The ontogeny of human laughter

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Summary

During positive social interactions, humans and other great apes often laugh. Human adult laughter is characterized by vocal bursts produced predominantly during exhalation ("ha-ha-ha"). In contrast, apes laugh while exhaling *and* while inhaling. The current study tested the hypothesis that the laughter of human infants changes from laughter similar to that of non-human apes to increasingly resemble the laughter of human adults over the course of early development. Specifically, we hypothesized that infant laughter would be produced increasingly during exhalation over the course of ontogeny. Moreover, we predicted that, due to social learning processes, the more laughter was produced on the exhale, the more positively it would be perceived by adult listeners. To test these predictions, novice (n = 102) and expert (phonetician, n = 15) listeners judged the extent to which human infant laughter (n = 44) was produced during inhalation or exhalation, and the extent to which they found the laughs pleasant and contagious. As predicted, the proportion of laughter produced on the inhalation was higher in infants as compared to adults, and the proportion of laughter occurring on the exhalation increased with age. Consistent with our second hypothesis, the more laughter was produced on the exhalation, the more positively it was perceived by adult listeners. These results were confirmed in a pre-registered replication study with a new set of 64 audio clips and a new group of novice listeners (n = 102). These results demonstrate that, likely through a combination of social learning and the anatomical development of the vocal production system, human infants' initial ape-like laughter transforms into laughter similar to that of adult humans over the course of early ontogeny.

Keyword: laughter, vocalization, positive emotion, affect, ontogeny, evolution, primates

Introduction

In social mammalian species, joint laughter contributes to the establishment and enhancement of social bonds (e.g., great apes: Davila Ross et al., 2009; Van Hooff, 1972; rodents: Panksepp & Burgdorf, 2003). Laughter evolved from the labored breathing of physical play, and in humans ritualized into a signal that is primarily produced during exhalation ("ha-ha"; Provine & Yong, 1991). Compared to human adults, infants have little control over their vocal production apparatus and have had limited opportunities for social learning. Based on these observations, we sought to test two hypotheses: 1) The extent to which human laughter is produced during exhalation increases over the course of early ontogeny, and 2) This change maps onto a shift in listeners' perception, such that laughter produced more during exhalation is perceived as more positive.

Similar to many other expressions of emotion, human laughter has its origins in ancestral nonhuman primate displays (Darwin, 1872; Gervais et al., 2005). Despite considerable similarities in laughter patterns across great apes and humans, some notable differences have also been established. In a study examining tickle-induced vocalizations from infant and juvenile great apes, including humans, Davila Ross and colleagues (2009) found that all non-human ape species produced laughter during exhalation (egressive), as well as during mixed exhalation-inhalation phases. In contrast, humans exclusively produced egressive laughter. The authors proposed that over the course of human evolution, egressive laughter may have been exaggerated after the divergence of hominins from a common ancestor with chimpanzees and bonobos. Davila Ross and colleagues included laughter from human infants of approximately one year and older. However, laughter emerges in human infants as young as three months old (Washburn, 1929; Addyman & Addyman, 2013). It may be that the production of laughter vocalizations changes over the course of development, since the vocal tract of a newborn infant is similar to that of a great ape (Stabel et al., 2013) and vocal production undergoes dramatic changes within the first two years of life (Negus, 1949). Compared to human adults, infant vocalizations are generally more likely to include ingressive sound production (Grau et al., 1995). We therefore hypothesized that infant laughter would be characterized by more ingressive vocalizations compared to adults, and that the degree of laughter occurring on exhalation would increase over ontogeny.

Laughter is intrinsically social (LaFrance, 1983; Young, 1973; Scott et al., 2014; Bryant et al., 2016). In fact, laughter is 30 times more likely to occur in social, as compared to solitary, situations (Provine & Fischer, 1989). When people laugh, it functions as a social glue: Contagious laughter is associated with longer social interactions in humans (Provine, 1992), as well as in other species (e.g., chimpanzees: Davila-Ross et al., 2011; geladas: Mancini et al., 2013). Shared laughter is particularly important early in ontogeny in order to strengthen the essential bond between the infant and the caregiver (Bowlby, 1969), and indeed young infants laugh a great deal: The frequency of laughter between mothers and infants over a period of 20 minutes is within the same range as that occurring in a 24-hour period for adults (Young, 1973). Social learning may shape laughter production, given that infants are strongly biased to learn communication skills that result in the caregiver satisfying the infant’s drives (Halliday, 1975). Through processes of mimicry, imitation and social learning, infants may learn that voiced, songlike laughs, which are typically produced during exhalation yield the most preferable outcomes in interaction partners (Bachorowski & Owren, 2001). Infants may thus come to produce more egressive laughter in order to elicit positive affect from listeners. We therefore hypothesized that the extent to which laughter was produced on the exhalation would be positively correlated with adult listeners’ judgments of the laughs’ contagiousness and pleasantness.

