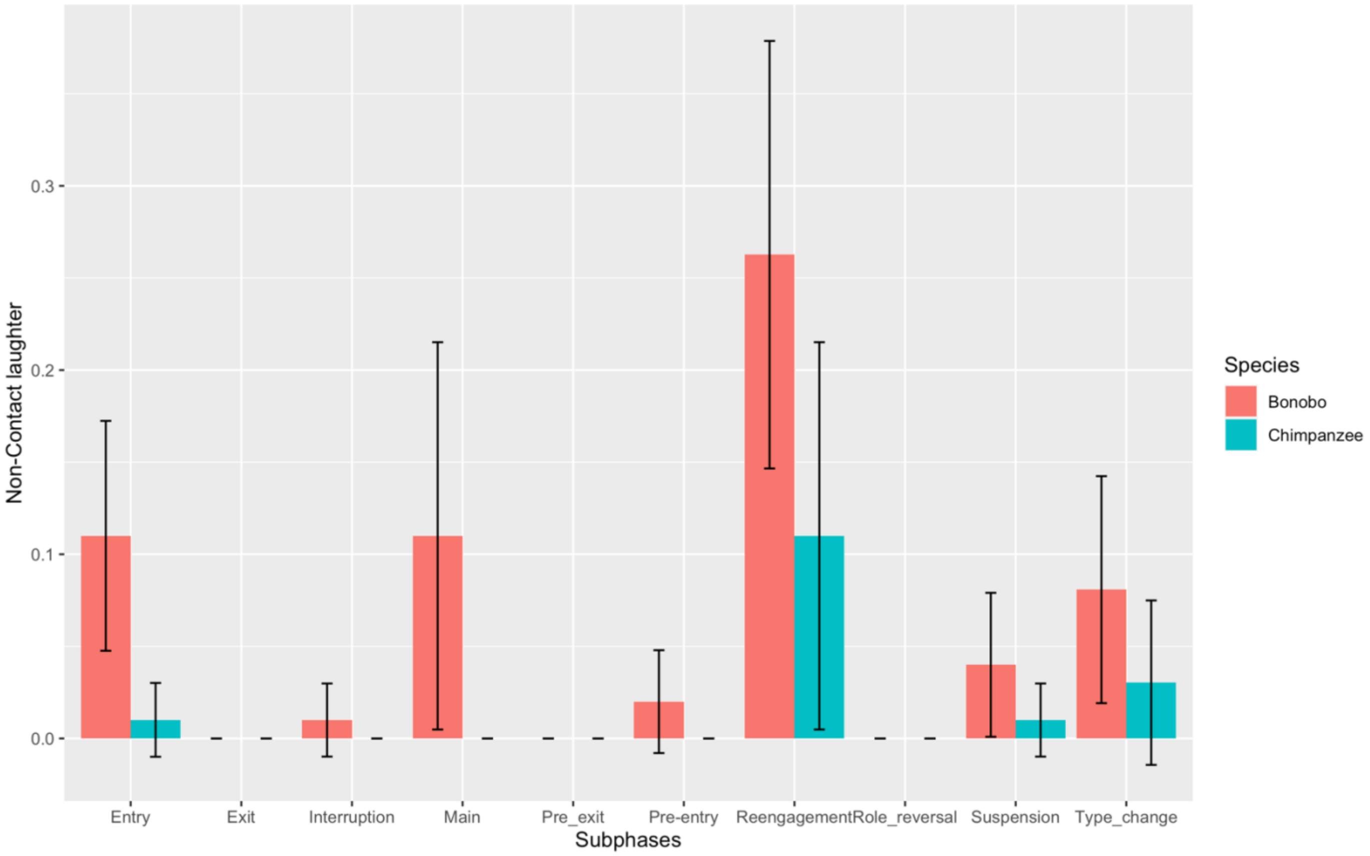
Contact Laughter per Species across Subphases



Note: The y axis represents the mean number of phases in which C laughter was present per species in each subphase, which are noted on the x axis. C laughter was mainly observed during the Main Body.

