Postural disturbances resulting from unilateral and bilateral diaphragm contractions: a phrenic nerve stimulation study

Alain Hamaoui,1 Anna L. Hudson,2,3,5 Louis Laviolette,2,3,6 Marie-Cécile Nierat,2,3 Manh-Cuong Do,7 and Thomas Similowski2,3,4

1Laboratory of Posture and Movement Physiology, University Champollion, Albi, France; 2Sorbonne Universités, UPMC Univ Paris 06, UMR_S 1158 “Neurophysiologie Respiratoire Expérimentale et Clinique”, Paris, France; 3INSERM, UMR_S 1158 “Neurophysiologie Respiratoire Expérimentale et Clinique”, Paris, France; 4AP-HP, Groupe Hospitalier Pitié-Salpêtrière Charles Foix, Service de Pneumologie et Réanimation Médicale (Département “RS”), Paris, France; 5Neuroscience Research Australia and University of New South Wales, Sydney, Australia; 6Centre de Recherche clinique de l’Institut Universitaire de Cardiologie et Pneumologie de Québec (CRIUCPQ), Quebec, Canada; and 7CIAMS Laboratory, UFR STAPS, University Paris-Sud, Orsay, France

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Hamaoui A, Hudson AL, Laviolette L, Nierat MC, Do MC, Similowski T. Postural disturbances resulting from unilateral and bilateral diaphragm contractions: a phrenic nerve stimulation study. J Appl Physiol 117: 825–832, 2014. First published August 22, 2014; doi:10.1152/japplphysiol.00369.2014.—Thoracoabdominal breathing movements are a complex source of postural disturbance, but there are contradictory reports in the literature with inspiration described as having either a backward or a forward disturbing effect. To elucidate the mechanisms underlying this phenomenon, the present study studied the postural disturbance caused by isolated contractions of the diaphragm. Eight male and four female healthy subjects followed an original paradigm of phrenic nerve stimulation (bilateral and unilateral) and “diaphragmatic” voluntary sniff maneuvers in the seated and standing postures. Center of gravity (CG) acceleration was calculated from force plate recordings, and respiratory kinematics were assessed with thoracic and abdominal sensor belts. CG and respiratory signals revealed that, while seated, bilateral phrenic stimulation and sniff maneuvers consistently produced expansion of the abdomen associated with a forward peak of CG acceleration. In the standing posture, the direction of the CG peak was reversed and always directed backward. Unilateral phrenic stimulation induced an additional mediolateral acceleration of the CG, directed toward the nonactive side while seated, but in the opposite direction while standing. These results suggest that isolated diaphragmatic contractions produce a constant disturbing pattern for a given posture, but with opposite effects between standing and seated postures. This could be related to the different biomechanical configuration of the body in each posture, corresponding to distinct kinematic patterns of the osteoarticular chain. In addition, the lateral component of the CG acceleration induced by unilateral diaphragm contractions could be clinically relevant in patients with hemidiaphragm paralysis.

posture; respiration; diaphragm

IN VERTEBRATES, breathing is the only vegetative function served by skeletal muscles (abdominal and thoracic respiratory muscles). Respiratory muscles exert their action on the rib cage and mobilize the costovertebral joints. In mammals, inspiratory diaphragm contractions generate positive abdominal pressure that exerts a caudal force on abdominal viscera. Therefore, breathing movements interfere with the biomechanical properties of the torso and are a source of postural disturbance (i.e., to the maintenance of body posture), particularly in humans, an erect, bipedal species. In healthy subjects, spinal stiffness is modulated by respiratory activity (25) and respiratory-related postural sway is reduced by apnea (6, 27) and increased by hyperventilation (16). This respiratory-related postural sway can be exaggerated by various factors, including the seated posture (3), restriction of postural chain mobility (i.e., reduction in the range of postural joint movements) (17), or diseases such as low back pain (12).

