

Aping Expressions? Chimpanzees Produce Distinct Laugh Types When Responding to Laughter of Others

Marina Davila-Ross, Bethan Allcock, Chris Thomas, and Kim A. Bard
University of Portsmouth

Humans have the ability to replicate the emotional expressions of others even when they undergo different emotions. Such distinct responses of expressions, especially positive expressions, play a central role in everyday social communication of humans and may give the responding individuals important advantages in cooperation and communication. The present work examined laughter in chimpanzees to test whether nonhuman primates also use their expressions in such distinct ways. The approach was first to examine the form and occurrence of laugh replications (laughter after the laughter of others) and spontaneous laughter of chimpanzees during social play and then to test whether their laugh replications represented laugh-elicited laugh responses (laughter triggered by the laughter of others) by using a quantitative method designed to measure responses in natural social settings. The results of this study indicated that chimpanzees produce laugh-elicited laughter that is distinct in form and occurrence from their spontaneous laughter. These findings provide the first empirical evidence that nonhuman primates have the ability to replicate the expressions of others by producing expressions that differ in their underlying emotions and social implications. The data further showed that the laugh-elicited laugh responses of the subjects were closely linked to play maintenance, suggesting that chimpanzees might gain important cooperative and communicative advantages by responding with laughter to the laughter of their social partners. Notably, some chimpanzee groups of this study responded more with laughter than others, an outcome that provides empirical support of a socialization of expressions in great apes similar to that of humans.

Keywords: evolution, positive expressions, laugh-elicited laughter, social play, chimpanzee

Humans have the ability to replicate the emotional expressions of others even when they are not in the same emotional states as their social partners. Positive expressions are used in such distinctive ways on an everyday basis, for instance, when individuals respond with polite laughter to the joyous laughter of their social partners (Gervais & Wilson, 2005; Mehu & Dunbar, 2008; Provine, 1992; Ruch & Ekman, 2001). These kinds of responses may lead to important advantages in cooperation and social communication, qualities that partly explain why laughter and smiles have become such integral tools of emotional intelligence (for skills of emotional intelligence, see Mayer & Salovey, 1997).

Recently, quantitative phylogenetic analyses provided evidence that human laughter emerged from an ancestral nonhuman primate display, present in all extant great apes (Davila Ross, Owren, & Zimmermann, 2009; for earlier works on the evolution of laughter, see van Hooff, 1972; van Hooff & Preuschoft, 2003). The current study focused on laughter of chimpanzees (*Pan troglodytes*) to test whether the ability to replicate the expressions of others with expressions of different socioemotional meaning is a human-unique trait.

Previous findings on laughter of humans and chimpanzees revealed both fundamental differences as well as commonalities among the species. Although laughter of humans is universally recognized as an expression of joy (Sauter, Eisner, Ekman, & Scott, 2010), it seems to have various functions and can be used in just about every situation imaginable (e.g., conversation: Vettin & Todt, 2004; Schadenfreude and taunting: Szameitat et al., 2009b). In contrast, great apes have only been documented to laugh during social play and tickling (Davila Ross, Owren, & Zimmermann, 2010; Matsusaka, 2004; Owren & Bachorowski, 2001; Provine, 2000; Vettin & Todt, 2005; van Hooff & Preuschoft, 2003). Within social play, however, laughter seems to have a similar effect across the Hominidae, that is, prolonging play actions in children (Rothbart, 1973) and chimpanzees (Matsusaka, 2004), possibly to a smaller degree also in orangutans (Davila Ross, 2009). Such a link between laughter and social play depicts laughter among these species as a display that promotes social affiliation and supports an interactive platform for young individuals to develop cooperative and competitive behaviors (for the social and cognitive impact of play on animals, see Bekoff & Allen, 2002). For instance, practice in play fights may lead to well-developed competitive skills

This article was published Online First February 28, 2011.

Marina Davila-Ross, Bethan Allcock, Chris Thomas, and Kim A. Bard, Centre for Comparative and Evolutionary Psychology, Department of Psychology, University of Portsmouth.

We thank David Leavens and two reviewers for their helpful comments on this article. The study was funded by the European Commission as part of the FEELIX GROWING project (EC-FP6-IST-045169) and by the Department of Psychology, University of Portsmouth. Special thanks also go to S. Bundell and V. Butler for assisting with the video coding. The data were collected in the Chimfunshi Wildlife Orphanage, Zambia, and we are grateful to S. Jones for logistic help and to M. Mulenga and E. van Leeuwen for assisting with the video recordings.

Correspondence concerning this article should be addressed to Marina Davila-Ross, Centre for Comparative and Evolutionary Psychology, Department of Psychology, King Henry Building, University of Portsmouth, PO1 2DY, Portsmouth, United Kingdom. E-mail: Marina.Davila-Ross@port.ac.uk

(van Leeuwen, Zimmermann, & Davila Ross, 2010). Gervais and Wilson (2005) claimed that laughter specifically and play in general must have helped ancestral primates to expand their physical, social, emotional, and cognitive repertoires and to further explore and build on their potentials, consistent with the broaden-and-build theory of positive emotions by Fredrickson (2001). Selection pressures might have favored individuals that used their laughter in socially distinctive ways (for a discussion on the neural substrates of laughter in apes and humans, see Meyer, Baumann, Wildgruber, & Alter, 2007).