Figure 5

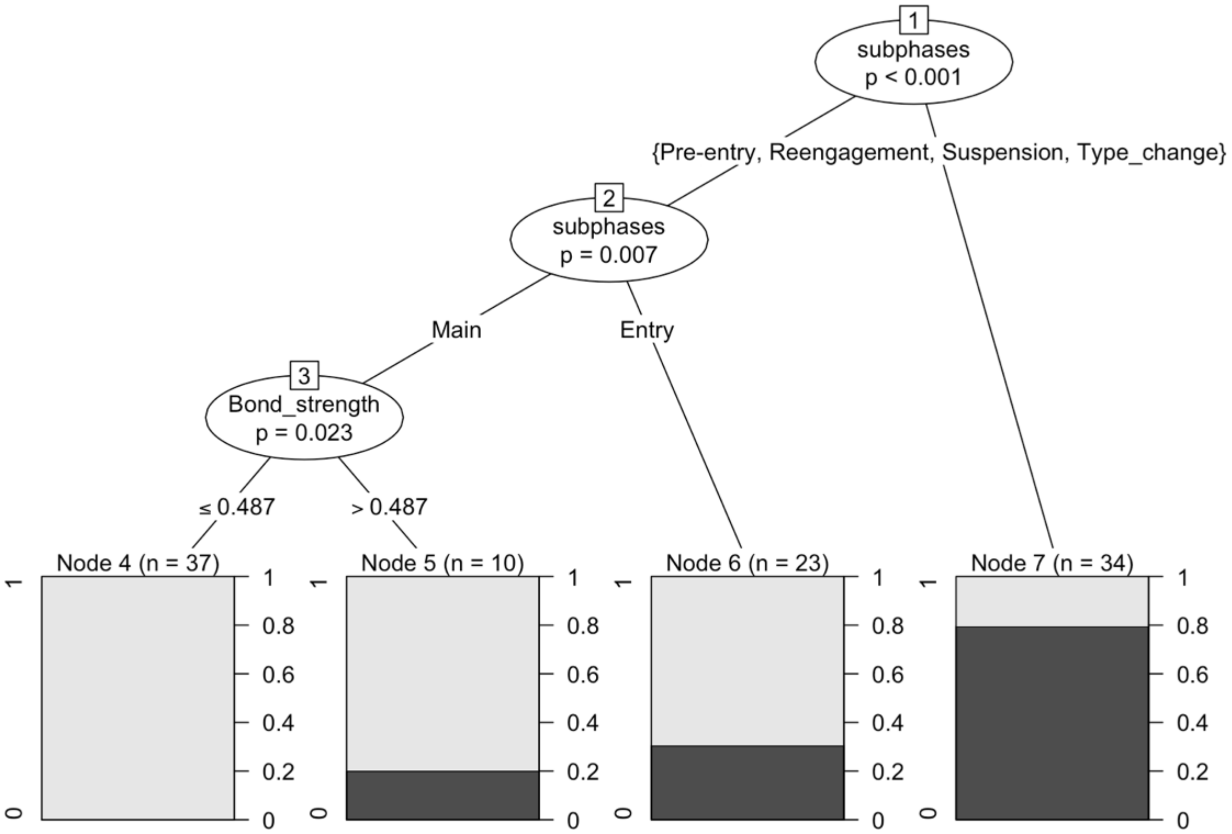
Non-contact Laughter per Species across Subphases



Note: The y axis represents the mean number of phases in which NC laughter was present per species in each subphase, which are noted on the x axis. NC laughter was mainly observed at Reengagement points.

Figure 6

Conditional Inference Tree Showing the Differential Effect of Species and of Subphases On Laughter Type



Note: In both species, moments of transition, and especially reengagement, are highly linked with non-contact laughter, whereas the Main Body is more linked with contact laughter and with Social Bond Strength. As this tree was computed using the ctree function in R, which operationally differs significantly from the statistical tests used in our final models, the p-values indicated are unreliable and do not necessarily coincide with those officially reported in our results section.

Table 2
Summary of Results from Models 1 and 2

	Model 1 : Laughter Presence			Model 2 : Laughter Type		
Predictors	Odds Ratios	CI	p	Odds Ratios	CI	p
(Intercept)	0.03	0.02 – 0.05	<0.001	92.88	6.30 – 1368.64	0.001
subphases [Reengagement]	5.44	3.05 – 9.70	<0.001			
species [Chimpanzee]	0.23	0.10 – 0.51	<0.001	0.71	0.13 – 4.02	0.699
ID Higher ranking	0.96	0.70 – 1.31	0.778	1.22	0.65 – 2.28	0.536
Bond strength	1.04	0.83 – 1.31	0.709	0.42	0.17 – 1.02	0.054
subphases [Other subphases]				0.01	0.00 – 0.10	<0.001
subphases [Other subphases] × Bond strength				2.95	1.14 – 7.60	0.026
Random Effects						
σ^2	3.29			3.29		
τ_{00}	0.37 $_{\text{dyad}}$			0.80 $_{\text{dyad}}$		
ICC	0.10			0.20		
N	74 $_{\text{dyad}}$			39 $_{\text{dyad}}$		
Observations	1658			104		
Marginal R^2 / Conditional R^2	0.207 / 0.287			0.593 / 0.673		