There are conflicting descriptions of respiratory-related forces that challenge body balance and their compensation, potentially due to differences in posture. Gurfinkel et al. (11) reported a backward movement of the torso during inspiration while standing, but with full compensation by antiphasic displacements of the hips and cervical spine. In contrast, Hunter and Kearney (15) found a substantial proportion of postural sway due to respiratory activity during paced respiration, and considered respiratory-related body movements as an important disturbance to posture. Still, in the standing posture, Hodges et al. (14) described a backward inspiratory displacement of the torso, with complete or almost complete compensation, but with no fixed compensation pattern. However, in seated subjects, Bouisset and Duchêne (3) reported a forward displacement of the center of pressure (CP) during inspiration, suggesting an incomplete compensation in this posture. This is the only study that suggests a forward respiratory-related postural disturbance, perhaps related to the outward displacement of the abdomen induced by diaphragm contraction, enhanced by the seated posture of the subjects. Of note, the pattern of recruitment of inspiratory muscles influences respiratory-related disturbances. Hamaoui et al. (13) showed that “rib cage breathing” (that favors the intercostal and neck muscles over the diaphragm) creates more postural disturbances than “abdominal breathing” (that favor the diaphragm). These differences may result from biomechanical differences between the thoracic and abdominal compartments of the chest wall (13).

Therefore, respiratory-related disturbances to posture are complex and are difficult to characterize because postural sway represents the net result of both the disturbing forces and their compensation. Furthermore, respiratory-related disturbances to posture are likely to depend on baseline posture (namely standing vs. sitting). The aim of the present study was to
investigate respiratory-related postural disturbance, namely the effect of posture and the degree of compensation. To do this, we systematically compared the postural effects of isolated diaphragmatic contractions, considered to be the main inspiratory agonist during resting breathing in humans. Thus, in healthy subjects, in the standing and seated postures, phrenic nerve stimulation was used to produce isolated diaphragmatic contractions (independent of any other respiratory muscle activity) with a sufficiently high velocity to limit the effects of feedforward compensatory mechanisms. We also compared the postural disturbances induced by bilateral and unilateral phrenic nerve stimulation. As diaphragmatic contraction pushes the viscera downward and forward (i.e., diaphragm-related abdominal expansion) (21), a systematic forward disturbing effect was expected in the seated posture, in which the postural chain is restricted to the head and torso. A less consistent effect was expected in the standing posture, which offers a wider range of kinematic patterns because of the extended postural chain.

METHODS

Subjects

Twelve subjects (8 men, 4 women) free of any neurological, musculoskeletal or respiratory disease, took part in the study. Their mean age (±SD) was 32 (±7) yr, with a mean weight of 70 (±13) kg, a mean height of 174 (±8) cm, and a mean body mass index of 23 (±3) kg/m². Appropriate legal and ethical clearance according to the French law by the “Comité de Protection des Personnes Ile-de-France 6, Pitié-Salpêtrière” (no. 33–2012) was obtained. All subjects gave written informed consent prior to the experiments.

Experimental Set-Up

Force plate. A six-channel force plate (model FP4080, Bertec, Columbus, OH), which records the forces and moments acting on the top surface in the three orthogonal planes, was used to calculate acceleration of the center of gravity. The coordinate system is centered on the top surface of the plate, with the anterior-posterior axis (X) oriented forward, the medial-lateral axis (Y) oriented on the left side, and the vertical axis (Z) oriented downward (Fig. 1).

Thoracoabdominal sensor belts. Respiratory kinematics were assessed using two custom sensor belts that measured changes in rib cage and abdominal circumference. The belts were composed of two nonstretch Velcro bands joined by a small elastic band with a draw wire sensor (WPS 250 model, Micro Epsilon, Ortenburg, Germany) strapped onto both sides of the elastic band. The belts were fastened around the upper rib cage and abdomen, at the level of the axilla and umbilicus, respectively.