In the present study we thus sought to empirically test two predictions on breathing patterns in laughter vocalizations over the course of early ontogeny. Firstly, we predicted that the proportion of laughter produced on the exhalation would be lower in infants than in adults, and that the proportion of egressive laughter would increase over the course of infant development (3-18 months). Secondly, we sought to test whether egressive laughter would be positively associated with perceived positive affect, potentially making the shift in vocal production of laughter functionally adaptive in terms of social relationships.

Method

The study consisted of two experiments, with Experiment 2 being a pre-registered replication of Experiment 1 (https://osf.io/j2d5w). In Experiment 1, 102 novices (89 female, mean age 23.5 years, range 18-58 years) and 15 phoneticians (14 female, mean age 35.3 years, range 26-58 years) participated. The judgments made by the novices closely matched those made by the experts (see Table S1), and consequently only novices were included in Experiment 2 (102 novices; 94 female, mean age 19.1 years, range 18-23 years). All participants gave informed consent, and the studies were approved by the local ethics committee of Leiden University (CEP16-1206/365 and CEP19-1015/503).

Sound clips of infant laughter were collected from video-sharing websites (e.g., YouTube) and the authors' personal networks. The lower age limit was set to three months, in order to include the youngest age at which infants have been found to produce laughter (Addyman & Addyman, 2013). The number of clips was 44 in Experiment 1 and 64 in Experiment 2. No selection criteria other than the age of the infant and audio quality (no interruptions, dominant background noise, or vocalizations produced by others) were employed. For each clip, the infant's age, sex, and the cause of the laughter was noted (see Table S2 and S3). In addition, we included adult laughter sounds (5 clips for the novices in Experiment 1, and 8 clips for the experts in Experiment 1 and the novices in Experiment 2) in order to test whether, compared to adults, infants would laugh more on the inhalation. All clips had a duration between 4 and 7 seconds.

Before the start of the main survey, participants were familiarized with ingressive (produced during inhalation) and egressive (produced during exhalation) vocalizations by listening to ingressive and egressive non-laughter vocalizations produced by human adults (one clip of each). Then, the laughter clips were played in a fixed random order, and participants were asked, for each clip, to state their agreement with the following four statements: 1) *The laugh is produced during inhalation*; 2) *The laugh is produced during exhalation*; 3) *The laugh is pleasant to listen to*; 4) *The laugh is contagious (when listening to this laugh, I feel like laughing too)*. The response format for all judgments was a 5-point scale with one-decimal accuracy. The scales ranged from *never* to *always* for the first two statements and from *strongly disagree* to *strongly agree* for the last two statements.

A proportion score for egressive laugther was calculated by dividing the perceived exhalation score by the sum of the perceived inhalation and exhalation scores. A combined positive affect score was calculated by taking the average value of the pleasantness score and the contagiousness score[1].

Results

A paired samples t-test comparing perceptions of laughter produced by infants to that of adults confirmed that the proportion of laughter produced during exhalation was significantly lower in infants than in adults (Experiment 1: $M_{infants}$ = .62 *(SD = .09)*, M_{adults} = .74 *(SD = .16)*, $t(114) = -9.09$, $p < .001$; Experiment 2: $M_{infants}$ = .59 *(SD = .09)*, M_{adults} = .62 *(SD = .12)*, $t(101) = -3.26$, $p < .01$).

To test our hypothesis that laughter would be produced increasingly on the exhalation over the course of infancy, two identical linear multilevel models were generated, one for each

[1] A proportion score for exhalation was calculated because the inhalation and exhalation scores were highly negatively correlated (Experiment 1: r = -.91, $p < .001$; Experiment 2: r = -.85, $p < .001$). The pleasantness and contagiousness scores were combined because they were highly positively correlated with each other (Experiment 1: r = .76, $p < .001$; Experiment 2: r = .72, $p < .001$).

experiment. Infant age was used as a predictor variable, and the proportion of laughter produced during exhalation as an outcome variable. As hypothesized, egressive laughter was found to increase with age (Experiment 1 $F(1, 5146) = 123.98$, $p < .001$, Table S4, Figure 1A; Experiment 2 $F(1, 6526) = 337.49$, $p < .001$, Table S5, Figure 1C).

