Consequences of postural changes and removal of vestibular inputs on the movement of air in and out of the lungs of conscious felines

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Arshian M, Holtje RJ, Cotter LA, Rice CD, Cass SP, Yates BJ. Consequences of postural changes and removal of vestibular inputs on the movement of air in and out of the lungs of conscious felines. J Appl Physiol 103: 347–352, 2007. First published April 12, 2007; doi:10.1152/japplphysiol.00211.2007.—A variety of experimental approaches have established that the vestibular system contributes to regulation of respiration. In cats, the surgical elimination of labyrinthine signals produced changes in the spontaneous activity and posture-related responses of a number of respiratory muscles. However, these effects were complex and sometimes varied between muscle compartments, such that the physiological role of vestibulo-respiratory responses is unclear. The present study determined the functional significance of vestibulo-respiratory influences by examining the consequences of a bilateral labyrinthectomy on breathing rate and the pressure, volume, and flow rate of air exchanged during inspiration and expiration as body orientation with respect to gravity was altered. Data were collected from conscious adult cats acclimated to breathing through a facemask connected to a pneumotach during 60° head-up pitch and ear-down roll body rotations. Removal of vestibular inputs resulted in a 15% reduction in breathing rate, a 13% decrease in minute ventilation, a 16% decrease in maximal inspiratory airflow rate, and a 14% decrease in the maximal expiratory airflow rate measured when the animals were in the prone position. However, the lesions did not appreciably affect phasic changes in airflow parameters related to alterations in posture. These results suggest that the role of the vestibular system in the control of breathing is to modify baseline respiratory parameters in proportion to the general intensity of ongoing movements, and not to rapidly alter ventilation in accordance with body position.

A VARIETY OF EXPERIMENTAL approaches have established that the vestibular system contributes to making adjustments in the activity of thoracic and abdominal respiratory pump muscles, as well as muscles that regulate the resistance of the upper airway. In animal models, stimulation of vestibular afferents through delivery of electrical pulses to the eighth cranial nerve or rotating the head evoked prominent changes in activity of nerves innervating a variety of respiratory muscles (18–21, 28). In particular, experiments in decerebrate cats recorded activity from the phrenic, hypoglossal, and abdominal nerves during dynamic rotations and static tilts of the head in vertical planes and horizontal yaw rotations, following denervations that eliminated nonlabyrinthine signals that could be produced by the head movement (18, 19). These studies showed that stimulation of vestibular afferents through static tilts, particularly in the pitch plane, were highly effective in altering respiratory nerve activity, although yaw rotations were ineffective. Experiments in humans have also suggested that vestibular inputs contribute to the control of breathing (7–9, 12, 15, 22).

Alterations in the discharges of respiratory muscles can also be elicited by stimulation of brain areas processing vestibular inputs. These regions include circumscribed areas of the caudal vestibular nuclei (26) and three portions of the cerebellum: the rostral fastigial nucleus, the anterior lobe (lobules I–V), and the uvula (lobule IX) (2, 3, 13, 16, 27). These data show that multiple brain regions that process labyrinthine inputs participate in respiratory regulation.

We have additionally conducted experiments in conscious cats that compared alterations in the activity of the diaphragm, abdominal muscles, and the tongue protruder muscle genioglossus during postural changes before and after removal of labyrinthine inputs (4, 5). In vestibular-intact cats, 60° head-up pitch and roll tilts elicited a significant increase in abdominal muscle activity, although the responses to head-up rotations were much larger in magnitude (5). However, changes in body orientation had little effect on electromyogram activity recorded from the diaphragm. Elimination of vestibular inputs greatly diminished the augmentation in abdominal muscle activity that previously occurred during pitch tilts, and additionally resulted in a large increase in the spontaneous activity of this musculature (5). The spontaneous discharges of the diaphragm were also significantly larger following the lesions (5). More complex responses were recorded from genioglossus during whole body tilts (4). Both pitch and roll body tilts produced modifications in muscle firing, but the relative effects of the rotations on genioglossal activity were variable from animal to animal (4). The response variability observed might reflect the fact that genioglossus is composed of many compartments and participates in a variety of tongue movements; in each animal, electromyogram recordings presumably sampled the firing of different proportions of fibers in the various compartments and subcompartments of the muscle. Nonetheless, despite this variability in the effects of body rotations on genioglossus activity, the responses were attenuated by removal of labyrinthine inputs (4).