Electromyography. Diaphragm electromyograms were obtained using silver/silver chloride surface electrodes positioned on the mid-clavicular line, with the active electrode in the 7th–8th intercostal space and the reference electrode over the adjacent rib (interelectrode distance about 20 mm). This electrode montage has been shown to minimize the risk of contamination of the diaphragm motor response to phrenic nerve stimulation by costimulated muscles (26).

Phrenic nerve stimulation. The right and left phrenic nerves were stimulated at the neck using handheld monopolar electrodes. With this system, the handle-mounted cathode can be positioned very precisely over the anatomical landmarks of the phrenic nerve while the anode is fixed (adhesive gel electrode just below the sternoclavicular junction) (Fig. 1). Stimulations were triggered with a footswitch allowing simultaneous production of an analog current pulse for subsequent synchronization purposes. Stimulating square wave pulses of 0.1-ms duration and adjustable intensity were delivered by a constant-current electrical stimulator (Digitimer DST7, Welwyn Garden, UK). Supramaximal stimulation was attempted as follows (24). First, the phrenic nerve was identified by means of low stimulating currents (~10 mA). A recruitment curve was then constructed by increasing the stimulation intensity in a stepwise manner with direct visual feedback of the amplitude of the diaphragm potentials. Supramaximal activation of the stimulated phrenic nerve fibers was assumed when a stimulating current 15–20% above the intensity producing the largest potential could be used. However, when increasing current intensity resulted in brachial plexus costimulation, phrenic nerve stimulation was performed by using the maximal intensity allowing the operator to obtain pure diaphragm contractions, irrespective of supramaximality.

Data acquisition. For the purposes of subsequent analysis, all data from the recording and stimulating devices (11 channels) were collected at 1,000 Hz with a 16-bit A/D converter board (model CompactDAQ with 9,215 modules, National Instruments, Austin, TX) controlled by a custom code written in Labview software (National Instruments). EMG signals from both hemidiaphragms were recorded in duplicate for online display during the recruitment curve procedures (see above) and during the phrenic nerve stimulation sessions. For this purpose, diaphragm EMGs were amplified (10,000×) and...
filtered (band-pass 10 Hz–1 kHz) using a 1902 signal conditioner (Cambridge Electronic Design, Cambridge, UK), digitized at 10 kHz using a CED Power 1401 MKII data-acquisition interface (Cambridge Electronic Design). Data recorded from the force plate and respiratory belts were filtered with a Butterworth second-order low-pass digital filter, with a cut-off frequency of 40 Hz.

**Procedures**

**Diaphragm twitches.** To determine displacements of the center of gravity (CG) following selective unilateral and bilateral diaphragm contractions, phrenic nerve stimulation was performed. Subjects either stood or sat on the force plate, barefoot and with their upper limbs relaxed alongside their trunk (Fig. 1). They were asked to remain as still as possible and to breathe normally while focusing their gaze in front of them. In the standing condition, their feet were shoulder-width apart, and in the seated condition, subjects sat on a rigid stool with their hips and knees flexed to 90°. A first experimenter, positioned behind the subject, applied the phrenic nerve stimulation electrodes while avoiding any bodily contact with the subject other than via the stimulating electrode. A second investigator monitored the respiratory and force plate signals. A third investigator managed the stimulation to avoid any transmission of the first investigator’s movements to the subject. The stimulation was triggered at the end of expiration, so that subjects were always in the same phase of the respiratory cycle. A fourth investigator checked the amplitude of the diaphragm EMG responses on-line to ensure consistent stimulation. A web cam placed above the experimental field was used to take pictures and videos during the trials. The investigator in charge of performing phrenic nerve stimulation took every effort to selectively deliver stimuli to the phrenic nerve. The absence of costimulation of the brachial plexus was determined by visual inspection (absence of arm movement or visible arm muscle contractions) and by inspection of the diaphragm EMG response (absence of obvious changes in shape and latencies). To ensure that CG displacements curves were exclusively related to diaphragm contractions and not to accidental upper limb movements produced by brachial plexus costimulation, we deliberately tested the effect of costimulation of the phrenic nerve and brachial plexus in each experimental condition. This costimulation led to different diaphragm EMG and biomechanical traces to those obtained after pure phrenic nerve stimulation and these trials were used as a framework to exclude unsatisfactory trials during off-line analysis.

