Patterns of Laryngeal Electromyography and the Activity of the Respiratory System During Spontaneous Laughter


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INTRODUCTION

One of the human behaviors that communicate information about a person’s emotional state is laughter. When viewed in its entirety, laughter is a very complex behavior (Bachorowski et al., 2001; Ruch and Ekman 2001), but at its core it involves the production of a characteristic sound pattern. This pattern is recognizable across cultures and because it is present in 11–21-wk-old infants (Nwokah et al., 1993), it appears to be innate. Previous studies that have visualized the glottis have observed that the vocal folds open and close rapidly during laughter (Citardi et al. 1996; Moore and von Leden 1958). Studies of the acoustic properties of laughter (Bachorowski et al. 2001; Provine and Yong 1991) have found that the repetition rate of laryngeal movements is about 4–5 Hz. It is also known that there are phasic lung pressure variations superimposed on an active expiratory effort (Filippelli et al. 2001). Laughter generally takes place when the lung volume is low, near functional residual capacity (FRC) and is terminated near residual volume (RV) (Bright et al. 1986; Filippelli et al. 2001).

Although these observations make it clear that both the laryngeal and respiratory system are active in laughing, the details of their coordination are not known. Such an analysis requires that both systems be monitored simultaneously, and it does not appear that such studies have been reported. The present report is based on data provided by two previous studies in which laryngeal EMG and direct and indirect measures of the behavior of the respiratory system were recorded. These data provide new detail on the coordination between these systems. The results of the analysis are discussed in terms of the degree to which the coordination of the respiratory and laryngeal actions during laughter is the result of a central pattern generator, one possibility being that the peri-aqueductal gray (PAG) is involved in this behavior.

METHODS

Subjects

This report is based on two groups of subjects. The larger group (experiment 1) was composed of 17 individuals who spontaneously laughed during the recording of laryngeal electromyographic (EMG) activity. This group was a subset of 31 subjects who were involved in a previous study that compared laryngeal muscle activity of young and old people who were neurologically normal with laryngeal activity of people who had idiopathic Parkinson disease (Baker et al. 1998; Luschei et al. 1999). The 17 people who laughed were all neurologically normal, except for two individuals who had Parkinson disease. There were 10 female and 7 male subjects who laughed. Nine subjects were relatively young (22–32 yr of age) and 8 subjects were older (66–79 yr of age).

A second group of 4 subjects was those who spontaneously laughed during a previous experiment (experiment 2) in which a direct measure of tracheal pressure was recorded, as well as laryngeal muscle activity (Finnegan et al. 1999, 2000). Three of these subjects were female, and one was a male. They ranged in age from 25 to 39 yr. All of these subjects were neurologically normal.

Procedures common to both experiment 1 and experiment 2

Although experiment 1 and experiment 2 were conducted entirely independent of one another, they used many of the same techniques and procedures. Variable inductance plethysmograph bands were placed around the chests and abdomens of 13 of the 17 subjects in experiment 1. All subjects in experiment 2 had these bands. These
bands were not calibrated, so they provided only relative measurements of changes in lung volume. After these bands were positioned, the subject was seated in a dental chair, the back which was lowered to place the subjects in a semirecumbent position. Descriptions of procedures used to insert the laryngeal EMG electrodes have been published elsewhere (Finnegan et al. 1999, 2000; Luschei et al. 1999). In brief, bipolar hooked wire electrodes made from bifilar insulated stainless steel wire—each strand 0.002 inch in diameter—were inserted by an otolaryngologist into the laryngeal muscles of each subject. After locally anesthetizing the skin overlying the ventral portion of the larynx, a 1.5-inch, 25-gauge hypodermic needle, carrying the wire in the lumen, was inserted through the cricothyroid (CT) membrane, and then directed into one of three laryngeal muscles: CT, thyroarytenoid (TA), or lateral cricoarytenoid (LCA) in experiment 1 or CT or TA in experiment 2. The needle was then withdrawn. Even with as many as four electrodes inserted into the laryngeal muscles, the subjects were able to speak and swallow normally without discomfort. Each EMG electrode was evaluated to determine whether it was in the intended muscle. Standard behavioral criteria were used for this purpose—for example, CT was very active for high pitch phonation, but not low pitch phonation or neck flexion. These criteria are described more fully in Luschei et al. (1999). Following these insertions, the back of the dental chair was raised to place the subjects in comfortable sitting positions.