Using linear multilevel models, we investigated whether the degree to which laughter was produced on the exhalation would predict the amount of positive affect evoked in adult perceivers. Proportion exhalation was used as a predictor variable and listener positive affect as an outcome variable. As hypothesized, the proportion of laughter produced on the exhalation positively predicted positive affect scores (Experiment 1 $F(1, 5146) = 135.35$, $p < .001$, Table S6, Figure 1B; Experiment 2 $F(1, 6526) = 126.17$, $p < .001$, Table S7, Figure 1D). Thus, the more the laughter was produced on the exhalation, the more positively it was perceived.

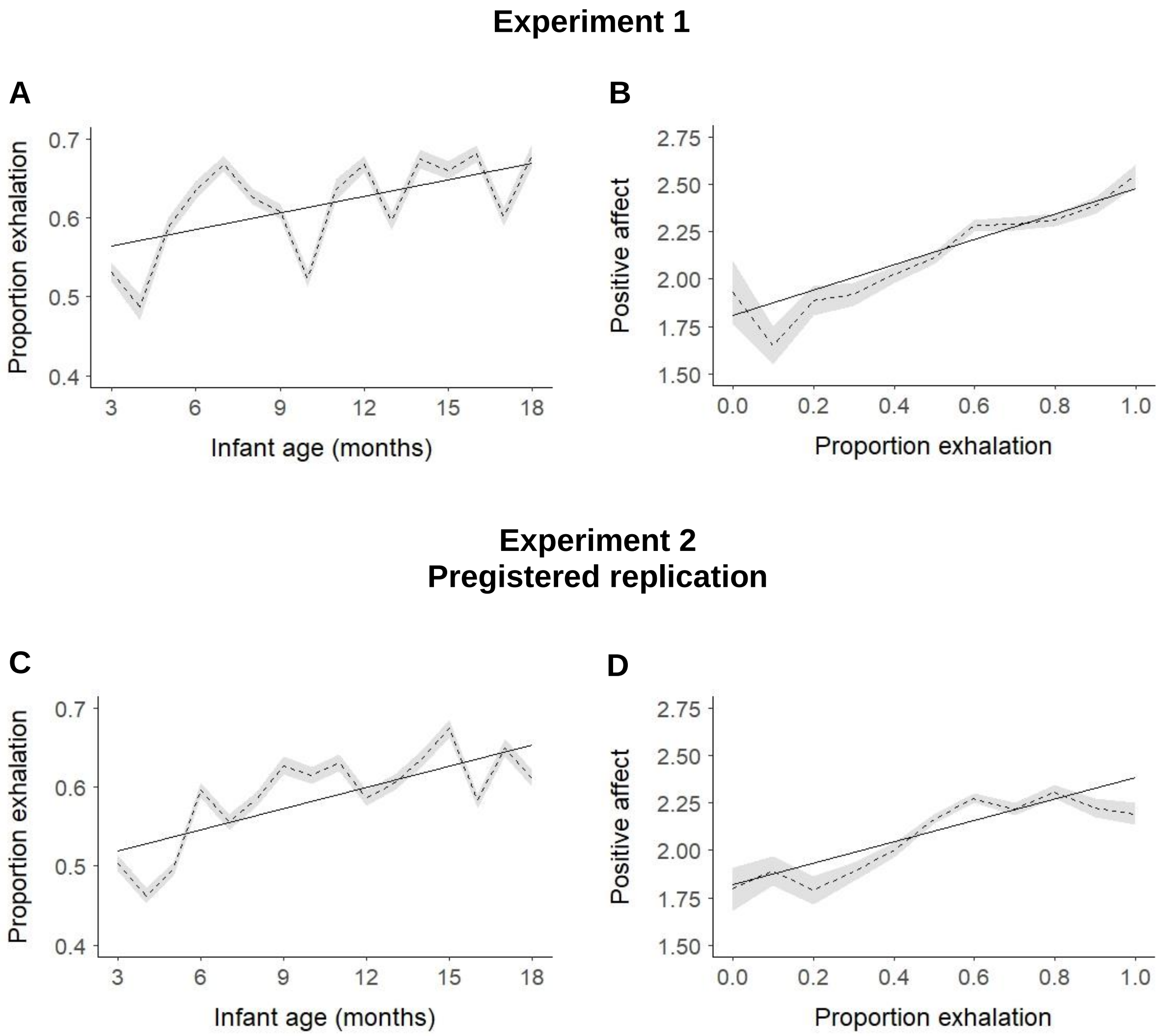

Figure 1. Proportion of laughter produced during exhalation (**A, C**) and positive affect scores (**B, D**) in Experiment 1 (top panel) and Experiment 2 (bottom panel). The solid line shows predicted data based on a linear multilevel model with audio clips nested in participants. The dashed line shows observed data and the shaded error band indicates 1 SE.

Discussion

The present study examined changes in the production of human laughter in early ontogeny. In two experiments, we found that the proportion of laughter produced during exhalation is lower in infants than in adults, and that the older the infants, the more their laughter was egressive. Over the course of early development, human laughter thus deviates increasingly from the laughter vocalizations of nonhuman primates (Davila Ross et al., 2009). Our findings also point to a likely role of social feedback in developmental changes of laughter, with laughs produced more on the exhalation eliciting more positive affect in adult listeners.

Two pathways may explain the shift towards egressive laughter over ontogeny and the enhanced interpersonal effects of egressive laughter. Firstly, developmental changes of the acoustic features of laughter are likely to relate to human anatomical development: The vocal tract of human infants initially resembles that of nonhuman primates (Stabel et al., 2013), but undergo major developmental changes during the first years (Mugitani & Sadao Hiroya, 2012). Functionally, infants greatly improve in terms of vocal control (Gaultier & Gallego, 2005) as they start to produce proto-speech vocalizations like babbling around 7-8 months (Oller, 1980; Stark, 1980). Early human infant laughter may thus resemble the laughter of nonhuman primates in part due to similarities in terms of vocal production systems and associated (lack of) vocal control.

Secondly, developmental changes in laughter production may also reflect social learning processes. Infants as young as six months have been found to mimic sounds produced by their caregivers (Imafuku et al., 2019), and infants are highly receptive to caregivers' responses to their pre-linguistic vocalizations (Albert et al., 2018). In particular, infants adapt subsequent vocalizations based on social feedback (Gaultier & Gallego, 2005) and human