The experimental conditions comprised crossover posture (standing, seated), and phrenic nerve stimulation (left, right, and bilateral), resulting in six different experimental conditions (2 posture conditions × 3 stimulation conditions). Two 1-min trials were carried out for each condition, with stimuli delivered every 10 s, with a 1-min rest period between trials, and a 3-min rest period between series.

**Sniff maneuvers.** To determine displacements of the center of gravity following voluntary, high-intensity sniff maneuvers performed in such a way as to ensure predominantly diaphragm contraction, subjects performed short, sharp inspiratory efforts through the nose following the end of a relaxed expiration. They were given feedback of the abdominal and thoracic displacement signals that were continuously monitored by an investigator, and were trained to sniff while “projecting their abdomen outward.” A sniff maneuver was considered to predominantly involve the diaphragm, if and only if abdominal expansion coincided with an initial decrease in upper rib cage circumference. Trials with any decrease in abdominal circumference were rejected (i.e., with predominant contribution of extradiaphragmatic inspiratory muscles). Trials in which upper rib cage circumference increased from the very beginning of inspiration were also discarded. Subjects performed two 1-min runs, with sniff maneuvers interspersed with one or two quiet breaths. A 1-min rest period was observed between runs, and a 3-min rest period was observed between conditions (seated and standing).

**Data Analysis**

Data analysis focused on the relationship between respiratory kinematics and posture. The signals derived from the thoracic and abdominal respiratory belts (RespTh, RespAb, respectively) were used as indicators of respiratory kinematics. Because diaphragm contractions induced relatively high-frequency movements (~5 Hz for diaphragm twitches, ~1 Hz for sniff maneuvers), center of pressure data (CP) were considered to be unreliable to describe postural changes. Indeed, CP is usually considered to be very close to the vertical ground projection of the center of gravity (CG) during the low-frequency (below 0.4 Hz) postural sway that occurs during quiet standing, but the CP and CG projections have been shown to diverge during higher-frequency movements (5, 11).

Therefore, postural variations during sniff maneuvers were described in terms of CG acceleration in the anterior-posterior (Xg) and medial-lateral (Yg) axes. These variables were calculated as the ratio between the ground reaction forces and the subject’s mass (m), both provided by the force plate. Xg = (−Fx/m) and Yg = (−Fy/m), where Fx and Fy are the forces applied by the subject on the plate in the anterior-posterior and medial-lateral axes, respectively. According to Newton’s third law (action-reaction principle), (−Fx) and (−Fy) represent reaction forces of the plate applied on the subject.

Respiratory and CG variables (RespTh, RespAb, Xg, Yg) were first described in terms of their general time-course and curve shape. In view of the “ballistic-like” nature of diaphragm twitches and sniff maneuvers, respiratory thoracic and abdominal peaks recorded from respiratory belts (RespThP and RespAbP, used as descriptors of the disturbance) were expected to occur in phase with postural respiratory peaks of CG acceleration (XgRP and YgRP, used as descriptors of the respiratory disturbance to posture) (in line with CG data observed during ballistic upper limb movements, see Ref. 4). The effects of posture (seated vs. standing) and the type of diaphragm activation (unilateral or bilateral phrenic nerve stimulation, sniff maneuvers) were then studied qualitatively (direction) and quantitatively (magnitude) from the peaks. It should be noted that signals were carefully inspected trial-by-trial, to eliminate from the analysis uninterpretable trials due to failure to obtain selective phrenic nerve stimulation or the failure of the subjects to perform adequate sniff maneuvers.