Respiratory airflow was measured in tracheal pressure. The repetition interval and duration of the EMG bursts observed in experiment 1 were determined for the occurrences of laughter. These were recognized primarily by the “bursting pattern” (see following text) of the TA and/or LCA. When EMG from PCA was available, it was noted that a bursting pattern also occurred during laughter. The record of the microphone (mike) often displayed repetitive sound bursts associated with the EMG bursts. When the mike records were played on a speaker, after D/A conversion, they sounded like laughter. Listening to the sound provided a reliable way to differentiate laughter from coughing or throat-clearing, which also showed short bursts of EMG.

When a laugh event was found, it and the activity before and after were parsed from the record and saved as a separate subfile. The mike channel of each subfile was converted to a “wave” file format. Compact disks (CDs) were made of the randomly ordered 106 laugh event voice files that were found in experiment 1, and these CDs were sent to five individuals who were asked to judge the sounds. The five individuals were native speakers of English who were academic professionals whose research interests were in the field of speech pathology. None, however, had any involvement with experiment 1 or CT or TA in experiment 2. The needle was then withdrawn leaving the cannula in place. After the cannula was in place, as confirmed by visual inspection of the trachea through the open glottis, the subject was moved to the laboratory. The outer end of the cannula was connected to a thin silicone rubber tube connected to a pressure transducer having a very low volume. The frequency response of the pressure-measuring system was flat ±3 dB to 40 Hz.

Analysis

The digital records of all subjects in experiments 1 and 2 were examined for the occurrences of laughter. These were recognized primarily by the “bursting pattern” (see following text) of the TA and/or LCA. When EMG from PCA was available, it was noted that a bursting pattern also occurred during laughter. The record of the microphone (mike) often displayed repetitive sound bursts associated with the EMG bursts. When the mike records were played on a speaker, after D/A conversion, they sounded like laughter. Listening to the sound provided a reliable way to differentiate laughter from coughing or throat-clearing, which also showed short bursts of EMG.

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Each spontaneous laugh event subfile was qualitatively examined to determine the general response pattern between the EMG, microphone recording, airflow, chest and abdominal movement, and, in the case of data from experiment 2, tracheal pressure. The repetition interval and duration of the EMG bursts observed in experiment 1 were determined for all records of spontaneous laughter having at least five EMG bursts.

The repetition interval of the EMG bursts was defined as the time from the beginning of a burst until the beginning of the next burst. For data from experiment 2, all laughs having at least four EMG bursts were analyzed. A lower number of bursts for inclusion was adopted for experiment 2 to increase the number of laughs to analyze from this experiment. This analysis was done by marking, on the computer, the

Procedures unique to experiment 1

One of the laryngeal muscles, the posterior cricoarytenoid (PCA), is the primary abductor of the vocal folds. Electrodes cannot be placed in the PCA along the route used for the other muscles. In experiment 1, repeated attempts to place an electrode in PCA using an intraoral route were unsuccessful. Electrodes were successfully placed in the PCA in three subjects of experiment 1, however, by inserting the needle through the skin lateral to the larynx while, at the same time, manually twisting the subject’s larynx so the PCA was more oriented to the side of the insertion.

Procedures unique to experiment 2

In experiment 2, a 20-gauge cannula was placed with its open end in the subject’s trachea. This was done in a minor procedure room in the clinic of the Department of Otolaryngology Head and Neck Surgery of the University of Iowa Hospitals and Clinics. First, the skin overlying the first and second tracheal ring was injected with local anesthetic. The needle carrying the local anesthetic was then advanced carefully until the tip rested against the tracheal wall, and more anesthetic was then injected. A 25-gauge hypodermic needle, which fit snugly inside the 20-gauge cannula, was inserted through the cannula with the needle tip extending beyond its end. The tracheal end of the cannula had been electropolished so that there was a smooth tapered junction where the end of the cannula contacted the shaft of the 25-gauge needle. This needle/cannula assembly was inserted through the skin and then the wall of the trachea. The 25-gauge needle was then withdrawn leaving the cannula in place. After the cannula was in place, as confirmed by visual inspection of the trachea through the open glottis, the subject was moved to the laboratory. The outer end of the cannula was connected to a thin silicone rubber tube connected to a pressure transducer having a very low volume. The frequency response of the pressure-measuring system was flat ±3 dB to 40 Hz.

