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ORIGINAL PAPER

Activity patterns of the diaphragm during voluntary movements in awake cats

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Abstract The diaphragm is an important inspiratory muscle, and is also known to participate in the postural function. However, the activity of the diaphragm during voluntary movements has not been fully investigated in awake animals. In order to investigate the diaphragmatic activity during voluntary movements such as extending or rotating their body, we analyzed the electromyogram (EMG) of the diaphragm and trunk muscles in the cat using a technique for simultaneous recordings of EMG signals and video images. Periodic respiratory discharges occurred in the left and right costal diaphragm when the cat kept still. However, once the cat moved, their periodicity and/or synchrony were sometimes buried by non-respiratory activity. Such non-periodic diaphragmatic activities during voluntary movements are considered as the combination of respiratory activity and non-respiratory activity. Most of the diaphragmatic activities started shortly after the initiation of standing-up movements and occurred after the onset of trunk muscle activities. Those activities were more active compared to the normal respiratory activity. During rotation movements, left and right diaphragmatic activities showed asymmetrical discharge patterns and higher discharges than those during the resting situation. This asymmetrical activity may be caused by taking different lengths of each side of the diaphragm and trunk muscles. During reaching movements, the diaphragmatic activity occurred prior to or with the onset of trunk muscle activities. It is likely that diaphragmatic activities during reaching movements and standing-up movements may have been controlled by some different control mechanisms of the central nervous system. This study will suggest that the diaphragmatic activity is regulated not only by the respiratory center but also by inputs from the center for voluntary movements and/or sensory reflex pathways under the awake condition.

Keywords Diaphragm · EMG · Voluntary movement · Respiration · Posture

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Introduction

The diaphragm is not only the primary muscle of inspiration but is also known to participate in postural function, and its activity is influenced by various factors, such as posture changes under anesthesia [1, 2] and walking [3–5] in cats. Changes in posture can affect the length of the diaphragm requiring additional activity to maintain stable ventilation. It has also been reported that the diaphragm is involved in the control of postural stability during rapid and repetitive voluntary movement of the limbs in human [6, 7].

In the walking cat, the diaphragm always shows a predominant inspiratory activity [8] and the influence of other inputs is weak [3]. Fitting et al. [9] measured end-expiratory length and tidal shortening of the diaphragm in the awake dog with body position changes. Their results suggested that the main compensatory mechanism for changes in operational length of diaphragm is a phasic expiratory contraction of the abdominal muscles rather than an increase in diaphragmatic electromyogram (EMG) activity. However, there has been no report describing how the diaphragm and trunk muscles on the left and right sides are recruited during various symmetric or asymmetric voluntary movements. Such information is essential to know how the centers for the voluntary movements, controlling posture and respiration, coordinately control the diaphragm and trunk muscles using various afferent feedbacks.

In the present study, we analyzed EMGs of the diaphragm and trunk muscles during standing-up, rotation, and reaching movements, which were selected from free movements and were voluntary and typical movements in which animal used trunk muscles.