adults have a preference for voiced, songlike laughs which are produced during exhalation (Bachorowski & Owren, 2001). Processes of imitation and social learning may thus support the development of gradually more adult-like laughter (Snowdon & Hausberger, 1997). Since laughter induces positive affect in others (Bachorowski & Owren, 2001), infants may over time come to produce laughter with a higher proportion of exhalation in order to elicit maximally positive responses from their social environment.

The present study establishes developmental changes in breathing during laughter production. Further work will be needed to examine whether these findings map onto changes in other important acoustic features of laughter, such as duration, spectral center of gravity, and Harmonics-to-Noise-Ratio (e.g., Szameitat et al., 2009; Lavan et al., 2016). Moreover, future work might examine whether other types of nonverbal vocalizations (e.g., crying) have similar or different trajectories in terms of the development of egressive vocal production. Another potential avenue for future research would be to determine whether similar developmental changes occurs in the laughter vocalizations of nonhuman primates.

In conclusion, this study provides novel insights into the ontogeny of human laughter. Our findings demonstrate that infants increasingly produce egressive laughter over the course ontogeny, with more egressive laughter also being perceived more positively by adults. Thus, human laughter changes over ontogeny from vocalizations similar to those of other great apes to laughter resembling that of human adults.

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Supplemental Information

Table S1

Results from the linear multilevel model predicting proportion of laughter produced during exhalation from infant's age (in months), expertise (novice vs expert), and their two-way interaction in Experiment 1. The multilevel structure of the model was defined by audio clips nested in participants.

Fixed Factors	**F**	**df1**	**df2**	***p*-value**
Corrected model	43.745	3	5144	.000
Infant's age	59.845	1	5144	.000
Expert knowledge	3.151	1	5144	.076
Expert knowledge * Infant's age	0.154	1	5144	.695
Random Factors	**Estimate**	**SE**	**Z**	***p*-value**
Intercept [subject = ID] Variance	.006	.001	6.660	.000

In order to investigate the reliability of lay judgments in Experiment 1, a multilevel model with the infant's age, expertise (novice vs expert), and their two-way interaction as predictors was created. The proportion of laughter produced during exhalation was used as the outcome variable. The main effect of expertise was not significant [$F(1, 5144) = 3.16$, $p = .076$], nor was the interaction between expertise and infant age [$F(1, 5144) =0.15$, $p = .695$]. This demonstrates that the judgments of the proportion exhalation laughter made by novices were similar to those made by experts. These findings suggest that novices were able to make accurate judgements.