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beginning and end of each EMG burst in the laugh event. The EMG channel having the most clearly defined bursts of activity was used for this marking. The marking of the beginning and end of each EMG burst was done by one experimenter (E.S.L.) for both experiment 1 and experiment 2. To estimate the reliability of this marking, 18 of the 50 laughs that were used in the rate analysis were marked a second time after deleting the marks from the original marking. For the repetition interval, the mean difference ± 1 SD between the original and second marking was 7% ± 6%; for the marking of the burst duration, these values were 8% ± 5%.

Statistics

The effects of laugh burst number (first, second, third, and so forth), experiment, and their interaction on burst repetition interval and duration were analyzed using nested repeated measures models, that is, laugh repetition intervals were nested within laughs that were repeated within subjects. Laugh burst number and experiment (1 or 2) were treated as fixed effects while subject and laugh were considered random effects. Because burst duration depended on laugh burst number (they were positively correlated), missing data were not missing at random. Therefore only the first four laugh bursts were included in analysis of burst duration as all laughs had at least four bursts. All statistical tests were two-sided with \( P = 0.05 \) significance levels.

RESULTS

Acoustic judging

The five judges listened to 106 voice recordings of what the experimenters considered laugh events, based on EMG responses and their own perception of the acoustic response. Of these, 83 laugh events were spontaneous, that is, not prompted by the instruction “to laugh.” The 23 stage laughs were eliminated from further analysis, though it is noteworthy that four or five of the judges correctly identified 18 of them. Four spontaneous laugh events were marked as “other,” by two or more judges, and these were eliminated from further analysis. There was agreement by four or five of the judges on the type of laugh for 35 of the remaining 79 spontaneous laughs. Most of the disagreement between judges came from assigning the word “chuckle” to the recordings. For purposes of the following report, all of these 79 laugh events will be referred to as “laughs” irrespective of how they were rated by the acoustic judges.

Qualitative observations of the EMG patterns

Figure 1 illustrates the repetitive bursting of laryngeal EMG activity of an individual during strong “ha ha” laughter. The top record, which is 18 s long, begins just before the termination of a prolonged period of vocalization resulting from the instruction to “sustain an ‘ah’ for as long as you can.” At the termination of the vocalization, the subject’s lungs are presumably at or near RV. This is followed by a deep inhalation, in which the PCA exhibits high-amplitude activity. During the subsequent time interval, the experimenter comments, jokingly, “You’ve been practicing, haven’t you?” This comment, though perfectly understandable, is in the background, and does not appear clearly in the mike record. A vigorous laugh immediately follows this comment. The subject, a 24-yr-old female, then begins to breathe normally as the instruction is given to produce “one more” sustained vocalization. This is followed by a deep inhalation and the beginning of another vocalization.

The bottom of Fig. 1 is a shorter record (3.0 s) of the laugh illustrated in the top record of this figure. The brief high-amplitude bursts of TA activity, occurring at a rate of about 5 Hz, were typical of all of the laughs that were studied. The activity of PCA could be observed in this subject, and it is clear that the PCA also exhibits bursts, which are, however, out of phase with the EMG bursts of the TA. A typical feature of this record is that the EMG bursts continue long after sound bursts have ceased being produced, during the initial part of the inspiratory phase of this breath cycle. The presence of EMG bursts in the TA and/or LCA that were not accompanied by a temporally related burst of phonation was seen in 61% of the laugh records that were analyzed. On average there were 2.9 ± 1.7 EMG bursts without accompanying vocalization. In the vast majority of these cases, the unaccompanied EMG burst occurred at the end of the laugh where the plethysmograph bands indicated that exhalation had ended and in some cases where inhalation was clearly progressing. There were, however, a few instances of EMG bursts without accompanying vocalizations in the middle of the laugh bout, during the expiratory phase. The voiced sound bursts of laughter occurred only during exhalation, though there were, in some cases, unvoiced “breath” noises during the inhalation at the end of a bout of laughter. A surprising feature of the TA and LCA muscles is that the burst of activity precedes the laugh sound.
burst and typically ends before or shortly after its beginning. Thus, it might seem that these adductor muscles are not associated with sound production. An explanation of this relationship that leaves the adductors responsible for producing the sound of laughter, however, is offered in the discussion.