Methods

Surgical procedures

Experiments were performed on four cats (2.2–3.7 kg). The anesthesia was induced and maintained by pentobarbital sodium (initial dose 30–35 mg/kg i.p., supplements of 3.0–5.0 mg/kg/h i.v.). The trachea was intubated and animals spontaneously breathed. All surgical procedures were performed under aseptic conditions. Atropine sulfate was administered before surgery. The electrocardiogram (ECG) and rectal temperature were monitored during surgical operation. Body temperature was maintained at a range of 37–38°C with a heating pad. Bipolar EMG electrodes consisted of stainless steel wires (AS632; Cooner Wire, USA) were implanted in the diaphragm costal region of both sides and trunk muscles (the latissimus dorsi, LD; the external oblique, EO; and the rectus abdominis, RA). The electrodes for trunk muscles were placed bilaterally near the diaphragm. Two pairs of electrodes were placed at different locations in EO muscles such as the thoracic region rostral to the 12th rib, and the abdominal region (Fig. 1). The diaphragm was approached through the abdominal cavity. To explore target muscles, an abdominal muscle incision measuring smaller than 25 mm was made along the muscle fiber. Electrode wires were passed into the target muscle. The parts of wires remained in the muscles were uncoated for 1–2 mm. Each wire was then knotted outside the muscles and fixed to the muscle surface with the adhesive. After implanting electrodes, the peritoneum and overlaid muscles were carefully closed. All the wires were passed under the skin to the connector that was attached to the skull with titanium screws and dental cement. The incision was washed by warm Ringer's solution with antibiotic and then closed. The animals were treated with an antibiotic for 3 days. They were observed very carefully and their behavior in cages quickly reached preoperative levels. After recovery from surgery, animals did not show any signs of discomfort, pain, or neurological symptoms, and were not nervous about their operated regions. All experimental procedures were approved by the Ibaraki Prefectural University of Health Sciences Animal Experiment Committee, and were in accordance with the guiding principles for care and use of animals in the field of physiological sciences of the Physiological Society of Japan.

Recording and data analysis

Electromyograms were recorded both under anesthesia and awake conditions. EMGs were amplified (AB610J; Nihon Kohden, Japan) and filtered with the range of 150 Hz to 3 kHz. The data were recorded on digital recorder of 8 channels (PC-208AX; Sony, Japan). Under anesthetized condition, EMGs were recorded from animals lying in a lateral recumbent position with left side up. To identify inspiration and expiration phases, respiratory airflow was monitored by the sensors which were set on the intubation tube and spirometer (MacLab /8s and MacLab ML141 Spirometer; AD Instruments, Australia) while cats breathed room air spontaneously under anesthesia. EMG from each muscle was recorded under the normal spontaneous breathing for a few minutes. The interval and the amplitude of EMGs of the diaphragm were stable if the condition of anesthesia was constant (4.7 ± 0.6 s, range 4.5–6.2 s, 3 records), although the interval seemed to be affected by the depth of the anesthesia. Also, we examined the EMG activities in response to CO_2 inhalation, sneeze, and cough

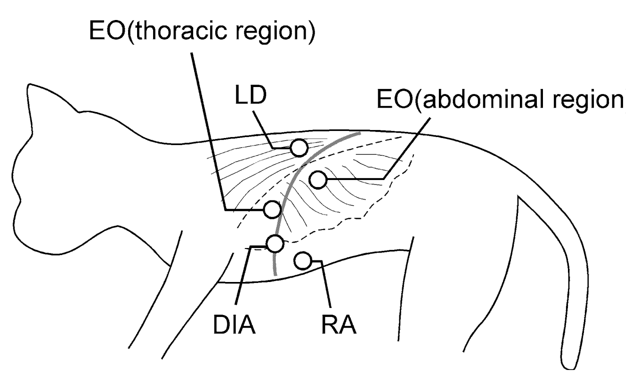

Fig. 1 Positions of EMG electrodes. EMG electrodes are indicated by *circles*. *Dotted lines* indicate the border of the latissimus dorsi and external oblique. *Thick line* indicates the position of the diaphragm. *DIA* Diaphragm, *LD* latissimus dorsi, *EO* external oblique, *RA* rectus abdominis. These abbreviations are common to all the figures

under anesthesia to verify whether the electrodes were properly placed in the diaphragm and trunk muscles. We first recorded the activities of the diaphragm in response to CO_2. CO_2 was added to the room air until the end tidal CO_2 reached 10%. After the administration of CO_2, the interval of each cycle became shorter (1.6 ± 0.2 s, range 1.4–1.8 s, 3 records). Then, the inspiratory gas was changed to the room air so that respiration returned to normal and the anesthesia became light enough to induce a sneeze or cough reflex. To examine whether the target muscles worked physiologically, EMGs were recorded during sneezing by inserting a thin thread into the nasal cavity, and during coughing by inserting a small suctioning tube from the tracheal tube.