Since vestibular lesions affected both the spontaneous activity and posturally related responses of a number of respiratory muscles, and sometimes these effects differed between muscle compartments, on the basis of prior data it is difficult to ascertain the physiological role of labyrinthine inputs in ad-
justing the movement of air in and out of the lungs. The objective of the present study was to determine this role by examining the consequences of a bilateral labyrinthectomy on breathing rate and the pressure, volume, and flow rate of air exchanged during inspiration and expiration as body orientation with respect to gravity was altered. We tested the hypothesis that, following removal of vestibular inputs, the volume, pressure, and flow rate of air inspired and expired at the onset of whole body tilts is diminished, due to a reduction in rapid compensatory changes in respiratory muscle activity.

**METHODS**

All experimental procedures conformed to the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the University of Pittsburgh’s Institutional Animal Care and Use Committee. Data were collected from 10 adult female cats obtained from Liberty Research (North Rose, NY). Animals were spayed before being included in this study to eliminate cyclic changes in hormonal levels and were acclimated to experimental procedures over ~2 mo before the initiation of data collection. Parameters regarding the movement of air in and out of the lungs were ascertained using a Hans Rudolph (Kansas City, MO) model RSS-100HR research pneumotach system, coupled with a heated model 8410 flow sensor. Airflow was monitored before and during nose-up pitch (10 animals) and ear-down roll (6 animals) static tilts of the whole body at 60° amplitude. In six of the animals, labyrinthine inputs were also surgically eliminated, and the effects of these lesions on airflow were determined before and during whole body rotations.

**Surgical procedures.** A recovery surgery was required for each animal to secure a bolt to the skull to permit head fixation. This surgery was performed using sterile procedures in a dedicated operating suite. Animals were initially anesthetized using an intramuscular injection of ketamine (15 mg/kg) and acepromazine (0.2 mg/kg). Subsequently, an endotracheal tube and intravenous catheter were inserted. Anesthesia was then maintained using 1–2% isoflurane in O2 such that areflexia was present and heart rate was stable. Ringer lactate solution was infused intravenously to replace any fluid loss during surgery, and a heating pad was used to maintain rectal temperature near 38°C. The animal’s head was secured in a stereotaxic frame, and the head fixation bolt was implanted as described in a previous publication (11). Animals recovered for at least 3 wk after this surgery before data collection was initiated. For 72 h following the surgery, analgesia was provided through the transdermal delivery of 25 μg/h fentanyl (Janssen Pharmaceutical Products, Titusville, NJ). In addition, 50 mg antibiotic (amoxicillin) were administered orally twice daily for 10 days following surgery to prevent infection.

A second recovery surgery was performed in six of the animals following initial data recording to eliminate vestibular inputs. Anesthesia was produced using the same procedures as employed in the initial surgery. The tympanic bulla on each side was exposed using a dorsolateral approach and opened to expose the cochlea. A drill was used to remove temporal bone near the base of the cochlea, thereby producing a labyrinthectomy that rendered the vestibular apparatus dysfunctional. This procedure also provided access to the internal auditory canal. The eighth cranial nerve was then transected under microscopic observation within the internal auditory canal. Thus two independent lesions affecting the vestibular system were made on both sides to ensure that vestibular inputs were removed. In no case did nystagmus or a tonic deviation in eye position occur after the surgery, suggesting that the peripheral lesions were complete. Furthermore, postmortem histological examinations performed as part of our previous studies utilizing this surgical method revealed that it is always completely effective in eliminating vestibular inputs (4, 5, 11).

To prevent the occurrence of postsurgical pain, 3 mg/kg Ketoprofen (a nonsteroidal anti-inflammatory drug with analgesic effects) was administered intramuscularly every 12 h for 3 days following the removal of labyrinthine inputs.