Figure 2 top is another long record (21 s) showing activity before and after a laugh. The record begins with rest breathing (A). Then the subject, a 79-yr-old male, yawns (B), during which there is strong activity in LCA but not TA. In “yawning speech,” the subject then says “take a nap” (C). The experimenter comments, “Don’t go to sleep on me” (D). The subject then says, “Yeah, go to sleep” (E), and this is followed by three bouts of “heh heh” laughter (F). The subject then clears his throat (G) and swallows (H). The bottom record of Fig. 2 shows a shorter record (2.6 s) of the second and third laugh bouts shown in the top record. Note the synchronous EMG bursts in these two adductors and the fact that they precede the sound bursts. Distance between the EMG traces equals 1.5 mv for both RTA and RLCA. The chest and abdomen traces of the bottom record are shown at twice the gain of those in the top record.

FIG. 2. A long (top) and shorter (bottom) record of a laugh composed of three laugh “bouts,” defined as the laugh sound bursts occurring on one exhalation-inhalation breath cycle. The segmented line below the mike record, with the alphabetic designations, is a timeline used, in the text, to describe the events that occurred during this 21 s record. The bottom record (2.6 s) is an expansion of the second and third laugh bouts shown in the top record. Note the synchronous EMG bursts in these two adductors and the fact that they precede the sound bursts. Distance between the EMG traces equals 1.5 mv for both RTA and RLCA. The chest and abdomen traces of the bottom record are shown at twice the gain of those in the top record.

Figure 3 depicts two different laughs from another subject in whom PCA activity could be observed. The records of both laughs illustrate typical features: strong phasic bursts of bilateral symmetric activity in the TA muscles, relatively weak modulation of the CT muscle, activity of PCA that is out of phase with the TA muscles, and bursts of muscle activity that continue after the cessation of sound production. What is unusual about both records from Fig. 3 is that they initially start with brief bursts of activity that occur at approximately twice the rate of the subsequent bursts—that is, approximately 10 Hz. The bottom record of Fig. 3 was classified as a “giggle” by four of the five judges. Two other laughs from this subject that had the same 10-Hz bursts of EMG activity were classified as a “giggle” by four or five of the judges.

In most records from experiment 1, the traces from the plethysmograph bands, showing the relative movement of the chest and abdomen, were entirely smooth (Fig. 1, bottom). The fact, however, that there was, in at least some laughs, rhythmic respiratory activity at a rate similar to the EMG bursts was revealed by records such as that shown in Fig. 4 (top). These

FIG. 3. Two laughs from the same subject illustrating the relationship between laryngeal muscle EMG and the accompanying acoustic record. Note rapid brief EMG bursts in the RTA and LTA at the very beginning (top) and in the first half (bottom) of the laughs. Time base: 1.7 s for both top and bottom records. Distance between EMG traces equals 63 μV for RCT, 1 mv for LTA, 0.5 mv for RTA, and 125 μV for LPCA for both top and bottom records.
tracheal pressure, which produced vocalization six times, does not appear to be closely correlated with the four EMG bursts seen in the TA muscles. In Fig. 5 (bottom), the tracheal pressure initially shows positive pressure pulses, only one of which produces vocalization. Following, during the inspiratory phase of respiration, the tracheal pressure pulses are negative, but still temporally correlated with the EMG bursts. Listening to a playback of this recording, there are, however, very quiet but perceptible repetitive breath sounds following the initial vocalization. They are produced by the small exhalations and inhalations seen in the derivative of the airflow record.

The peak tracheal pressure during the laughs ranged between 1.8 and 3.0 kPa for seven of the laughs from experiment 2. The other two had peak values of 0.74 (Fig. 4, bottom) and 0.9 kPa; both of these sounded very quiet compared with the other seven. Pressure at the onset of phonation ranged between 0.45 and 0.85 kPa for all of the laugh sound bursts.