We took great care about electrical cross-talk between electrodes in muscles, especially in cross-talk to the diaphragm from trunk muscles during free movement recording sessions in alert condition. After the bipolar electrodes were implanted into the diaphragm, LD, EO, and RA, trunk muscles (LD, EO, and RA) were stimulated directly through the implanted electrodes to make sure the electrical cross-talk from these muscles to the diaphragm, using rectangular pulses with duration of 150 μs. The stimulation intensity was threshold (×1Th), twice (×2Th), and 5 times (×5Th) of contraction. There was no response elicited by the any of these intensities of stimulation. This result indicated that no EMG activities of trunk muscles influenced the activities of the diaphragm. In this study, we could not find differences of EMGs between the thoracic and the abdominal EO under anesthesia or during free movement, although it has been reported that EO shows the different activities due to the morphological features in the thoracic and abdominal portions [10, 11]. Therefore, we did not distinguish between the thoracic and the abdominal EO, although we implanted EMG electrodes in both portions.

More than 2 days after operation, EMGs were recorded during free movement in a cage (width 60 cm, length 55 cm, height 90 cm). Connecting wires from the head connector of the cat were long enough to move freely and were connected to the amplifier through the ceiling of the cage. To induce a variety of movements, the cats were sometimes intervened by the moving toy rod at the outside of the cage. Three typical movement patterns [standing-up, rotation (U-turn) and reaching movements] were selected from recordings. To induce animals to make the reaching movement, we set the blocks of the food in the stock case (width 8 cm, length 15 cm, height 8 cm) on the cage wall. To bring the block of food out of the case, the cats needed to insert left forelimb into the case, catch the food, and withdraw the forelimb to eat. The video image and EMG data were recorded simultaneously for 30 s for each recording session through the recording system developed using LabVIEW (National Instruments, USA). The sampling frequency of EMG data was 30 kHz, and that of the video image was 30 Hz. Raw EMG signals for 30 s were full-wave rectified, and the resulting signal was integrated by using LabVIEW software. The integration was done as follows. One epoch (0.1 s) for the integration had 3,000 data points. The next epoch was obtained from the second data point of the previous epoch to the next 3,000 data points. Each epoch overlapped with the next epoch by 2,999 points. A series of integrated data was derived from the successive integration for the whole length (30 s) of EMG data.

A respiratory cycle period is the period between the onset time to the next onset time of the diaphragmatic activities. In the present study, the respiratory cycle period was computed as the average of 3 cycle periods. In order to determine respiratory cycles, we analyzed the recordings containing adequate periods during the resting state before standing-up movements. The activity onset time of other muscles were measured when integrated EMG became larger than the baselines. The baselines were determined by the values during inactive periods of each muscle. Data are expressed as mean ± SD. Differences were considered significant at $P < 0.05$ with a Student's t test.

Results

Sixty-three records with the typical movements were analyzed. Of the 63 records, 36 were obtained in the standing-up with extending and raising the trunk in 4 cats, 18 in the rotation in 3 cats, and 9 in the reaching movements in 2 cats.