**Statistical Analysis**

Statistical analysis was performed to assess the qualitative and quantitative characteristics of the four peaks (RespThP, RespAbP, XgRP, YgRP) as a function of experimental conditions, namely changes in posture (seated, standing) and diaphragm activation mode (right stimulation, left stimulation, bilateral stimulation, sniff maneuver). First, McNemar’s test (matched pairs) was used to compare the direction of XgRP (forward, backward) and YgRP (right, left) peaks. Second, the magnitude of each peak, which was averaged per subject, was assessed by a two-way repeated-measures analysis of variance (ANOVA). The interaction between the two independent variables (posture and diaphragm activation mode), was also tested for the four peaks. When statistical significance was reached, the ANOVA was followed by a within-subject analysis of contrasts to compare the levels of each independent variable. Differences were considered significant when the probability P of a type I error was <0.05. All tests were performed with SPSS 14.0 statistical package.

**RESULTS**

**General Characteristics of Respiratory and CG Curves**

**Phrenic nerve stimulation.** Visual inspection of RespAb and RespTh traces revealed that stimulated diaphragm contractions were systematically associated with an abdominal and a thoracic peak (RespAbP and RespThP, respectively). RespAbP
had an outward direction (inspiratory) in every case, with an onset latency of 61 ± 7 ms. RespThP had an inward direction, representing the paradoxical “expiratory” effect of the negative intrathoracic pressure produced by diaphragm contractions on the upper rib cage, and attesting to the isolated nature of diaphragm contraction (20) in every case, with an onset latency of 44 ± 5 ms (Fig. 2).

$X^g$ and $Y^g$ curves consistently displayed polyphasic waves starting concomitantly with the respiratory peaks (Fig. 2). The first peak of the wave was considered to be the respiratory peak of CG acceleration along the anterior-posterior ($X^gRP$) and medial-lateral ($Y^gRP$) axes. According to the second law of Newton, which defines the relationship between CG acceleration and force, the acceleration peak must be generated by a force. Under stimulated contraction conditions, which are not anticipated by the subjects, the first peak can only result from a diaphragm contraction. However, the following peaks could be related to reflex or voluntary reactions to the stimulation.

**Sniff maneuvers.** The respiratory and postural traces observed during sniff maneuvers were generally similar to their “stimulation” counterparts, but with greater magnitudes (Fig. 3).

### Qualitative Assessment of Respiratory and Postural Peaks

All modalities of phrenic nerve stimulation (bilateral, left, and right) produced a forward $X^gRP$ in the seated posture. This was also consistently the case in response to sniff maneuvers. In contrast, $X^gRP$ was systematically directed backward in the standing posture, regardless of the type of stimulation and during sniff maneuvers (Fig. 4). All seated vs. standing comparisons were therefore highly significant for stimulated contractions ($P = 0.0039$ for bilateral stimulation, $P = 0.002$ for right stimulation, $P = 0.001$ for left stimulation) and for sniff maneuvers ($P = 0.001$).

During bilateral phrenic nerve stimulations and sniff maneuvers, $Y^gRP$ was present in most trials and indifferently oriented toward the left or right side. In contrast, unilateral phrenic nerve stimulation produced $Y^gRP$ that were consistently oriented toward the opposite side in the sitting posture (leftward in response to right phrenic nerve stimulation and vice versa) (Fig. 5). The direction of $Y^gRP$ was reversed in the standing posture in 8 of the 12 subjects ($P = 0.0078$ for right stimulation and $P = 0.002$ for left stimulation), with $Y^gRP$ directed toward the side of stimulation (Fig. 5).

### Quantitative Assessment of Respiratory and Postural Peaks

All peak measurement results are presented in Table 1. Analysis of peak magnitudes revealed that RespAbP, RespTh, and $X^gRP$ were greater in response to bilateral phrenic nerve stimulation compared with unilateral (right or left) phrenic nerve stimulation ($P < 0.05$ for RespAb, $P < 0.002$ for RespTh, and $P < 0.05$ for $X^gRP$). Conversely, higher mean values of $Y^gRP$ were observed in response to unilateral phrenic nerve stimulation compared with bilateral phrenic nerve stimulation, with a significant difference only between bilateral and left stimulations ($P = 0.035$).