Table S2

Overview of the infant’s age, the infant’s gender, and the laughter-eliciting context for the 44 audio clips used in Experiment 1.

#	Age (months)	Gender	Context
1	3	Female	Caregiver tickles the infant
2	3	Female	Caregiver plays with rubber duck and makes funny noises
3	4	Male	Infant looks in the mirror for the first time
4	4	Male	Interaction with caregiver
5	5	Male	Caregiver rips a piece of paper
6	5	Female	Caregiver rips a piece of paper
7	5	Male	Caregiver changes the duvet cover
8	6	Female	Caregiver makes funny noises
9	6	Male	Caregiver plays with stuffed animal and makes funny noises
10	7	Male	Caregiver plays with stuffed animal and makes funny noises
11	7	Male	Caregiver interact with the infant and makes funny noises
12	7	Male	Caregiver interacts with the infant and repeats the same sentence
13	8	Male	Caregiver makes funny noises
14	8	Female	Caregiver makes funny noises
15	8	Male	Infant watches a dog that plays with a ball

16	8	Male	Caregiver rips a piece of paper
17	9	Male	Caregiver repeatedly squeezes a toy that then makes a funny noise
18	9	Male	Caregiver plays together with the infant
19	9	Female	Caregiver scrapes paint of the window frame
20	9	Male	Caregiver engages in social interaction with the infant
21	10	Male	Caregiver tickles the infant
22	10	Male	Baby sister crawls around
23	10	Male	Ripping paper
24	11	Male	Caregiver makes funny noises
25	11	Male	Caregiver tickles the infant
26	11	Male	Caregiver makes funny noises
27	12	Female	Caregiver tickles the infant
28	12	Male	Caregiver is making silly noises
29	12	Female	Brother stumbles
30	13	Male	Older sibling makes funny noises
31	13	Male	Caregiver making silly noises
32	13	Male	Caregiver engages in social interaction with the infant
33	14	Male	Social interaction
34	14	Male	Caregiver pretends to be clumsy by repeatedly dropping books on the floor
35	15	Male	Caregiver tickles the infant

36	15	Male	Infant watches a TV show for kids
37	15	Male	Unknown
38	16	Female	Caregiver tickles the infant
39	16	Male	Uncle cheers when the infant scores while playing basketball
40	16	Female	Caregiver engages in social interaction with the infant
41	17	Female	Caregiver tickles the infant
42	17	Male	Caregiver makes silly noises
43	18	Male	Caregiver engages in social interaction with the infant and they play together
44	18	Female	Caregiver tickles the infant

Note: Three of the clips belong to the same infant (ID = 25); they were recorded at 8, 11, and 14 months of age.

Table S3

Overview of the infant's age, the infant's gender, and the laughter-eliciting context for the 64 audio clips used in Experiment 2.

#	Age (months)	Gender	Context
1	3	Female	Caregiver making silly noises
2	3	Female	Caregiver tickles the infant
3	3	Male	Caregiver making silly noises
4	3	Male	Caregiver tickles the infant
5	4	Female	Unclear (no physical contact)
6	4	Female	Caregiver tickles the infant
7	4	Male	Caregiver repeatedly saying "I love you" in a high-pitched voice
8	4	Male	Caregiver tickles the infant
9	5	Female	Caregiver whistles
10	5	Female	Caregiver tickles the infant
11	5	Male	Caregiver uses a paper tongue whistle
12	5	Male	Caregiver tickles the infant
13	6	Female	Parent making sounds by blowing raspberries
14	6	Female	Caregiver tickles the infant
15	6	Male	Parent making sounds by blowing raspberries