Standing-up movement

The standing-up movement of animals consisted of the following series of movements. The onset of movement was the time which the animal raised a forelimb from the floor. Then, the animal lifted up their upper body and kept the upright posture. Finally, the animal returned to quadrupedal posture. In 12 of 36 records in standing-up movements, resting state with enough length of time was observed before standing-up movements, but not in the other 24 records. In 30 of 36 records, entire standing-up movements were recorded but not in the other 6 records because the animals kept their standing-up posture and recording time of 30 s had run out before the cats downed their forelimb. Figure 2 shows a representative standing-up movement. During rest or walking state before the standing-up movements, rhythmic activities that alternately repeated active and inactive phases were observed in the diaphragm (12 records). Since these rhythmic activities were similar to that during spontaneous respiration under anesthetized condition, we considered these activities were respiratory activities. The respiratory cycle period was 1.2 ± 0.3 s (range 0.53–2.0 s, 12 records). Just before the onset of standing-up movements, the respiratory cycle period tended to be shorter. Prior to the onset of movement, 5 or more sequential respiratory cycle periods in resting condition were able to be measured in 6 of 12 records. Although there was no significant difference, the average length of the last 3 cycle periods was shorter than that of the first 3 cycle periods in 4 of these 6 records. We did not analyze the other 6 records, because the number of respiratory cycles was not enough. During standing-up movements, the amplitude of diaphragmatic EMG of both sides became larger and the activities continued longer compared with those of the rhythmic activity in resting condition (Fig. 2). The periods of these activities varied depending on movements during standing-up and after standing-up. For example, in the case of Fig. 2, the large diaphragmatic activity appeared and was followed by a small diaphragmatic activity before the EMG returned to baseline (Fig. 2b). These prolonged activities in the diaphragm during standing-up movement occurred coincident with the EO or LD, and overlapped with the RA active period in certain cases. In the case of Fig. 2, the left diaphragmatic activities were occurred with EO and LD, and the right side was with RA.

We considered these prolonged activities seen in the present study as the non-respiratory activities. Non-respiratory activities often had a larger peak point than that of the respiratory cycle period, and occurred coincident with the EO which is a major expiratory muscle, or with the LD, a back muscle, and in certain cases overlapped with the active period of RA which is an abdominal muscle.

The non-respiratory activity in the diaphragm started shortly after (0.33 ± 0.37 s, $n = 32$) the onset of the standing-up movement in most cases. The periods between the onsets of the non-respiratory diaphragmatic EMG and those of LD or EO of both sides were measured in 15 or 16 records of EMGs, respectively (Fig. 2b). The onset of activities in the diaphragm tended to be later than that in LD or EO. The periods between the onset time of the diaphragm and LD (LD-diaphragm) was 0.31 ± 0.39 s ($n = 30$, both sides in 15 records) and diaphragm and EO (EO-diaphragm) was 0.23 ± 0.36 s ($n = 32$, both sides of 16 records). We examined differences in diaphragmatic activities between the cases when animals stood up raising the right forelimb and when raising the left forelimb. Since there was no difference in the activity between the cases ($P > 0.05$ for all cases), we analyzed records without distinguishing whether the right or left forelimb was raised first. Also, there were no significant differences between left and right sides of LD-diaphragm nor EO-diaphragm ($P > 0.05$ for all cases). The period between the onset times of diaphragm and RA were not measured because it was difficult to find the onset time due to no activity or the continuous activity.