Laugh responses that are triggered by the laughter of others seem to be deeply rooted in primate evolution. In humans, such laugh responses appear already during infancy (Nwokah, Hsu, Dobrowolska, & Fogel, 1994) and may occur merely upon hearing prerecorded laugh sounds (Provine, 1992). Apes and monkeys also replicate the vocal and facial expressions of their social partners (e.g., Bard, 2007; Ferrari et al., 2006; Mitani & Gros-Louis, 1998; Palagi, Leone, Mancini, & Ferrari, 2009; Paukner & Anderson, 2006; Wich et al., 2009), where the replications were found to resemble the replicated expressions in their forms (see Palagi et al., 2009; Wich et al., 2009). Previous findings further indicated that apes, like humans, may replicate facial expressions of others as fast as within 1 s, a rapidity that suggests these expressions to be automatic and affective (Davila Ross, Menzler, & Zimmermann, 2008; for humans, see Dimberg & Thunberg, 1998; Dimberg, Thunberg, & Elmehed, 2000). Such responses appear to be coupled with mirror neuron activations (see Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Kohler et al., 2002). Therefore, replications of expressions in social interactions might serve similar adaptive functions in humans and chimpanzees, that is, promoting social affiliation and coordination, in addition to the learning of new behaviors (Bard, 2007; Bourgeois & Hess, 2008; Byrne, 2003; Hatfield, Cacioppo, & Rapson, 1994). By extension, even the imitation of monkeys' object use by humans seems to facilitate the formation and maintenance of social bonds (Paukner, Suomi, Visalberghi, & Ferrari, 2009).

The ubiquitous use of human laughter probably is based on the ability of humans to emit non-Duchenne laughter (laughter that is purely controlled, detached from any emotion). However, it is also important to note that humans often produce laughter that is a blend of both Duchenne (affective) laughter and non-Duchenne laughter (Gervais & Wilson, 2005). Moreover, it can be difficult for humans to emit an entirely fake laugh in a persuasive manner, probably because the neural pathways of both laugh types are partly interdependent (Wild, Rodden, Grodd, & Ruch, 2003). Whether great apes use their laughter in similar ways still needs to be investigated. Acoustic research on great apes suggests some form of vocal management. Captive chimpanzees and bonobos produce novel vocalizations that are absent among wild populations (Hopkins, Taglialatela, & Leavens, 2007; Taglialatela, Savage-Rumbaugh, & Baker, 2003), and orangutans and chimpanzees may even reproduce human sounds (Hayes & Hayes, 1951; Wich et al., 2009). Chimpanzees may also modify their vocalizations in acoustic structure because of changes in their social surrounding (Marshall, Wrangham, & Arcadi, 1999).

It is important to note, however, that the ability of great apes to vocally manage is significantly limited compared with such abilities of humans as well as animals that vocally mimic a wide range of complex species-untypical sounds, for example, parrots (Schachner, Brady, Pepperberg, & Hauser, 2009; also see Egnor & Hauser, 2004). We therefore predict that chimpanzee laughter does not involve a

purely cognition-driven process. Nonetheless, chimpanzee laughter with its strong impact on social play might still be partly managed and be partly automatic and affective, similar to laughter and various other behaviors of humans (e.g., intuitive parenting is neither reflexive nor planned in advance, see Papoušek & Papoušek, 1987).

In the current study, laughter was assessed in chimpanzees of four social groups during their naturally occurring social play. Previously, pilot tests with games and with video- and audio-playbacks revealed that great ape laughter cannot be systematically evoked in experimental set-ups other than through tickling (Davila-Ross, 2004–2007). These limitations seem to reflect that laughter of great apes is an emotional expression that is closely bound to the positive interactions of social play. Thus, a noninvasive methodological approach was most appropriate for this study. Parenthetically, experimental research on the production of emotional expressions in humans faces similar methodological challenges, where it can be, for instance, difficult to systematically obtain recordings of Duchenne laughter and smiles (see Bachorowski, Smoski, & Owren, 2001; Szameitat et al., 2009b; Wild, Erb, Eyb, Bartels, & Grodd, 2003).

The approach of the present work was first to examine the form and occurrence of laughter in chimpanzees to compare between laugh replications (laughter after the laughter of others) and spontaneous laughter (Part 1). It was then tested whether the laugh replications of Part 1 were laugh-elicited laugh responses (laughter triggered by the laughter of others) by applying a quantitative method designed to measure responses to specific behaviors in natural social settings (Part 2). If the results of Part 1 and Part 2 were to indicate laugh-elicited laughter in chimpanzees that is distinct in both form and occurrence, then this study would provide first empirical evidence that nonhuman primates replicate the expressions of their social partners with expressions that differ in their socioemotional meaning. The ability of humans to produce such distinct responses represents an important component of emotional intelligence and empathy (see Mayer & Salovey, 1997; Preston & de Waal, 2002).

For the laugh replications of the subjects in this study, two time domains were selected in accordance with previous findings on replications of positive expressions in humans; automatic affective responses occurred rapidly, that is, between 0.5 and 1.0 s (Dimberg & Thunberg, 1998; Dimberg et al., 2000), and nonautomatic responses were more delayed (Hatfield et al., 1994; Wild et al., 2003a). In the current study, findings on such rapid and delayed responses in subjects would imply two types of expressions in nonhuman primates when replicating others, that is, expressions that are purely affective and expressions that have a blend of both affective and of nonautomatic traits. However, it also needs to be noted that response latencies might be affected by internal and external factors (e.g., motivational states and distraction by group members). Recent research on mirror neurons in macaques revealed a suppression of discharge during action observation that might explain the inhibition of their own movements because such suppression was absent when the subjects performed the tasks themselves (Kraskov et al., 2009).

In addition, it was examined whether chimpanzees replicate laughter differently across their colonies and their age classes. Previous findings have already revealed that the emotional and cognitive development of chimpanzees is affected by their social surrounding and upbringing (van IJzendoorn, Bard, Bakermans-Kranenburg, & Ivan, 2009). The present work could provide empirical support that great

apes respond with their expressions flexibly with dependence on their social surrounding and upbringing, an outcome that would indicate strong parallels with findings of cross-cultural studies on human expressions (Eibl-Eibesfeldt, 1976; also see Malatesta & Haviland, 1982). Comparisons of laughter across age classes in this study would furthermore reveal whether laughter develops into an expression that is more directed to others in apes, as it does in humans (see Nwokah et al., 1994; Provine, 2000).