RespAbP was higher in response to sniff maneuvers than in response to bilateral phrenic nerve stimulation ($P = 0.0001$), on average five- to sixfold higher in magnitude. A similar phenomenon, but to a lesser degree, was observed for RespThP ($P = 0.027$). In contrast, no significant variation of $X^gRP$ and $Y^gRP$ was observed between these two experimental conditions.

Pooled data across all conditions show that RespAbP and RespThP did not vary according to posture, but $X^gRP$ and $Y^gRP$ were significantly greater in the seated compared with the standing posture ($P = 0.0001$) (Fig. 6).
For any measure (XgRP, YgRP, RespAbP, or RespThP), statistical analysis did not reveal a significant interaction between posture and diaphragm activation mode.

DISCUSSION

The main finding of this study is that isolated diaphragm contractions induce a specific postural disturbance that varies according to posture. It also shows that respiratory-related disturbances may comprise a lateral component, not only during unilateral diaphragm contractions, but also during voluntary sniff maneuvers.

Qualitative analysis of respiratory and postural displacements in our subjects showed that the postural disturbance resulting from diaphragm contractions has a systematic pattern. While seated, Xg was always directed forward regardless of the source of diaphragm contraction (bilateral stimulation, unilateral stimulation, or sniff maneuver). In contrast, in the standing position, Xg was systematically directed backward. To our knowledge, this reversal of the direction of a respiratory-related disturbance of posture according to body position has not been reported previously for isolated diaphragm contraction, but our findings are consistent with available data (see Introduction). Reversal of respiratory-related postural disturbance could be related to differences between the nature and biomechanical characteristics of the postural chain in the seated and standing positions. While seated, the pelvis is in direct contact with the supporting surface and the lower limbs are not included in the postural chain. It can then be assumed that forward displacement of the abdominal mass induced by diaphragm contraction (21) is transmitted to the whole body CG, with limited antiphase movements along the chain. In standing, the postural chain includes the lower limbs and therefore presents more degrees of freedom, including, for example, translation of the pelvis that is no longer limited by friction forces with the seat. Consequently, multisegmental movements may occur along the postural chain in reaction to abdominal mass displacements (third law of Newton), e.g., torso extension, with an inverse effect on the whole body center of mass. This hypothesis could be tested by assessing the segmental mobility of the postural chain during diaphragm contractions (e.g., angular motions of the neck, hip, knee, and ankles).

In addition, one can also assume that the flattening of the lumbar lordosis and the posterior pelvic, which occur with a change from the standing to seated posture (10, 18, 23), may vary the postural disturbance induced by the displacement of the neighboring abdominal mass. Finally, the biomechanical action of the diaphragm itself, namely the crural portion which inserts on the spine, will also be altered by a change in posture by mechanisms such as altered muscle length and configuration.

Fig. 4. Acceleration of the center of gravity along the anterior-posterior axis (Xg) and respiratory traces (RespTh, RespAb; B) during bilateral phrenic nerve stimulation (Stim.) in a representative subject, in the seated (A) and standing postures (B). Positive slopes represent forward accelerations (Xg).

Fig. 5. Acceleration of the center of gravity along the medial-lateral axis (Yg) and respiratory movements (RespTh, RespAb) during left phrenic nerve stimulation (Stim.), in the seated (A) and standing (B) postures. Positive slopes represent leftward accelerations (Yg).
Table 1. **Magnitude of thoracoabdominal** (RespThP, RespAbP) and postural (X"gRP, Y"gRP) respiratory peaks in response to stimulated contractions (Stim) and sniff maneuvers (SniffAb) 