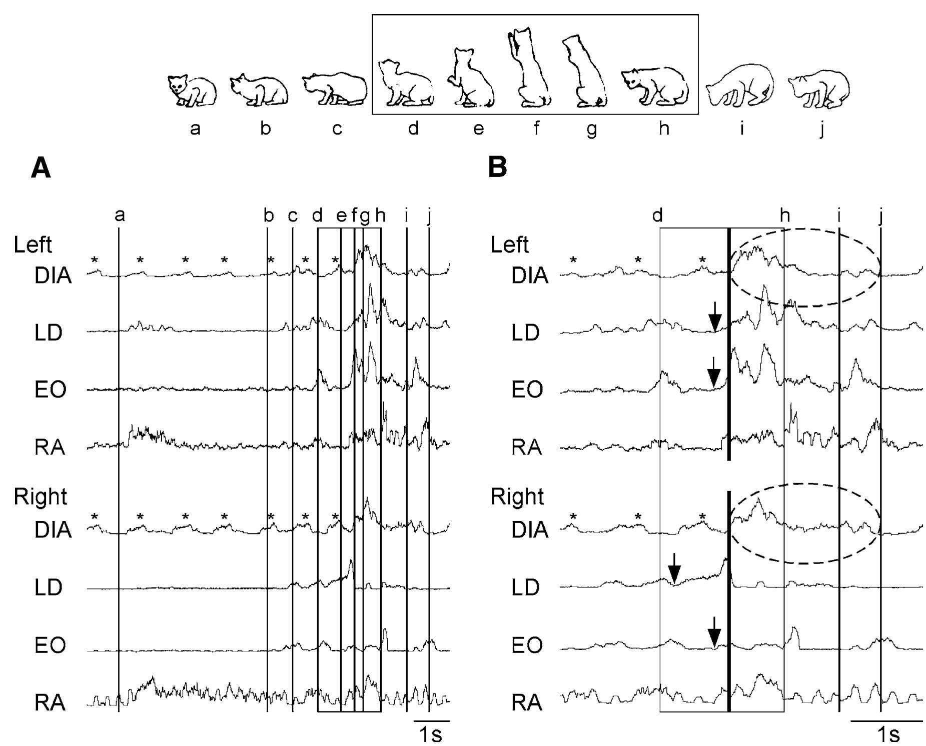

Fig. 2 EMGs during standing-up movements. *Frames* indicate the period of standing-up movement from lifting their forelimbs up to putting down. **a** EMGs from resting (*a–c*) to standing-up movement (*d–h*). '*d*' The onset of the standing-up movement and '*h*' the end of the standing-up movement. The *vertical line* and the *alphabet* correspond with the body positions illustrated on the *top* of the figure. *Asterisks* show rhythmic respiratory activities in the diaphragm. **b** Time scale expanded recording of (**a**). *Asterisks* show rhythmic respiratory activities in the diaphragm, and *dotted circles* indicate the non-respiratory activities. The *vertical thick lines* indicate the onset of non-respiratory activity of the diaphragm. The *arrows* indicate onsets of LD and EO activities

Rotation movement

In the present study, rotation movements ($n = 18$) were selected from free movement recordings. Rotation movements were movements with turning-around of the animal's body. In many cases, animals walked round without turning around their body, and such movements were excluded from further analysis. Figure 3 shows an example of EMGs during clockwise rotating movement. The left and right diaphragmatic activities were seen alternately beginning from the left side. The symmetrical activity of the diaphragm was not detectable and asynchronous activities occurred during rotation movement in all cases ($n = 18$). However, the pattern of diaphragmatic activity varied depending on each rotating movement, and we were not able to find the particular similarity or difference in EMGs between clockwise and counterclockwise rotating movement. We could not find any unification pattern in other trunk muscle activities either.

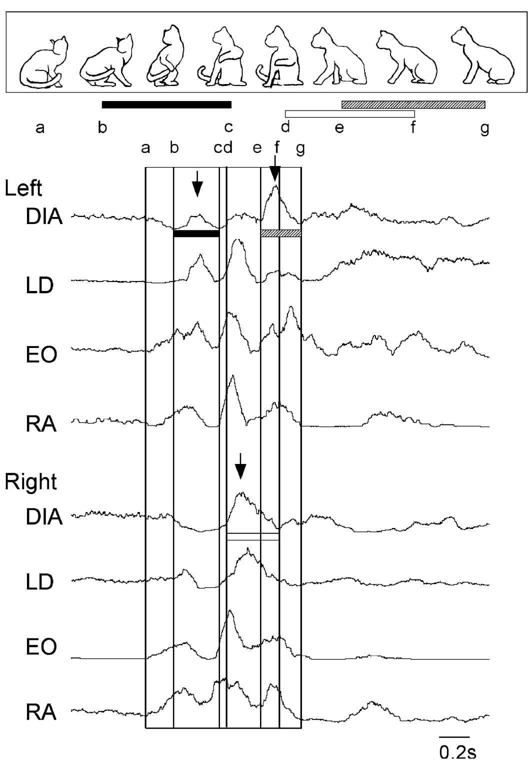

Fig. 3 EMGs during rotating movement. *Frames* indicate the rotating movements (the clockwise rotating movement). The *vertical lines* and the *alphabet* show the body positions in accordance with illustration on the *top* of the figure. The non-respiratory activities when the contralateral diaphragm was not active are indicated by the *arrows* and the *underlines*. *Black thick underlines* the first asymmetrical activity of left diaphragm, *white thick underlines* the first asymmetrical activity of right diaphragm. *Hatched thick underlines* the second asymmetrical activity of left diaphragm