Part 1

Method

Subjects

The subjects were 59 chimpanzees, living in four multimale-multifemale group enclosures at the chimpanzee sanctuary Chimfunshi in Zambia. The enclosures ranged from 5 to 500 acres and were large enough for the chimpanzees to travel either alone or in groups. The chimpanzees of two of these enclosures were grouped together within the past 5 years (new colonies), and the chimpanzees of the remaining two enclosures were grouped together more than 14 years ago (old colonies). The new colonies had three times fewer chimpanzees than the old colonies. Members of all age classes were represented in each of these colonies. For an overview of the subject representation in the sample and the chimpanzees living in the colonies, see Table 1.

The chimpanzees of the new colonies were orphans (with the exception of one mother-reared infant). In their earlier years, they seem to have been transferred to different places with limited or no contact with other chimpanzees. The adult chimpanzees of the old colonies (with the exception of three adults) were also once brought as orphans to the sanctuary, but most of them have their own families now (second and third generation). All infants, juveniles, and adolescents and three adults of the old colonies were thus raised by their mothers in a familiar social environment. In sum, the chimpanzees of the newly established colonies must have had fewer opportunities to play with others in their past than the chimpanzees of the old colonies.

Design and Procedure

A total of 466 dyadic play bouts were video recorded at a distance of 10 m and less. Dyadic play bouts began when two playmates showed a play action and ended when at least one playmate stopped showing these actions for more than 20 s or when a third individual interfered. Nine mutually exclusive and exhaustive categories of play actions were coded for each play-

mate (chase, approach, tickling, grabbing, wrestling, gnawing, hitting, jumping, and games). The occurrence of laugh series was additionally coded for each playmate during play bouts. A laugh series consisted of consecutively emitted calls (elements of acoustic energy) of laughter with intercall intervals of less than 1 s.

Two researchers coded the play actions. Their interobserver reliability ($\kappa = 0.86$) was calculated based on 89 randomly selected play bouts (19% of all play bouts). Laughter was then coded by two additional researchers, each assessing all laugh series of this study. Only the laugh series that were found in agreement by both coders were included for further analyses. Videos were analyzed using Interact 8 (Mangold, Arnstorf, Germany).

The present work distinguished between laugh replications (laughter that followed laughter of a playmate within 5 s) and spontaneous laughter (laughter that did not follow laughter of a playmate within 5 s). Laugh replications were measured for two time domains, that is, within the first second after the onset of a laugh sound produced by the other playmate (rapid laugh replication) and within the next 4 s (delayed laugh replication). The time domains were selected based on human replication latencies that were measured for positive expressions (see Dimberg & Thunberg, 1998; Dimberg et al., 2000; Wild et al., 2003a; also see Hatfield et al., 1994).

The three categories of laughter (rapid laugh replications, delayed laugh replications, and spontaneous laughter) were compared in their acoustic form and in their occurrence across the chimpanzee colonies and across the age classes. For the acoustic analysis, three variables were selected based on the impact that related acoustic features seem to have had on the evolution of chimpanzee laughter (see Davila Ross et al., 2009): The number of unvoiced laugh series (with irregular vocal-fold vibrations), of laugh series with alternating airflow directions (exhalation and inhalation), and of calls per laugh series were counted. The acoustic analysis included all laugh series for which judgments on voicing and airflow direction could be made. Spontaneous laugh series, however, were only acoustically measured during play bouts without laugh replications. These judgments were made by the first author by both eye and ear. For each of the three acoustic variables, the intercoder reliability ($\kappa = 0.77$ – 0.87) was tested on 829 calls in a previous study (Davila Ross et al., 2009).

The play bouts with laugh replications, with spontaneous laughter, and without laughter were furthermore compared in their lengths. The bouts that were measured for spontaneous laughter were absent of laugh replications. For all repeated statistical comparisons of present work, α levels were adjusted using Hommel-Hochberg corrections.

Table 1
Overview of the Subject Representation in the Sample and the Members of the New and Old Colonies

Colonies	Number of laughers	Number of playmates	Number of members
New	2 infants, 8 juveniles, 5 adolescents, 1 adult	3 infants, 9 juveniles, 5 adolescents, 4 adults	4 infants, 10 juveniles, 5 adolescents, 5 adults
Old	5 infants, 14 juveniles, 2 adolescents, 5 adults	8 infants, 16 juveniles, 3 adolescents, 11 adults	19 infants, 16 juveniles, 7 adolescents, 30 adults

Results and Discussion

In this study, 687 laugh series were found during 195 play bouts from 42 chimpanzees (of a total of 466 play bouts from 59 study subjects). Altogether, 20 chimpanzees produced rapid laugh replications (77 laugh series), 19 subjects produced delayed laugh replications ($n = 38$), and 42 chimpanzees produced spontaneous laughter ($n = 572$). Rapid laugh replications occurred predominantly 0.70 to 0.80 s (mean \pm standard error: 0.74 ± 0.04) after the onset of the playmates' laughter, whereas the event peak of the delayed laugh replications was between 2.00 and 3.00 s (mean \pm standard error: 2.54 ± 0.26).

Figure 1a presents the acoustic data. Laugh replications had significantly fewer calls per laugh series than spontaneous laughter (two-tailed Mann-Whitney U with Hommel-Hochberg corrections; $U = 202$, $N = 16 + 32$ subjects, $p = .014$), depicted in Figure 1b. No significant difference was found in the number of calls per laugh series between the rapid and delayed laugh replications ($p > .050$). No significant differences were found when comparing the three laugh categories either in unvoiced laugh series or in airflow directions ($ps > .050$). For a representative spectrogram of a laugh replication produced by a chimpanzee, see Figure 1c.