<table>
<thead>
<tr>
<th></th>
<th>RespAbP, mm</th>
<th>RespThP, mm</th>
<th>X&quot;gRP, m/s²</th>
<th>Y&quot;gRP, m/s²</th>
</tr>
</thead>
<tbody>
<tr>
<td>StimBiSit</td>
<td>2.393±1.521</td>
<td>1.204±0.777</td>
<td>0.087±0.040</td>
<td>0.030±0.020</td>
</tr>
<tr>
<td>StimBiStand</td>
<td>1.439±1.150</td>
<td>1.033±0.710</td>
<td>0.034±0.006</td>
<td>0.010±0.009</td>
</tr>
<tr>
<td>StimRSit</td>
<td>0.681±0.574</td>
<td>0.571±0.463</td>
<td>0.050±0.022</td>
<td>0.034±0.010</td>
</tr>
<tr>
<td>StimRStand</td>
<td>0.342±0.362</td>
<td>0.634±0.409</td>
<td>0.031±0.011</td>
<td>0.011±0.006</td>
</tr>
<tr>
<td>StimLSit</td>
<td>0.563±0.699</td>
<td>0.520±0.350</td>
<td>0.032±0.015</td>
<td>0.041±0.018</td>
</tr>
<tr>
<td>StimLStand</td>
<td>0.418±0.475</td>
<td>0.633±0.379</td>
<td>0.022±0.008</td>
<td>0.011±0.003</td>
</tr>
<tr>
<td>SniffAbSit</td>
<td>14.847±6.476</td>
<td>1.722±0.910</td>
<td>0.080±0.040</td>
<td>0.026±0.032</td>
</tr>
<tr>
<td>SniffAbStand</td>
<td>13.937±5.208</td>
<td>2.141±1.199</td>
<td>0.033±0.020</td>
<td>0.009±0.014</td>
</tr>
<tr>
<td>P (Sit/Stand)</td>
<td>NS</td>
<td>NS</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>P (StimBi/StimR)</td>
<td>0.010</td>
<td>0.002</td>
<td>0.020</td>
<td>NS</td>
</tr>
<tr>
<td>P (StimBi/StimL)</td>
<td>0.010</td>
<td>0.004</td>
<td>0.010</td>
<td>0.035</td>
</tr>
<tr>
<td>P (StimBi/SniffAb)</td>
<td>0.00</td>
<td>0.03</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

Values are means ± SD. Peaks were measured during bilateral (StimBi), right (StimR) and left (StimL) stimulations, in the seated (Sit) and standing (Stand) postures. The P values of the ANOVA are presented at the bottom of the table; P values >0.05 were considered to be nonsignificant (NS).

Of note, X"gRP and Y"gRP (representing the respiratory disturbance to posture) were significantly higher in the seated than standing posture (P < 0.0001), whereas RespAbP and RespThP (representing the disturbing source) remained almost constant. Therefore, for a similar breathing pattern, the respiratory-related postural disturbance is greater while sitting than standing, suggesting that a shorter postural chain is less efficient to compensate for respiratory disturbances, consistent with previously published studies (1, 3, 17). As stimulated diaphragm contractions did not allow a feedforward compensatory mechanism, it can be assumed that this variation was exclusively related to the passive characteristics of the postural chain. Therefore, compensation for reactive forces consequent on diaphragm shortening during breathing is not only the result of active counter-disturbing mechanisms as shown by Hodges et al. (14), but also involves passive dampening mechanisms, which could be related to the viscoelastic properties of the soft tissues surrounding the bony chain (13).