Reaching movement

Reaching movement is composed of the forelimb lifting up, extending, withdrawing and putting down. Reaching movement was analyzed in 9 records. During reaching movement, animals did not change their trunk position vigorously compared with standing-up movement. Figure 4 shows an example of the result during reaching movement. All reaching movements were performed by the left forelimb. During reaching movement, the non-respiratory activity of the bilateral diaphragm appeared.

The diaphragmatic EMG showed rhythmic respiratory activities before reaching movements in 5 of 9 records (both sides of diaphragm in 3 records, one side in 2 records). The cats kept quiet before the reaching movements, and the diaphragmatic activities were returned to the baseline during inactive phase. Although the diaphragm clearly showed the rhythmic activity before reaching movements, this rhythmic activity became unclear or hard to be recognized after the initiation of reaching movements. In the remaining 4 of 9 records, the diaphragmatic EMG did not show the clear rhythmic activity but showed a weak and little modulated activity before reaching movements. However, the diaphragmatic EMG showed the non-respiratory activities during reaching movements.

We could also examine the time difference between the onset time of diaphragmatic EMG activities and the initiation of reaching movement. The non-respiratory diaphragmatic activities started shortly after the initiation of reaching movement (left 0.11 ± 0.28 s, right 0.19 ± 0.25 s, $n = 4$). For this analysis, we used only 4 of 9 records, because they did not contain the apparent respiratory rhythmic activity, nor the activity which was elicited by other trunk movements at the initiation time of the reaching movement. If we included the remaining 5 records, the results of this analysis would be confusing because, in those records, the apparent respiratory rhythmic activity overlapped the initiation of the movement in 3 of 5 records, and there were the activities which were elicited by other trunk movements in 2 of 5 records. Although those movements did not include vigorous changes in their trunk position, we excluded those records for comparison.

In Fig. 4, LD showed clear asymmetric activity during the reaching movement. For example, the left LD was active when the left forelimb was lifted up (a–b) and the right LD was active when the forelimb was extended to the feedbox (b–d). On the other hand, the diaphragm showed synchronous activity on both sides. When the diaphragm was active, RA activities were almost silent, but most of EO activities, especially left EO, showed small amplitudes compared with other detectable activities.

The latencies from the onset of the diaphragm to the onset of LD and EO were measured in 9 records. The