Figure 2a shows the occurrence of laughter across the chimpanzee colonies. Data indicated that the laugh replications were underrepresented in the old colonies compared with the new colonies. In the old colonies, significantly more chimpanzees produced spontaneous laughter than either rapid laugh replications (two-tailed Binomial with Hommel-Hochberg corrections; $p = .006$) or delayed laugh replications ($p = .003$). In the new colonies, no

significant differences were found when comparing chimpanzees across the laugh categories ($p > .050$). The data of this study showed that the chimpanzees of the new colonies responded more to the laughter they received (12% of the times, measured for each subject) than the chimpanzees of the old colonies (6%), even though their overall laugh series were similar (a mean of 41 and 49 laugh series per hour of play, respectively).

The occurrence of laughter in chimpanzees from infancy to adulthood is presented in Figure 2b. Chimpanzees of every age class, with the exception of infants, produced laughter of all three categories. Whereas most of the infants laughed spontaneously, only one infant (2.6 years of age) replicated laughter rapidly, and no infants exhibited delayed laugh replications. The juveniles were the most frequent laughers and playmates of all the subjects. They were equally represented across the colonies (new colonies: 50% of all laughers and 43% of all playmates; old colonies: 54% of all laughers and 42% of all playmates).

These findings suggest that the laugh replications and the spontaneous laughter of the subjects differ in their acoustic form and occurrence and, consequently, in their socioemotional meaning. Chimpanzees thus seem to produce distinct types of laughter. No differences, however, were found between rapid and delayed laugh replications.

In addition, Figure 3 presents the durations of play bouts when subjects laughed and when they were silent. The play bouts lasted significantly longer when they were accompanied by laugh replications compared to spontaneous laughter (two-tailed Mann-Whitney U with Hommel-Hochberg corrections; $U = 433$, $N = 22 + 41$ subjects, $p < .001$). Play bouts with spontaneous laughter, on the other hand,

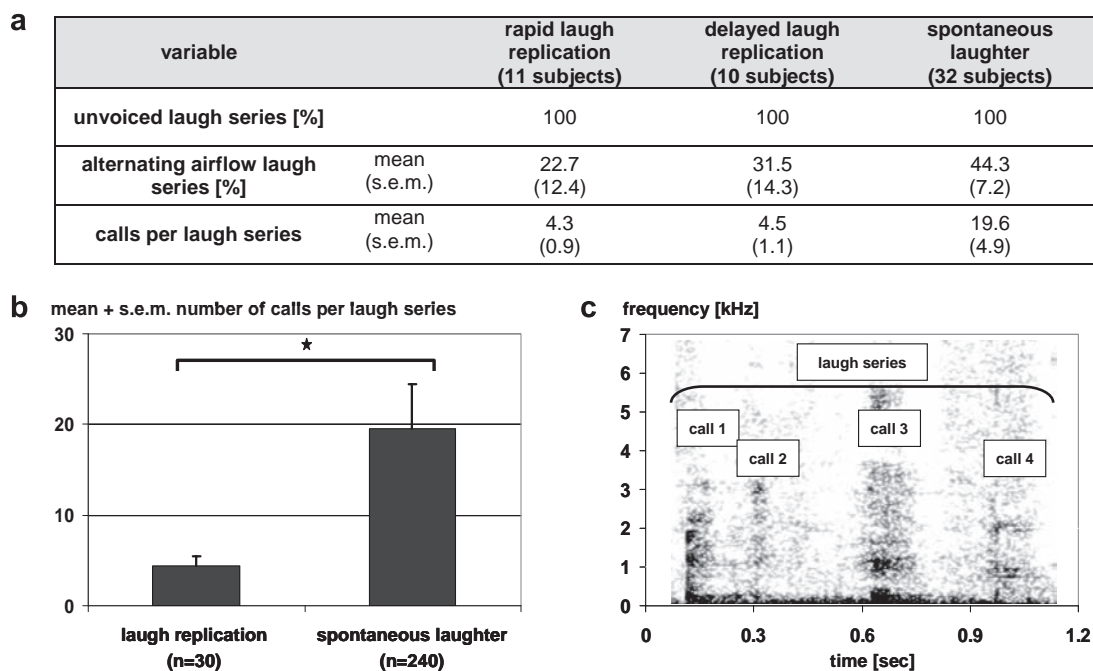


Figure 1. Bioacoustics of chimpanzee laughter. (a) Means (+ standard errors) of the acoustic variables for each laugh category. (b) Mean (+ standard error) number of calls per series of laugh replications and spontaneous laughter measured for every subject. (c) A representative spectrogram of a laugh replication. Acoustic analysis was conducted for laugh series where judgments could be made on voicing and airflow direction and only for spontaneous laugh series during play bouts without laugh replications ($n = 30$ laugh replications; $n = 240$ spontaneous laugh series).

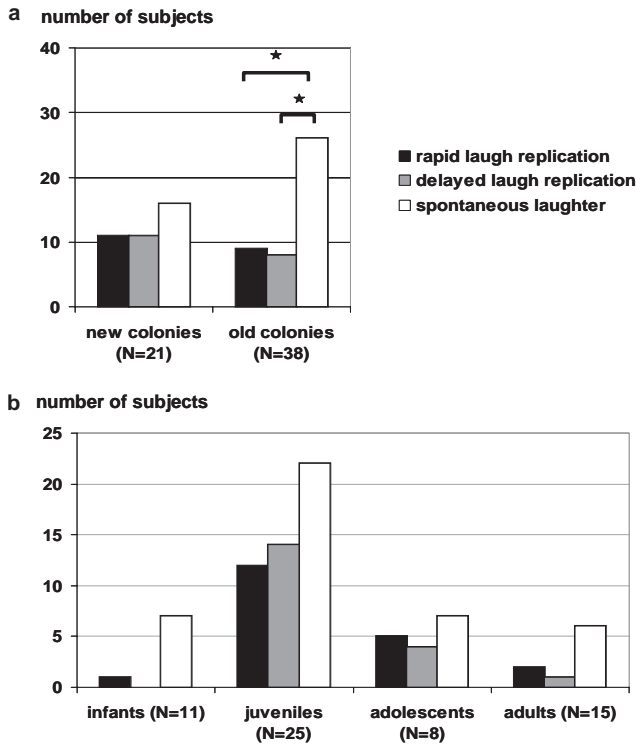


Figure 2. Number of chimpanzees producing laughter (a) across colonies and (b) across age classes. The total number of subjects is shown in parentheses.

were significantly longer than play bouts without laughter ($U = 516$, $N = 41 + 57$, $p < .001$). No significant difference in the play bout durations was found between the rapid and delayed laugh replications ($U = 170$, $N = 20 + 19$, $p > .050$).