**Laugh repetition interval and burst duration**

Graphs of the repetition interval versus the burst number in the laugh (first, second, third, and so forth) is shown in Fig. 6. Results from the two different experiments are shown separately. It appears from inspection that the laugh repetition interval was somewhat shorter for experiment 2 than experiment 1. This observation was confirmed by the statistical analysis; laugh repetition interval does not differ by burst number ($P = 0.92$), but it does differ by experiment ($P = 0.03$). Figure 7 shows the graphs of EMG burst duration versus the burst number in the laugh. By use of the same statistical model to analyze these data, it was found that burst duration does increase during the laugh ($P = 0.01$) but burst duration did not differ significantly between the two experiments ($P = 0.11$).

It should be noted that the data from one of the subjects in experiment 1 were not included in the analysis of repetition interval or burst duration; this was the subject who laughed with a “giggle” (see Fig. 3, bottom). Many of the EMG bursts within this subject’s laughs occurred with a repetition interval of around 100 ms. These laughs seemed to be of a qualitatively different type, and including them in the analysis would have considerably increased the variance and decreased the means, making them somewhat misrepresentative of the vast majority of the data.

Although Fig. 6 is useful for showing that the repetition interval does not change as the laugh bout progresses, it does not reveal the source of the variability of these graphs. It could be that each laugh had very steady intervals, but these intervals varied widely from one laugh to another. At the other extreme, it could be that all laughs tended to have the same mean interval or burst duration; this was the subject who laughed with a “giggle.” It plots the mean versus SD of the intervals within each laugh. Each symbol represents an individual laugh; it is clear that both the mean interval and the intervals within a laugh are quite variable. It is also clear that laughs recorded in experiment 2 have shorter mean intervals than those from experiment 1, but that they have similar variability within a laugh. The open triangle symbols of Fig. 8 represent 5 laughs made by the same individual.

oscillatory perturbations were small compared with the excursions of the chest and abdomen occurring during the breath cycle during the laugh.

Recordings of laughs from experiment 2 showed, in eight of nine laughs that had adequate records of tracheal pressure, very clear increases of tracheal pressure occurring after each EMG burst (Fig. 4, bottom). In most cases, these pressure increases were large enough to reach the pressure needed to sustain vocalization, and therefore the laugh sounds were in register with the tracheal pressure pulses. Figure 4 bottom shows one of these eight laughs. The record of airflow shown in Fig. 4 (bottom) also illustrates the fact that expiratory flow increased between each burst of phonation; this airflow without voicing created the aspiration noise of the “h” in “ha ha.” This noise is relatively quiet and composed of frequencies that are too high to be recorded faithfully at the bandwidth of the data recording system (2.5 kHz), however, so they are not visible in the microphone record between the voiced sound bursts.

Although nine laughs from experiment 2 exhibited tracheal pressure pulses during the laugh, two records suggest that the linkage between laryngeal EMG bursts and tracheal pressure pulses can be quite flexible. In Fig. 5 (top), the modulation of tracheal pressure, which produced vocalization six times, does not appear to be closely correlated with the four EMG bursts seen in the TA muscles. In Fig. 5 (bottom), the tracheal pressure initially shows positive pressure pulses, only one of which produces vocalization. Following, during the inspiratory phase of respiration, the tracheal pressure pulses are negative, but still temporally correlated with the EMG bursts. Listening to a playback of this recording, there are, however, very quiet but perceptible repetitive breath sounds following the initial vocalization. They are produced by the small exhalations and inhalations seen in the derivative of the airflow record.

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DISCUSSION

Laryngeal behavior during laughter

One of the primary findings of our study is that the TA, LCA, and PCA laryngeal muscles show vigorous bursts of EMG activity during laughter, with the PCA being out of phase with the other two muscles. It is known from earlier studies using either videoendoscopy (Citardi et al. 1996) or high-speed laryngeal photography (Moore and von Leden 1958) that the glottis opens and closes repetitively during laughter. Thus, our results are consistent with prior studies on this topic. Although the activity of the CT muscle was active during laughter, its activity was not modulated (Fig. 4, bottom), or much less modulated than the TA, LCA, and PCA muscles (Fig. 3). Although the CT muscle is classified as an adductor of the vocal folds, it is more importantly a muscle that tenses the medial edge of the vocal folds and thereby controls the fundamental frequency ($F_0$) of the voice (its “pitch”). Although the typical excursion of $F_0$ during a laugh sound burst is appreciable (Bachorowski et al. 2001), presumably it is less than it would be if CT were strongly modulated. One cannot be certain about the functional significance of the differing behavior of CT, but perhaps the lack of very pronounced $F_0$ modulation during the sound burst is a salient feature that

![Image](http://jn.physiology.org/DownloadedFrom)
allows a laugh to be correctly recognized as such. From a neurophysiological standpoint, the differing behavior of CT would at least suggest that the motor program underlying laughter is capable of controlling the laryngeal muscles in an individual manner.