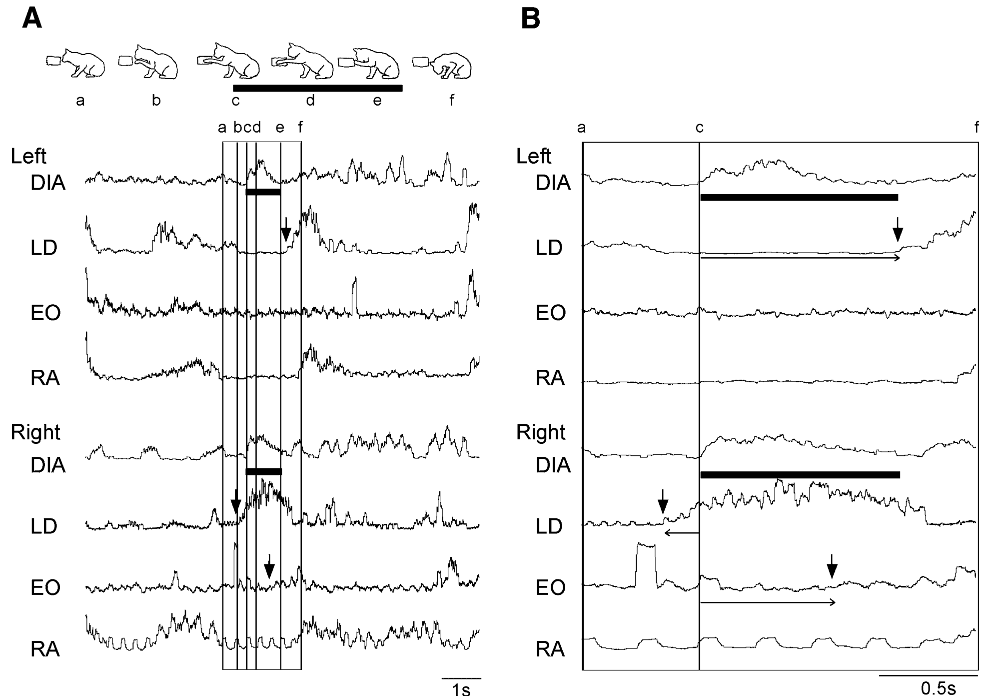

Fig. 4 EMGs during reaching movements. *Frames* indicate the reaching movements. **a** EMG recordings during reaching movement. **b** Time scale expanded graph of (**a**) during reaching movement. ECG signal mixed in the record of right RA. The *vertical line* '*c*' indicates the onset of non-respiratory activity of the diaphragm. The *arrows* indicate onsets of LD and EO activities. The differences in the times of onset between DIA and LD or EO are indicated by *horizontal arrows*. In this case, onset of the right LD was prior to that of the diaphragm and the onset of left EO was not able to be measured

period between the onset times of diaphragm and RA was not measured because it was difficult to find the onset time of RA activity. Most EMG activities in the diaphragm occurred prior to the onset of EMGs on LD and EO, though in the case of the Fig. 4, the left side LD activated prior to the left diaphragm. The periods between onset time of the diaphragm and LD or EO were as follows: left diaphragm-LD, 0.53 ± 0.73 s ($n = 8$); right diaphragm-LD, 0.020 ± 0.27 s ($n = 8$); left diaphragm-EO, 0.49 ± 0.60 s ($n = 7$) and right diaphragm-EO, −0.011 ± 0.66 s ($n = 8$). Though the activities of LD tended to be asymmetrical, there was no significant difference in latencies between left and right sides of diaphragm-LD ($P \geq 0.05$, Wilcoxon signed-rank test; 8 paired data). There was significant difference in diaphragm-EO ($P \leq 0.05$, Wilcoxon signed-rank test; 7 paired data).

Discussion

Activities during free movement

In order to check the EMG cross-talk from trunk muscles to the diaphragm, we stimulated the trunk muscles. However, evoked trunk muscle activities did not show any effects on EMG of the diaphragm, suggesting no cross-talk during free movement.

In the present study, the activity of the diaphragm during resting and walking showed active (inspiratory) and inactive phases (expiratory) alternately in non-restrained awake cats. The period of each cycle was 1.2 ± 0.3 s. In awake condition, the period of each cycle in the diaphragm was significantly shorter and more variable than that in anesthetized condition (4.7 ± 0.6 s).

Since the active and the inactive phases could clearly be separated and diaphragmatic activity was silent in the inactive phase, we considered this activity pattern as the respiratory activity. On the other hand, the diaphragmatic activities showing larger amplitude and longer duration were observed during voluntary movements. This prolonged pattern of diaphragmatic activity was considered as the non-respiratory activity. We were able to distinguish the inspiration phase from the expiration phase, although the rhythmic activity of the diaphragm was sometimes difficult to detect during free movement. The indistinguishable activities might be due to the combination of respiratory and non-respiratory activities because the activity of the diaphragm is known to be influenced by the non-respiratory inputs [2–5, 12]. Also, it has been reported that under anesthetized condition and when the posture is changed, the cycle length and intensity of the activity of the diaphragm change due to the non-respiratory input [2, 12].

The length and configuration of the diaphragm always change in accordance with changes in posture, and such changes would be expected to affect the mechanical efficiency of the diaphragm. The effect of postural changes on respiration was investigated in anesthetized cats by applying body tilt [2]. The results suggested that respiratory modulation minimizes the changes in lung volume which was externally induced during postural changes [2].