Part 2

Method

Subjects and Coding

The same chimpanzees and coded data were used as in Part 1.

Design and Procedure

Because Part 1 of this study revealed that the subjects produced laughter that followed the laughter of their playmates (laugh replications), Part 2 of this study further tested whether these vocalizations represented responses that were triggered specifically by the laughter of their playmates (laugh-elicited laughter). For this test, a highly controlled quantitative method designed to gauge responses to a specific stimulus in natural social settings was used (Davila Ross et al., 2008).

Here, it was examined whether there was a pattern of congruency in the laugh behavior of the subjects when their playmates laughed (scene 1) and when the same playmates were silent (scene 2). Subjects who laughed in scene 1 and were silent in scene 2 showed congruent behaviors. In contrast, subjects who were silent

in scene 1 and laughed in scene 2 showed noncongruent behaviors (a method scheme is depicted in the right panel of Figure 4). If a significantly greater number of subjects were to show congruent behaviors than noncongruent behaviors, then the current study would provide evidence of laugh-elicited laughter in chimpanzees. This analysis was conducted twice, once for each time domain (within 1 s; from >1 to 5 s).

The search for scene 1 of a subject, A, began with the first occurrence of laughter that was produced by the other playmate, B, within a randomly selected play bout. Then, the search for scene 2 of subject A and playmate B began. An important control of this method was that each individual, A and B, must have shown the same type of play actions in scenes 1 and 2. To find such play situations that resembled each other as much as possible across the two scenes, the search for scene 2 started as early as 1 s after scene 1 ended, with the onset of silence by playmate B. If scene 2 could not be found within the same play bout as scene 1, it was then searched for within randomly selected play bouts. This procedure was followed for each subject.

This method to test for laugh-elicited laughter offered two important advantages compared with the mere counting of laugh replication events (Part 1). First, the data were standardized for the context of play, with every subject and playmate being assessed during the same play actions across the two scenes, respectively. Coordination in laughter caused by laugh-eliciting play actions (e.g., hitting or chasing) would therefore not affect the results. Second, the laugh rates of every subject were controlled. Because only congruent and noncongruent behaviors were statistically compared, data on subjects laughing in both or none of the complementary scenes had no effect on the results of these tests. This technique also controlled for individual differences. The data of laughers with many laugh series would thus not override the data of laughers with few laugh series.

mean + s.e.m. play bout duration of every subject [sec]

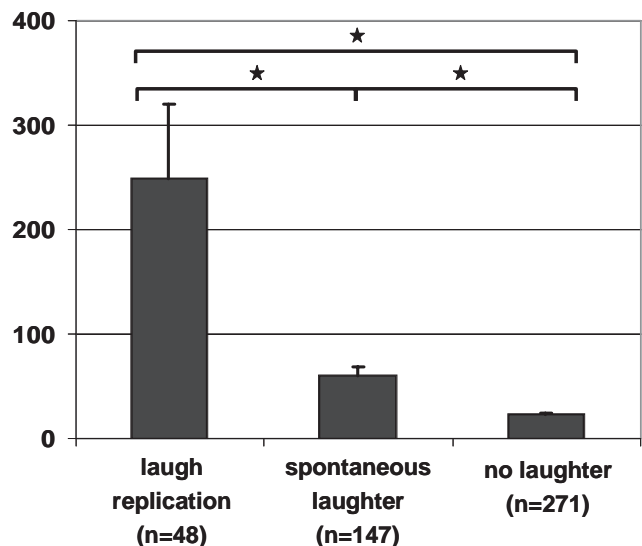


Figure 3. Mean (+ standard error) of play bouts with laughter and without laughter of every subject. For each category of laughter, the total number of play bouts is shown in parentheses.

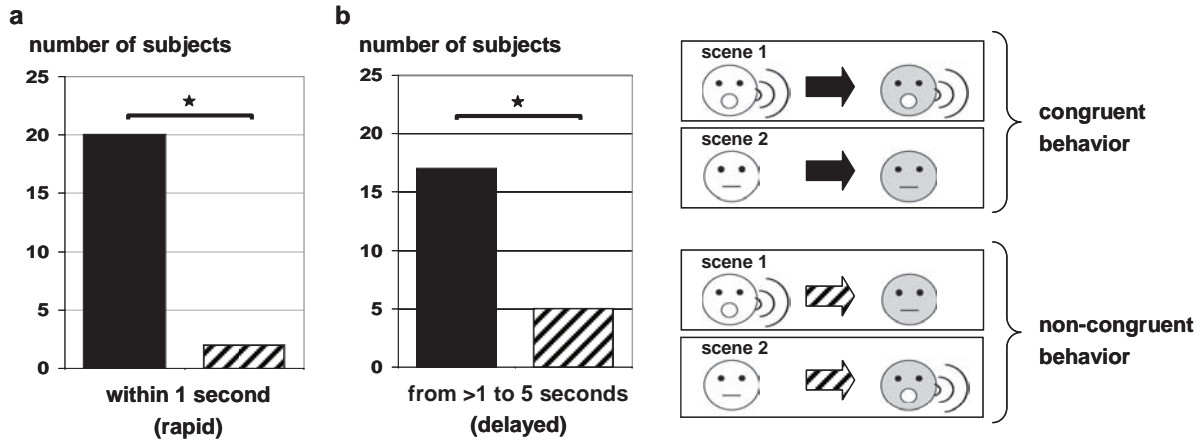


Figure 4. The number of chimpanzees that behaved congruently and noncongruently to their playmates, measured for (a) rapid and (b) delayed laugh replications. The method scheme on the right side depicts the laugh behaviors of the subjects (gray faces) after the behaviors of their playmates (white faces) in scenes 1 and 2, which were assessed for both congruent behaviors and noncongruent behaviors.