One noteworthy feature of our results is that the activity of TA and LCA, the primary adductors of the vocal folds, precedes the sound burst, and ends before or slightly after its beginning. Further, the activity of the PCA “overlaps” the sound burst to a considerable degree. These observations could suggest that the role of these muscles is reversed during laughter, compared with the role they ordinarily have in sound production. In our view, this seems unlikely. The contraction time of human laryngeal muscles will cause a delay in having the vocal folds move from their open position (a result of the preceding activity of PCA) to a closed position where voicing can occur. The precise value of this delay is not known, but it is relevant to note that electrical stimulation of the TA muscle in a human holding a singing note can produce a “twitchlike” change in the voice $F_0$ that has a “contraction time” of about 50 ms (Titze et al. 1994). This study involved essentially an isometric contraction; the TA contraction during laughter would be, in contrast, much more like an isotonic contraction and would therefore presumably require >50 ms for the EMG to achieve its ultimate mechanical effect. The overlap of the PCA burst and the sound burst can also be explained as the result of the contraction time of the PCA. In this view, the important role of the PCA is to abruptly stop the vibration of the vocal folds by pulling them apart.

Another important reason the TA and LCA bursts precede the sound burst is simply that the tracheal pressure pulse, which is essential to the creation of voicing, appears to be delayed relative to the start of the EMG. Whether this timing is “planned” by the motor control for laughing cannot be determined from these data. It could be that the respiratory muscles are activated at the same time as the laryngeal adductor muscles, but it takes about as long for the respiratory muscles, once they are activated, to increase tracheal pressure as it does for the laryngeal muscles to close the vocal folds once they are activated. Further research combining EMG recording from both the laryngeal and respiratory muscles will be needed to resolve this question.

Rate of laughter

The mean repetition interval in the 50 laughs that were analyzed was 204 ± 30 ms. These values correspond to a rate of 4.95 ± 0.68 Hz. Prior studies have reported on mean laugh rate. Bachorowski et al. (2001) reported an average of 4.37 “calls” per second (their use of the term “call” is what has been called a “sound burst” in the present report). These authors did not, however, report on the variability of these measures. Filippelli et al. found active respiratory efforts superimposed on exhalation during bouts of laughter. These pulses of gastric and esophageal pressure occurred at a rate of 4.6 ± 1.1 Hz. According to Provine (1996) the typical repetition interval of laugh sounds is 210 ms, corresponding to a rate of 4.76 Hz. If one assumes that the repetition rate of the EMG bursts, the acoustics, and the phasic respiratory efforts all represent the same underlying rhythm of the motor center for laughing, then our finding of a rate of 4.95 Hz is reasonably close to the results of prior studies.

Our finding that the laughs in experiment 2 have significantly shorter repetition intervals than those of experiment 1 was entirely unexpected, and the reason for this difference is not clear. The large majority (9 of 10) of the laughs in experiment 2 were produced by young females, so one might wonder whether this difference would disappear if they were compared with laughs produced by young females in experiment 1. When this is tested, however, the difference in repetition interval remains highly significant. Within experiment 1, there are no significant interactions by age, gender, or status (normal or idiopathic Parkinson disease), so laugh rate does not appear to be highly sensitive to these common variables. It is also noteworthy that all the measurements of interval and burst duration were made by the same individual. Subjects in both experiments were of European descent and shared the same basic culture. Thus, the only difference in these experiments that could be related to the rate of laughing is the difference in the region from which the subjects were drawn. It is not impossible that people from Iowa City, Iowa, laugh differently from people from Denver, Colorado, but it seems highly unlikely. Without further information, it seems just as likely to guess that this “difference” in laugh rate is a type I error.