As expected, the magnitude of the thoracoabdominal motions induced by bilateral diaphragm contraction was higher than the corresponding displacements following unilateral contractions, coincident with higher X"gRP values in response to bilateral phrenic nerve stimulation. Thoracoabdominal displacements were even greater in response to sniff maneuvers than to bilateral phrenic nerve stimulation. This result was also expected, as a maximal sniff maneuver produces four- to fivefold greater inspiratory pressure than a supramaximal diaphragm twitch (2). However, in contrast, X"gRP and Y"gRP were not significantly higher during sniffs than during bilateral twitches. Other possible mechanisms for the unaltered CG values include 1) a plateau in the relationship between respiratory movements and the ensuing postural changes at the twitch strength level; 2) slower sniff dynamics than twitch dynamics, as suggested by visual inspection of the signals; 3) the involvement of respiratory muscles other than the diaphragm during the sniffs, which might blunt the diaphragm-related postural disturbance; and 4) feedforward postural compensation mechanisms, insofar as self-paced sniffs result from cortical preparation (19, 22).

Unilateral diaphragm contractions induced lateral displacement of the CG (Y"gRP peak). In general, this peak was directed contralaterally to the side of stimulation while seated, and ipsilaterally during standing. Contralateral acceleration of the CG in the seated posture could be due to the oblique direction of the force produced by a single hemidiaphragm (in contrast with the cephalo-caudal force produced by bilateral contractions), as the abdominal contents are pushed downward and toward the contralateral side. Reversal of the direction of

![Fig. 6. Postural (X"gRP, Y"gRP) and thoracoabdominal respiratory (RespThP, RespAbP) peaks in the standing and seated postures. Mean (±SD) of each variable were calculated from all experimental conditions (bilateral and unilateral diaphragm twitches, sniff maneuver), in the standing and seated postures. Note that the large SD for ResAbP is due to much higher peaks in sniff maneuvers than in diaphragm twitches.](http://jap.physiology.org/doi/10.1152/japplphysiol.00369.2014)
the disturbance observed while standing could be derived from the same biomechanical hypothesis as described above for \( Z_{g} \), i.e., movement of other segments of the extended postural chain in an opposite direction to those of the abdominal contents.

Lateral acceleration of the CG in response to both bilateral phrenic nerve stimulation and sniff maneuvers was sometimes observed in the form of a \( Z_{g} \) peak, with a similar order of magnitude to that observed in response to unilateral phrenic nerve stimulation. Therefore, the lateral disturbing effects of the left and right hemidiaphragms appear to be asymmetrical and not “cross-compensated.” This may be due to heterogeneous distribution of the visceral mass underlying the diaphragm or to the known asymmetry of the length and curvature of the two hemidiaphragms in humans \( (7, 8, 28) \). Of note, although the contractions of both hemidiaphragms in response to central nervous commands are coupled, the peripheral neural pathway to the muscle is not perfectly symmetrical. Several phrenic nerve stimulation studies have evidenced longer phrenic conduction times on the left side \( (see \) Table 1 in Ref. 24) that could be responsible for a slight mechanical lag between the movements of the two hemidiaphragms. Whatever the origin of the sniff-related \( Z_{g} \), its existence suggests that respiratory kinematics have a disturbing effect not only along the anterior-posterior axis but also along the medial-lateral axis.

Several methodological issues need to be addressed. We tried, but failed, to use a phrenic nerve stimulation device that would avoid contact between the investigator and the subject and aid symmetrical stimulation \( (9) \). As a result, some of our observations may have been altered by involuntary electrode displacement, stimulation asymmetry during bilateral phrenic nerve stimulation, or transmission of a force from the investigator to the subject with a resulting postural compensation. However, the fact all experiments were conducted by a single, highly experienced investigator and the high level of intersubject homogeneity of the results suggests we limited technical error. In addition, we are aware that, as this study was based on isolated diaphragm contractions (induced by phrenic nerve stimulation and therefore not posturally compensated) and sniff maneuvers, our results do not pertain to physiological breathing observed at rest or during exercise. Nevertheless, our data indicate that the inspiratory action of the diaphragm has a specific, posture-dependent impact on body balance. Future studies are necessary to determine the relevance of our findings in clinical situations where diaphragm function is abnormal (e.g., thoracic hyperinflation in obstructive lung disease or uniaxial bilateral diaphragm paralysis).

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

REFERENCES


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