Results and Discussion

The controlled tests on laugh-elicited laughter of this study resulted in an overall pattern of congruency: Most chimpanzees laughed after the laughter of their playmates and were silent when their playmates were silent. Figure 4 specifically shows that a significantly greater number of chimpanzees behaved congruently to their playmates' laugh behavior than noncongruently. Moreover, this outcome was true for both measured time domains (within 1 s: two-tailed McNemar with Hommel-Hochberg corrections: $N = 20 + 2$ subjects, $p < .001$; from >1 to 5 s: $N = 17 + 5$, $p = .017$). These statistically significant findings indicate that both the rapid and delayed laugh replications of the subjects were laugh-elicited responses.

General Discussion

The outcomes of Part 1 and Part 2 in this study indicated that chimpanzees produce laugh-elicited laughter and that this vocalization differs in acoustic form and occurrence from their spontaneous laughter. The present work therefore provides empirical evidence that nonhuman primates replicate the expressions of their social partners by producing expressions that are distinct in their underlying emotions and their social implications.

In humans, particularly positive expressions are used in such distinctive ways to promote cooperation and social communication, where these expressions represent integral tools of emotional intelligence, closely linked to empathy (see Mayer & Salovey, 1997; Preston & de Waal, 2002). The results of this study suggest that laugh-elicited laughter might also provide chimpanzees with important social advantages, by helping them to prolong their social play. The data specifically showed that the study subjects played longest when laughter was replicated. Although it could be that the replications of various play activities promote play in chimpanzees, their laugh-elicited laughter seems to have a unique role here because even their laughter, in general, appears to prolong play to some degree (Matsusaka, 2004; also see this study, see Figure 3).

The laugh responses of chimpanzees in this study furthermore show a striking similarity to conversational laughter of humans. Both vocalizations are significantly short and seem to promote social interactions (Vettin & Todt, 2004; for a representative spectrogram of laugh replications in chimpanzees, see Figure 1c), suggesting that there may be deeply rooted links between short laughs and social coordination. Particularly the close relationship between laugh-elicited laughter and play maintenance of the subjects in this study implies that these laughs help to promote social cohesion and the development of communicative skills in chimpanzees more so than their spontaneous laughter. Ancestral hominids may thus well have had physical, social, emotional, and cognitive benefits by responding with laughter to the laughter of their social partners (see Fredrickson, 2001; Gervais & Wilson, 2005).

In addition, the present work compared the new and old chimpanzee colonies and revealed differences in the way the group members responded with laughter. Chimpanzees therefore seem to produce their laugh types flexibly with dependence on their populations, a finding that adds to previous findings that have indicated that the overall rates of an expression in chimpanzees may vary as a function of their social surrounding and upbringing (Bard, 1998, 2003). These outcomes of the current study represent first empirical support of a socialization of an expression in great apes that resembles that in humans, where a socially distinctive application of a specific expression is learnt from the social environment (for the socialization of replicating emotional expressions in humans, see Malatesta & Haviland, 1982; also see Eibl-Eibesfeldt, 1976).

The comparisons between the colonies specifically indicated that the orphans of the newly established groups with their less familiar members were those that predominantly replicated the laughter of their playmates, even though they must have had fewer opportunities to play in their early years than the chimpanzees of the old colonies (see Method, Part 1). It therefore seems likely that laugh replications have a more important role in the social communication of chimpanzees when their social partners are less predictable and/or when the need for social cohesion increases (for

the group establishing functions of laughter in humans, see Eibl-Eibesfeldt, 1970; Szameitat et al., 2009a).

Moreover, the results of this study indicate meaningful developmental changes in laughter of chimpanzees. Young infant chimpanzees seem to first produce spontaneous laughter and only start to replicate laughter over the course of years. A similar developmental pattern was found in orangutans, where the juveniles rapidly mimicked the facial displays of their playmates more often than the infants (Davila Ross et al., 2008). In humans, the use of laughter also seems to change developmentally as it shifts away from the generally emitted spontaneous laughter of 1 year olds (Nwokah et al., 1994) to become laughs that are more directed to the social partners in adulthood (see Provine, 2000; Vettin & Todt, 2004; for comparisons on the development of humans and chimpanzees, see Bard & Leavens, 2009).

The results of Part 2 further showed that the laugh responses of the study subjects occurred within the same time domains as affective (rapid) and controlled (delayed) responses of humans who replicate positive expressions (see Dimberg & Thunberg, 1998; Dimberg et al., 2000; Wild et al., 2003a). Although internal and external factors might have slowed affective responses down to over 1 s so that they could have been categorized as delayed responses (for a suppression of discharge in mirror neurons of macaques, see Kraskov et al., 2009), the results on response latencies indicate such an effect to be unlikely for the data of this study. Specifically, the results on the latencies of rapid and delayed laugh responses revealed two separate event peaks with an interpeak gap of more than 1 s (0.70–0.80 s and 2.00–3.00 s, respectively), indicating two distinctive responses. Chimpanzees may thus not only produce undirected affective laughter but also laughter that represents a blend of both affective and nonautomatic traits. Such laugh vocalizations are notably also present among humans (see Gervais & Wilson, 2005) and appear to reflect an evolutionary transition of Duchenne laughter and the later evolving non-Duchenne laughter. However, the ability of humans to laugh at any given situation, detached from any emotion, has not been documented for chimpanzees (see Gervais & Wilson, 2005; Owren & Bachorowski, 2001). Furthermore, this study revealed no significant differences in either form or occurrence between the rapid and delayed categories of laugh replications.