After all data recording was completed, animals were deeply anesthetized with an intraperitoneal injection of 40 mg/kg pentobarbital sodium and killed by transcardial perfusion with saline.

**Data recording procedures.** During data recording sessions, animals were restrained in the prone position on the tilt table. For this purpose, a vinyl bag with attached straps was placed around the animal’s body; the straps were secured to the tilt table to prevent the animal’s position from shifting during testing. Furthermore, the animal’s head was immobilized by inserting a screw into the bolt mounted on the skull. Animals were acclimated over an ~2-mo period to this restraint paradigm, as discussed in a previous publication (11). The data recording sessions had a duration of ~30 min; one to three recording sessions were conducted per day. During each recording session, only one direction of tilt (either nose-up pitch or roll, typically right ear down) was performed. Rotations of 60° amplitude from the earth-horizontal to the maximal pitch or roll position were performed rapidly, at a velocity of ~30°/s. Tilts persisted for ~20 s and were separated by ~40 s. Data were not analyzed from trials in which abrupt transients in airflow occurred as a result of vocalization, swallowing, or other activities, but <10% of trials were eliminated.

The numbers of trials performed for each animal are indicated in Table 1. Only pitch rotations were executed for animals 1–4, whereas animals 5–10 were subjected to approximately equal numbers of roll and pitch tilts.

To monitor the movement of air during inspiration and expiration, a tightly fitting anesthesia mask with a rubber diaphragm seal was secured over the animal’s mouth and nose using straps. The facemask was connected to the sensor of the Hans-Rudolph RSS100HR research pneumotach system using rubber tubing. The positioning of the mask was inspected to ensure that no leaks were present. In addition, airflow measurements were monitored at the onset of the recording session to ensure that the values did not drift (which is indicative of a leak) and that they were concordant with those previously recorded from the animal and other subjects. If any discrepancy was noted, the positioning of the facemask was adjusted. Voltages proportional to the flow rate, pressure, and volume of air delivered to the sensor were recorded digitally using a 1401-plus data collection system (Cambridge Electronic Design, Cambridge, UK) interfaced with a Macintosh (Apple Computer, Cupertino, CA) G4 computer; the sampling rate was 100 Hz. A potentiometer mounted on the tilt table provided a recording of table position; the voltage from this potentiometer was digitized and sampled at 100 Hz.

Table 1. Number of trials performed before removal of vestibular inputs, in the first week following elimination of labyrinthine signals, and in the subsequent 3 wk

<table>
<thead>
<tr>
<th>Animal No.</th>
<th>Prelesion</th>
<th>Postlesion, W1</th>
<th>Postlesion, W2-4</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>142</td>
<td>362</td>
<td>716</td>
</tr>
<tr>
<td>2</td>
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<td>364</td>
<td>799</td>
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</tr>
<tr>
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<td>371</td>
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</tr>
<tr>
<td>9</td>
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<td>544</td>
<td>1,073</td>
</tr>
<tr>
<td>10</td>
<td>2,004</td>
<td>509</td>
<td>1,148</td>
</tr>
</tbody>
</table>

Values are nos. of trials performed before removal of vestibular inputs (prelesion), in the first week following elimination of labyrinthine signals (postlesion, W1), and in the subsequent 3 wk (postlesion, W2-4). Only pitch rotations were delivered to animals 1–4, whereas animals 5–10 received approximately equal numbers of roll and pitch tilts.
Data analysis procedures. The Spike-2 software package (Cambridge Electronic Design) was used for analysis of signals obtained from the pneumotach that were related to the pressure, flow rate, and volume of air inspired and expired. The following parameters were obtained for the five breaths before the onset of each tilt, as well as the first 10 breaths after the body axis was pitched nose up or rolled ear down: tidal volume, maximal airflow rate during inspiration, maximal airflow rate during expiration, and the change in air pressure during the breath. Data obtained for the five breaths before the tilt were averaged to provide the baseline values for that trial. The time between each breath was used to determine breathing rate, and tidal volume and breathing rate values were employed to calculate instantaneous minute ventilation. Similar determinations were made for each pair of breaths after the body axis was reoriented (i.e., breaths 1–2, 3–4, 5–6, 7–8, and 9–10 after the tilt, reached maximal amplitude). The percent change in each airflow parameter from the pretilt baseline value was also calculated for each pair of breaths generated while the animal was oriented 60° head up or ear down.