Respiratory behavior during laughter

The direct measure of tracheal pressure that was available in experiment 2 provides strong evidence that the respiratory system is coordinated in a rather precise way with laryngeal activity during a laugh. In all but one laugh in experiment 2 there was a 1:1 relationship between the laryngeal bursts of EMG and the pulses in the tracheal pressure. It is noteworthy in Fig. 4 (bottom) that, although the tracheal pressure shows pressure pulses with laughing, the recordings of the chest and abdominal plethysmograph bands are completely smooth—that is, do not show oscillations. Thus, the smooth records of the chest and abdominal movements seen in most records of laughs
in experiment 1 (Fig. 1, bottom) cannot be taken to mean that there was no phasic respiratory activity in these subjects. In light of the evidence from experiment 2, it seems reasonable to suggest that phasic respiratory efforts were present in the laughs observed in experiment 1, but the plethysmograph bands were too insensitive in most cases to measure the small volume changes necessary to produce these pressure fluctuations. This interpretation is given more weight by the findings of Filippelli et al. (2001), who studied respiratory dynamics during laughing. They observed 4.6-Hz pressure fluctuations in both gastric and esophageal pressure in all of the 11 subjects they studied, which they interpreted as evidence for active respiratory efforts in association with laughing. They also noted that the exhalation during a laughing “fit” (their term for what has been called a “bout” in the present study) went well below functional residual capacity, an observation made earlier by Bright et al. (1986). Because our plethysmograph bands were not calibrated, we cannot confirm where the laugh exhalation ended with respect to FRC, but it is possible to note that all of our laughs, where the plethysmograph bands records were available, were typically associated with a large decrease in relative lung volume. The laugh illustrated in Fig. 4 top is an exception in this regard, a fact that perhaps explains why there were only three sound bursts in the laugh whereas the EMG bursts continue for about another 2 s.

Does the PAG coordinate the laryngeal and respiratory systems during laughter?

It has been demonstrated that focal chemical stimulation of the PAG in unanesthetized decerebrate cats causes two types of vocalization (howls and hisses), both of which are associated with emotional states in this animal (Zhang et al., 1994). Such vocalization involves the coordinated activation of laryngeal adductors (TA) whereas the respiratory muscles of the respiratory system produce increases in tracheal pressure. Davis et al. have further shown that these vocalizations depend on proper afferent input from the respiratory system (1993). Jürgens and Pratt (1979) have likewise presented evidence that the PAG is involved in emotional vocalizations in the squirrel monkey. As laughing in the human is a sound associated with a positive emotional state, and as we have shown coordination between the laryngeal and respiratory system during laughing, we suggest that the PAG in the human has at least some of the essential properties that have been demonstrated in animal experiments. This conclusion makes the assumption, of course, that emotionally laden sounds in the human are produced by or through the PAG. The human PAG has been specifically hypothesized as having a role in laughter (Wild et al. 2003, p. 2130). Davis et al. (1996) have gone further, however, in hypothesizing that the voiced and unvoiced sounds of speech as well as emotional sounds, such as laughing and crying, are coordinated by the neural systems in the human PAG. This view is given some weight by the observation that lesions of the PAG in the human causes complete and irreversible mutism (Esposito et al. 1999).

Although the bulk of our evidence suggests coordination between the laryngeal and respiratory system in the production of laughing, there is, as noted previously, a degree of “flexibility” in this relationship. In well over half of our laughs from experiment 1, we observed EMG bursts that were unaccompanied by sound bursts (see Figs. 1 and 3–5). In these cases, the respiratory system did not provide sufficient tracheal pressure to produce vocalization. Part of the explanation for these partially “silent” laughs (where only the EMG responses would indicate that a laugh was taking place) was that in our situation many of the laughs were of a “private,” subdued, nature. Our guess would be that, if these laughs had occurred in a social context where other people were laughing, the laryngeal EMG and tracheal pressure would have been more of a 1:1 relationship.

These examples imply that there are other neural systems, perhaps neocortical, that may be sensitive to context and “appropriateness” and that these systems can condition the laugh output, either directly by input to the lower coordinative centers (Jürgens and Zwirner 1996) or by inputs to the PAG (Davis and Zhang 1991). Our data do not bear on either of these two possibilities, but they do provide examples of the potential complexity of the neural system responsible for the motor coordination of human laughter.

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