We conclude that hominids emitted laugh-elicited laughter already five million years ago, when the last common ancestor of humans and chimpanzees still existed, whereas their management in laugh production seems to have been rather limited compared with the one of modern humans. Primordial laughter, in general, most likely had an important impact on these hominids (see Gervais & Wilson, 2005), an impact that must have increased throughout evolution along with the expansion of laughter into a wide range of social contexts, as it became a highly sophisticated tool of cooperation and social communication in humans.

References

- Bachorowski, J.-A., Smoski, M. J., & Owren, M. J. (2001). The acoustic features of human laughter. *Journal of the Acoustical Society of America*, *110*, 1581–1597.
- Bard, K. (2007). Neonatal imitation in chimpanzees (*Pan troglodytes*) tested with two paradigms. *Animal Cognition*, *10*, 233–242.
- Bard, K. A. (1998). Social-experiential contributions to imitation and emotion in chimpanzees. In S. Braten (Ed.), *Intersubjective communication and emotion in early ontogeny: A source book* (pp. 208–227). Cambridge: Cambridge University Press.
- Bard, K. A. (2003). Development of emotional expressions in chimpanzees (*Pan troglodytes*). In P. Ekman, J. J. Campos, R. J. Davidson, & F. B. M. de Waal, (Eds.), *Emotions inside out: 130 years after Darwin's The expression of the emotions in man and animals* (pp. 88–90). New York: *Annals of the New York Academy of Sciences*.
- Bard, K. A., & Leavens, D. A. (2009). Socio-emotional factors in the development of joint attention in human and ape infants. In L. Roska-Hardy & E. M. Neumann-Held, (Eds.), *Learning from animals? Examining the nature of human uniqueness* (pp. 89–104). London: Psychology Press.
- Bekoff, M., & Allen, C. (2002). The evolution of social play: Interdisciplinary analyses of cognitive processes. In M. Bekoff, C. Allen, & G. M. Burghardt, (Eds.), *The cognitive animal* (pp. 429–435). Cambridge, MA: The MIT Press.
- Bourgeois, P., & Hess, U. (2008). The impact of social context on mimicry. *Biological Psychology*, *77*, 343–352.
- Byrne, R. W. (2003). Imitation as behaviour parsing. *Philosophical Transactions of the Royal Society London B: Biological Sciences*, *358*, 529–536.
- Davila Ross, M. (2009). *Towards the evolution of laughter*. Saarbrücken: Südwestdeutscher Verlag für Hochschulschriften Aktiengesellschaft.
- Davila Ross, M., Menzler, S., & Zimmermann, E. (2008). Rapid facial mimicry in orangutan play. *Biology Letters*, *4*, 27–30.
- Davila Ross, M., Owren, M. J., & Zimmermann, E. (2009). Reconstructing the evolution of laughter in great apes and humans. *Current Biology*, *19*, 1106–1111.
- Davila Ross, M., Owren, M. J., & Zimmermann, E. (2010). The evolution of laughter in great apes and humans. *Communicative and Integrative Biology*, *3*, 191–194.
- Dimberg, U., & Thunberg, M. (1998). Rapid facial reactions to emotional facial expressions. *Scandinavian Journal of Psychology*, *39*, 39–45.
- Dimberg, U., Thunberg, M., & Elmehed, K. (2000). Unconscious facial reactions to emotional facial expressions. *Psychological Science*, *11*, 86–89.
- Egnor, R. S. E., & Hauser, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences*, *27*, 649–654.
- Eibl-Eibesfeldt, I. (1970). *Ethology: The biology of behavior*. New York: Holt, Rinehart & Winston.
- Eibl-Eibesfeldt, I. (1976). *Menschenforschung auf neuen Wegen. Die naturwissenschaftliche Betrachtung kultureller Verhaltensweisen*. Vienna: Molden.
- Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience*, *17*, 1703–1714.
- Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., Suomi, & S. J. (2006). Neonatal imitation in rhesus macaques. *PLoS Biology*, *4*, e302.
- Fredrickson, B. L. (2001). The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. *American Psychologist*, *56*, 218–226.
- Gervais, M., & Wilson, D. S. (2005). The evolution and functions of laughter and humor: A synthetic approach. *The Quarterly Review of Biology*, *80*, 395–430.
- Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1994). *Emotional contagion*. Cambridge, MA: Cambridge University Press.
- Hayes, K. J., & Hayes, C. (1951). The intellectual development of a homeraised chimpanzee. *Proceedings of the American Philosophical Society*, *95*, 105–109.
- Hopkins, W. D., Tagliatalata, J. P., & Leavens, D. A. (2007). Chimpanzees