Prior studies reported that compensation for the effects of vestibular lesions on regulation of respiration and blood pressure occurred after 1 wk (4, 5, 11). For this reason, data recorded in the first 7 days after the removal of labyrinthine inputs and in subsequent weeks were considered as separate groups during analyses. Statistical analyses were performed using SPSS version 11 software (SPSS, Chicago, IL). Statistical significance was set at  \( P < 0.05 \), and pooled data are presented as means \( \pm \) SE. For each animal, univariate ANOVA, in conjunction with the least significant difference test, was used to identify significant differences in each parameter from the pretilt baseline for each pair of breaths generated after the body axis was reoriented. To determine the effects of vestibular lesions on baseline airflow parameters recorded before tilts in each cat, an ANOVA, in combination with the least significant difference test, was also utilized. To determine the overall effects of whole body rotations on airflow parameters across the entire population, mean values from each animal were employed in a repeated-measures ANOVA, and Bonferroni’s multiple-comparison test indicated whether parameters for each pair of breaths after the body axis was reoriented deviated from those before tilts. A similar ANOVA method ascertained whether elimination of labyrinthine signals had a significant effect across the population on the airflow parameters determined while animals were oriented 60° head up or ear down.

RESULTS

Effects of body rotations on airflow parameters in vestibular-intact animals. The mean airflow parameters for all animals combined, determined in the prone position, are as follows: tidal volume, 50 \( \pm \) 3 ml; breathing rate, 52 \( \pm \) 4 breaths/min; minute ventilation, 2.6 \( \pm \) 0.2 l/min; maximal inspiratory airflow rate, 7.2 \( \pm \) 0.5 l/min; maximal expiratory airflow rate, 7.1 \( \pm \) 0.4 l/min; pressure change during breaths, 1.7 \( \pm \) 0.1 cmH\(_2\)O.

Figure 1 shows the percent changes in these parameters when the animals were pitched head up or rolled ear down by 60° before vestibular lesions. Pitch rotations produced a significant increase in tidal volume near the onset of tilts, although responses varied from animal to animal. However, as the animals were maintained in the head-up position, tidal volume returned to baseline values and was not significantly different from that determined before the onset of rotations. Roll tilts had little effect on tidal volume. Both directions of rotation produced an initial increase in breathing rate (9 \( \pm \) 4% for roll and 15 \( \pm \) 4% for pitch). As the animals were maintained in an ear-down position, breathing rate returned to pretilt levels. However, sustained head-up pitch resulted in an \( \sim \)7% decline in breathing rate from values ascertained when the animals were prone. Minute ventilation, inspiratory and expiratory airflow rates, and the pressure generated during breaths all increased significantly at the onset of roll and head-up pitch rotations, but returned to baseline values within a few breaths.

Effects of removal of vestibular inputs on the movement of air in and out of the lungs of prone animals. Figure 2A indicates the percent changes in airflow parameters, determined while animals were in the prone position, that resulted from the surgical elimination of labyrinthine inputs. Data from the first week after vestibular lesions and the subsequent 3 wk are provided separately. Removal of labyrinthine signals produced varying changes in tidal volume in different cats, but for the entire population no significant effects of the lesions on this airflow parameter were noted. However, in every animal, both breathing rate and minute ventilation were significantly reduced by the lesions. The reduction in baseline breathing rate was particularly strong (20–25%) in animals 6, 7, and 10. On average, breathing rate and minute ventilation were, respectively, 15 and 13% lower in the first week after the lesions compared with when vestibular inputs were present. Subsequently, the baseline breathing rate remained significantly depressed in four of the six animals, but in the other two animals a large rebound in respiratory frequency occurred,
such that this parameter became higher than when vestibular inputs were intact.