16	6	Male	Caregiver tickles the infant
17	7	Female	Caregiver shakes a box containing grain, which makes a rustling sound
18	7	Female	Older sibling tickles the infant
19	7	Male	Caregiver making silly noises
20	7	Male	Caregiver tickles the infant
21	8	Female	Caregiver makes silly noises
22	8	Female	Older sibling tickles the infant
23	8	Male	Caregiver pumping up a balloon
24	8	Male	Caregiver tickles the infant
25	9	Female	Caregiver throwing a toy towards the child
26	9	Female	Caregiver tickles the infant
27	9	Male	Caregiver making silly noises
28	9	Male	Caregiver tickles the infant
29	10	Female	Unclear (no physical contact)
30	10	Female	Caregiver tickles the infant
31	10	Male	Caregiver repeatedly making the same noise
32	10	Male	Caregiver tickles the infant
33	11	Female	Caregiver reading a book out loud and making silly noises
34	11	Female	Caregiver tickles the infant

35	11	Male	Caregiver pretends to be clumsy by purposely dropping things on the floor
36	11	Male	Caregiver tickles the infant
37	12	Female	Caregiver clowning around
38	12	Female	Caregiver tickles the infant
39	12	Male	Caregiver making silly noises
40	12	Male	Caregiver tickles the infant
41	13	Female	Child watches a video of an adult being clumsy
42	13	Female	Caregiver tickles the infant
43	13	Male	Caregiver making loud noise by slapping the couch the child is standing on
44	13	Male	Caregiver tickles the infant
45	14	Female	Unclear (no physical contact)
46	14	Female	Caregiver tickles the infant
47	14	Male	Caregiver plays with blocks together with the child
48	14	Male	Caregiver tickles the infant
49	15	Female	Unclear (no physical interaction)
50	15	Female	Caregiver tickles the infant
51	15	Male	Caregiver playing a hiding game with the child
52	15	Male	Caregiver tickles the infant
53	16	Female	Caregiver playing tag with child

54	16	Female	Dog tickles the infant
55	16	Male	Caregiver clowning around
56	16	Male	Caregiver tickles the infant
57	17	Female	Caregiver makes silly noises
58	17	Female	Caregiver tickles the infant
59	17	Male	Caregiver pretending to sneeze multiple times
60	17	Male	Caregiver tickles the infant
61	18	Female	Caregiver plays a hiding game with the child
62	18	Female	Caregiver tickles the infant
63	18	Male	Caregiver swinging around with a cloth
64	18	Male	Caregiver tickles the infant

Table S4

Results from the linear multilevel model predicting proportion of laughter produced during exhalation from infant's age, used to investigate the effect of age on egressive laughter in Experiment 1. The multilevel structure of the model was defined by audio clips nested in participants.

Fixed Factors	**F**	**df1**	**df2**	***p*-value**
Corrected model	123.981	1	5146	.000
Infant's age	123.981	1	5146	.000
Random Factors	**Estimate**	**SE**	**Z**	***p*-value**
Intercept [subject = ID] Variance	.007	.001	6.736	.000

Table S5

Results from the linear multilevel model predicting proportion of laughter produced during exhalation from infant's age, used to investigate the effect of age on egressive laughter in Experiment 2. The multilevel structure of the model was defined by audio clips nested in participants.

Fixed Factors	**F**	**df1**	**df2**	***p*-value**
Corrected model	337.489	1	6526	.000
Infant's age	337.489	1	6526	.000
Random Factors	**Estimate**	**SE**	**Z**	***p*-value**
Intercept [subject = ID] Variance	.008	.001	6.662	.000

Table S6

Results from the linear multilevel model predicting the perceiver's positive affect from proportion of laughter produced during exhalation, used to investigate the relationship between egressive laughter and perceived positivity in Experiment 1. The multilevel structure of the model was defined by audio clips nested in participants.

Fixed Factors	**F**	**df1**	**df2**	***p*-value**
Corrected model	135.353	1	5146	.000
Proportion exhalation	135.353	1	5146	.000
Random Factors	**Estimate**	**SE**	**Z**	***p*-value**
Intercept [subject = ID] Variance	.273	.038	7.206	.000

Table S7

Results from the linear multilevel model predicting the perceiver's positive affect from proportion of laughter produced during exhalation, used to investigate the relationship between egressive laughter and perceived positivity in Experiment 2. The multilevel structure of the model was defined by audio clips nested in participants.

Fixed Factors	**F**	**df1**	**df2**	***p*-value**
Corrected model	126.169	1	6526	.000
Proportion exhalation	126.169	1	6526	.000
Random Factors	**Estimate**	**SE**	**Z**	***p*-value**
Intercept [subject = ID] Variance	.342	.049	6.916	.000