- differentially produce novel vocalizations to capture the attention of a human. *Animal Behaviour*, 73, 281–286.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, 297, 846–848.
- Kraskov, A., Dancause, N., Quallo, M. M., Shepherd, S., & Lemon, R. N. (2009). Corticospinal neurons in macaque ventral premotor cortex with mirror properties: A potential mechanism for action suppression? *Neuron*, 64, 922–930.
- Malatesta, C. Z., & Haviland, J. M. (1982). Learning display rules: The socialization of emotion expression in infancy. *Child Development*, 53, 991–1033.
- Marshall, A. J., Wrangham, R. W., & Arcadi, A. C. (1999). Does learning affect the structure of vocalizations in chimpanzees? *Animal Behaviour*, 58, 825–830.
- Matsusaka, T. (2004). When does play panting occur during social play in wild chimpanzees? *Primates*, 45, 221–229.
- Mayer, J. D., & Salovey, P. (1997). What is emotional intelligence? In Emotional development and emotional intelligence: Educational implications. In P. Salovey, & D. Sluyter, (Eds.). *Emotional development and emotional intelligence: Educational implications* (pp. 3–31). New York: Basic Books.
- Mehu, M., & Dunbar, R. I. M. (2008). Relationship between smiling and laughter in humans (*Homo sapiens*): Testing the power asymmetry hypothesis. *Folia Primatologica*, 79, 269–280.
- Meyer, M., Baumann, S., Wildgruber, D., & Alter, K. (2007). How the brain laughs. Comparative evidence from behavioral, electrophysiological and neuroimaging studies in human and monkey. *Behavioural Brain Research*, 182, 245–260.
- Mitani, J. C., & Gros-Louis, J. (1998). Chorusing and call convergence in chimpanzees: Tests of three hypotheses. *Behaviour*, 135, 1041–1064.
- Nwokah, E. E., Hsu, H.-C., Dobrowolska, O., & Fogel, A. (1994). The development of laughter in mother-infant communication: Timing parameters and temporal sequences. *Infant Behavior and Development*, 17, 23–35.
- Owren, M. J., & Bachorowski, J.-A. (2001). The evolution of emotional expression: A “selfish-gene” account of smiling and laughter in early hominids and humans. In T. J. Mayne, & G. A. Bonanno, (Eds.). *Emotions: Current issues and future directions* (pp. 152–191). New York: The Guilford Press.
- Palagi, E., Leone, A., Mancini, G., & Ferrari, P. F. (2009). Contagious yawning in gelada baboons as a possible expression of empathy. *Proceedings of the National Academy of Sciences, USA*, 106, 19262–19267.
- Papoušek, H., & Papoušek, M. (1987). Intuitive parenting: A dialectic counterpart to the infant’s integrative competence. In J. Osofsky, (Ed.). *Handbook of infant development* (2nd ed.) (pp. 669–720). New York: Wiley.
- Paukner, A., & Anderson, J. R. (2006). Video-induced yawning in stump-tail macaques (*Macaca arctoides*). *Biology Letters*, 2, 36–38.
- Paukner, A., Suomi, S. J., Visalberghi, E., & Ferrari, P. F. (2009). Capuchin monkeys display affiliation toward humans who imitate them. *Science*, 325, 880–883.
- Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, 25, 1–72.
- Provine, R. R. (1992). Contagious laughter: Laughter is a sufficient stimulus for laughs and smiles. *Bulletin of the Psychonomic Society*, 30, 1–4.
- Provine, R. R. (2000). *Laughter: A scientific investigation*. New York: Viking Press.
- Rothbart, M. K. (1973). Laughter in young children. *Psychological Bulletin*, 80, 247–256.
- Ruch, W., & Ekman, P. (2001). The expressive pattern of laughter. In A. Kazniak, (Ed.). *Emotion, qualia and consciousness* (pp. 426–443). Tokyo: World Scientific.
- Sauter, D., Eisner, F., Ekman, P., & Scott, S. K. (2010). Cross-cultural recognition of basic emotions through nonverbal emotional vocalizations. *Proceedings of the National Academy of Sciences, USA*, 107, 2408–2412.
- Schachner, A., Brady, T. F., Pepperberg, I. M., & Hauser, M. D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. *Current Biology*, 19, 831–836.
- Szameitat, D. P., Alter, K., Szameitat, A. J., Darwin, C. J., Wildgruber, D., Dietrich, S., & Sterr, A. (2009a). Differentiation of emotions in laughter at the behavioral level. *Emotion*, 9, 397–405.
- Szameitat, D. P., Alter, K., Szameitat, A. J., Wildgruber, D., Sterr, A., & Darwin, C. J. (2009b). Acoustic profiles of distinct emotional expressions in laughter. *Journal of the Acoustical Society of America*, 126, 354–366.
- Tagliabue, J. P., Savage-Rumbaugh, S., & Baker, L. A. (2003). Vocal production by a language-competent *Pan paniscus*. *International Journal of Primatology*, 24, 1–17.
- van Hooff, J. A. R. A. M. (1972). A comparative approach to the phylogeny of laughter and smiling. In R. A. Hinde, (Ed.). *Non-verbal communication* (pp. 209–241). Cambridge, MA: Cambridge University Press.
- van Hooff, J. A. R. A. M., & Preuschoft, S. (2003). Laughter and smiling: The intertwining of nature and culture. In F. B. M. de Waal, & P. L. Tyack, (Eds.). *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 261–287). Cambridge, MA: Harvard University Press.
- van IJzendoorn, M. H., Bard, K. A., Bakermans-Kranenburg, M. J., & Ivan, K. (2009). Enhancement of attachment and cognitive development of young nursery-reared chimpanzees in responsive versus standard care. *Developmental Psychobiology*, 51, 173–185.
- van Leeuwen, E., Zimmermann, E., & Davila Ross, M. (2011). Responding to inequities: Gorillas try to maintain their competitive advantage during play fights. *Biology Letters*, 23, 39–42.
- Vettin, J., & Todt, D. (2004). Laughter in conversation: Features of occurrence and acoustic structure. *Journal of Nonverbal Behavior*, 28, 93–225.
- Vettin, J., & Todt, D. (2005). Human laughter, social play, and play vocalizations of non-human primates: An evolutionary approach. *Behaviour*, 142, 217–240.
- Wich, S. A., Swartz, K. B., Hardus, M. E., Lameira, A. R., Stromberg, E., & Shumaker, R. W. (2009). A case of spontaneous acquisition of a human sound by an orangutan. *Primates*, 50, 56–64.
- Wild, B., Erb, M., Eyb, M., Bartels, M., & Grodd, W. (2003a). Why are smiles contagious? An fMRI study of the interaction between perception of facial affect and facial movements. *Psychiatry Research: Neuroimaging*, 123, 17–36.
- Wild, B., Rodden, F. A., Grodd, W., & Ruch, W. (2003b). Neural correlates of laughter and humour. *Brain*, 126, 2121–2138.

Received April 25, 2010

Revision received August 23, 2010

Accepted September 17, 2010 ■