In every cat, both inspiratory and expiratory airflow rates were significantly lower in the first week following the lesions than when labyrinthine signals were present. On average, removal of vestibular inputs produced a 16% drop in the inspiratory airflow rate and a 14% decrease in the rate of expiratory flow. However, after 1 wk following the lesions, the flow rates tended to recover toward values recorded when the vestibular system was intact. The early effects of removal of vestibular inputs on the pressures generated during breaths were variable between animals. Nonetheless, in all cats the pressures tended to increase after the first week following the lesions. Figure 2 shows the average pressures generated during breaths for every week (W) following the removal of vestibular inputs. Stars indicate values that differed significantly from the pretilt responses (P < 0.05); error bars designate 1 SE.

Effects of removal of vestibular inputs on the changes in airflow accompanying postural alterations. Figures 3 and 4, respectively, show the effects of removal of vestibular inputs on the changes in airflow parameters elicited by 60° nose-up pitch and ear-down roll tilts. These figures illustrate pooled data for animals 5–10 and indicate the mean percent changes in parameters from values determined immediately before the onset of tilts. The alterations in respiratory parameters from baseline deviated by at most 4–5% before and after the removal of vestibular inputs, and thus no significant effects of the lesions were noted. ANOVA analysis P values for the different airflow parameters ranged from 0.35 to 0.86 (median of 0.54) for roll tilts and 0.12 to 0.91 (median of 0.82) for pitch tilts. It thus appears that the lesions did not appreciably alter the consequences of postural alterations on the movement of air in and out of the lungs.

DISCUSSION

A prior study demonstrated that removal of vestibular inputs produces >50% increase in the baseline activity of both the diaphragm and abdominal muscles in conscious animals (5). The present data extend these findings by showing that a bilateral vestibular neurectomy results in tonic alterations in the movement of air in and out of the lungs. In particular, respiratory frequency, minute ventilation, maximal inspiratory flow rate, and maximal expiratory flow rate were reduced significantly after the lesions, and the pressure generated during breaths increased progressively over time. Presumably, the changes in airway were a direct result of the tonic alterations in respiratory pump muscle discharges generated by the elimination of labyrinthine signals (5), although it is unclear whether the effects were due to removal of inputs from otolith organs or semicircular canals. Previous experiments also revealed that alterations in posture, particularly head-up tilts, are accompanied by increases or decreases in the activity of some muscles that participate in respiration, including abdominal musculature and genioglossus (4, 5, 18, 19). However, these responses were complex and varied between muscle compart-
changes in airflow during tilts were noted. Subsequent W2–4. No significant effects of removal of vestibular inputs on lines indicate mean parameters for W1 following the vestibular lesions and the subsequent W2–4. No significant effects of removal of vestibular inputs on changes in airflow during tilts were noted.

Fig. 4. Effects of removal of vestibular inputs on the movement of air in and out of the lungs during 60° roll tilts from the prone position. Averages of data collected from animals 5–10 are plotted; error bars designate 1 SE. Different lines indicate mean parameters for W1 following the vestibular lesions and the subsequent W2–4. No significant effects of removal of vestibular inputs on changes in airflow during tilts were noted.

ments (4, 5). Despite the fact that posturally related changes in respiratory muscle firing have been shown to be attenuated by elimination of labyrinthine signals (4, 5), the present study failed to demonstrate that a bilateral vestibular neurectomy appreciably affects the movement of air in and out of the lungs during alterations in body orientation. The present results therefore suggest that, from a functional standpoint, the most important role of the vestibular system in the control of breathing is to modify baseline respiratory parameters, and not to rapidly alter ventilation in accordance with body position.

Effects of vestibular lesions on the movement of air in and out of the lungs dissipated after a 1-wk recovery period, raising the possible concern that the consequences of lesions were related to indirect factors rather than the loss of vestibular signals. We minimized this potential through the surgical approach employed to eliminate labyrinthine inputs, which did not damage respiratory muscles and involved minimal tissue dissection. In general, it has been noted in animal models that the effects of peripheral vestibular lesions on autonomic regulation dissipate rapidly (4, 5, 11, 24). Patients with inner ear damage or disease also experienced only short-term effects on breathing (8). This rapid recovery may be related to the fact that spontaneous firing of vestibular nucleus neurons recovers within 1 wk after bilateral destruction of the inner ear (17), presumably due to “substitution” of nonlabyrinthine signals for inputs from the inner ear (10, 29). A subset of vestibular nucleus neurons even eventually regain directionally related responses to rotation of the body following the elimination of labyrinthine signals (29). Nonetheless, some of the effects of a bilateral vestibular neurectomy on respiration, such as the decrease in breathing rate induced by the lesions, were still present in four of six animals after a 1-mo recovery period. Another parameter, the pressure generated during breaths, tended to increase above prelesion values progressively over time following the removal of vestibular inputs, further suggesting that gradual plasticity was occurring instead of a transient indirect effect on respiration, such as discomfort related to surgery. Labyrinthine signals influence the discharges of inspiratory and expiratory respiratory motoneurons through several parallel neural pathways, including projections emanating from premotoneurons in the medullary respiratory groups (14, 20), medial medullary reticular formation (23), and upper cervical spinal cord (1). It would not be surprising if the consequences of removal of vestibular inputs on the activity within each of these pathways differed, potentially explaining why some parameters related to the movement of air in and out of the lungs recovered to baseline levels quickly after the lesions, whereas others changed slowly.

This is also the first study that systematically examined the consequences of postural alterations on the movement of air in and out of the lungs of vestibular-intact animals. Changes in respiratory muscle activity elicited by 60° head-up pitch tilts coupled with the mechanical constraints placed on the airway and thoracic cavity by the postural alteration produced a number of effects on the movement of air in and out of the lungs, mainly at the onset of rotations. These effects included a transient mean 14% increase in the maximal inspiratory flow rate, a 5% increase in the pressure generated during breaths, and a 9% increase in minute ventilation. However, these alterations in respiratory parameters were transient, and recovery toward baseline levels occurred within a few breaths after the body axis was reoriented. Similarly, roll tilts produced only momentary changes in the movement of air into and out of the lungs. These findings show that rapid compensation occurs to mitigate the effects of postural changes on the thorax and airway, presumably through adjustments in the activity of primary and ancillary respiratory muscles. Although modifications in abdominal and genioglossal muscle firing during whole body tilts are attenuated by elimination of labyrinthine signals (4, 5), in the present study vestibular lesions did not affect the movement of air in and out of the lungs. Apparently, signals from sensors such as pulmonary and airway receptors are adequate to evoke appropriate adjustments in airflow to compensate for mechanical constraints imposed on breathing when body position changes. Perhaps vestibular-elicited modifications in the activity of muscles with respiratory-related roles during reorientation of the body axis serve another function than regulating the movement of air into and out of the lungs. For example, increases in abdominal muscle discharges during head-up tilts (4, 18) could act to stabilize the body axis, while the mechanics of the contraction have little impact on ventilation.

In summary, the present study showed that removal of vestibular inputs results in a tonic reduction in a number of parameters related to the movement of air in and out of the lungs. However, adjustments in airflow during postural alterations were relatively unaffected by the lesions. These findings suggest that the physiological role of vestibular influences on respiration might be to regulate baseline ventilation in relation
to the intensity and frequency of movements that are occurring. The general level of activity of vestibular afferents and neurons receiving inputs from these cells varies in accordance with the magnitude and number of ongoing head movements (6, 25). Hence, a reduction of head movements and thus activity in the vestibular system should lead to a decrease in ventilation; an increase in vestibular activation seemingly has the opposite effect. Stimulation of vestibular nuclei neurons produces instantaneous changes in breathing (26), such that sudden increases in vestibular system activation under circumstances such as the onset of exercise could rapidly enhance ventilation, even before oxygen demands increase appreciably. Thus vestibulo-respiratory responses could augment chemoreceptor influences on breathing and other feedback mechanisms in ensuring that gas exchange in the lungs is adequate to meet metabolic needs. In contrast, inputs from pulmonary receptors, proprioceptors in the respiratory muscles, and other sensors appear to play the predominant role in eliciting the changes in activity of primary and ancillary respiratory muscles needed to compensate for the mechanical effects of postural alterations on the airway and thoracic cavity.

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