Further, the diaphragm responses to the stretch were compared before and after rhizotomy [13]. The results suggested that the afferents sensitive to changes in the operating length in the diaphragm contribute to compensatory alterations in phrenic motor drive.

It was suggested that systematic, reproducible, and posture-dependent changes in regional EMG activity of the diaphragm may be due to the changes in electrical environment surrounding the intramuscular electrodes by examining evoked regional diaphragmatic activity in dogs [14]. The asymmetrical non-respiratory activity in the left and right diaphragm was considered to be due to the changes in electrical environment [14]. However, it could not be the case in the present experiment, because the diaphragm in cats is smaller than that in dogs and small displacements by contraction may cause the relatively stable electrical recording environment. Moreover, recording wires were knotted from the surface of the diaphragm in the abdominal cavity and fixed to the muscle surface with adhesive, and we confirmed no effects on the diaphragm by passive movements after the implantation of the recording wires.

In the present study, most of the diaphragmatic activities started shortly after the initiation of standing-up movement, and those activities were more active than normal respiratory activity. Non-respiratory EMG activity in the diaphragm occurred after the onset of trunk muscles activities during standing-up movement. Left and right diaphragmatic activities showed different patterns during rotation movements and sometimes more active than that during the resting state. From these points, it was reasonable to consider that non-respiratory activities were not controlled voluntarily but affected by changes of length and tension which were induced by changes in mechanical conditions of the body due to the voluntary movements. The asymmetrical activity may be caused by different lengths of each side of the diaphragm and trunk muscle, but we were not able to find the particular difference between clockwise and counterclockwise rotating movements. In the present study, we selected the record of rotation movements from the records of free movements. Therefore, the movements of rotation varied. The variability of EMG activities may be due to the variation of each rotating movement.

On the other hand, EMG activity of the diaphragm occurred prior to or with the onset of trunk muscles during reaching movement. With rapid flexion of the shoulder to a visual stimulus in human, it was reported that the EMG activity in the diaphragm occurred about 20 ms prior to the onset of deltoid EMG and almost simultaneously with transverses abdominis [6]. Hodges and Gandevia [15] suggested that this preparatory action may aid truncal stability and cause a sustained increase in intra-abdominal pressure. There was no significant difference between left and right side of diaphragm-LD. However, LD tended to show asymmetric activity, although the diaphragm showed synchronous activity on both sides. And EO activities were small and RA activities were almost silent when the diaphragm was active. These motor patterns during reaching movement seem to be very different from that during the standing-up movement.

Our result suggest that the reaching movements and the standing-up movements may have some different control mechanisms from central nervous system. The standing-up movements are dynamic postural adjustments and need trunk muscle activities, thus the movement may be mainly controlled by the brain stem and spinal cord. In this situation, the diaphragm may work to adjust the respiratory condition after the postural change by the trunk muscle activities. As a result, non-respiratory diaphragmatic activities occurred after the onset of trunk muscle activities. On the other hand, during reaching movements, animals need to keep the posture without large postural changes, and to do goal-directed arm movements. It seems that this movement is mainly organized by the motor cortex and the diaphragm activity is preset in order to adjust the respiratory condition. Accordingly, the diaphragm may be activated prior to trunk muscles activities to control the stability of respiratory condition that was affected by the trunk muscle activities. Thus, non-respiratory diaphragmatic activities occurred prior to or with the onset of trunk muscle activities.

Postural functions of the diaphragm

It is known that the intercostal muscles take an active part in the postural function [9, 16]. The tonic activity without respiratory rhythm is found to the greatest extent in the intercostal muscles that have the high concentration of muscle spindles, and this tonic activity shows the important role of the gamma loop that plays in the activation of these muscles [17]. In the present study, the diaphragm showed ventilatory activity, and also phasic activity during trunk movement. It suggested that the diaphragm may receive an input from the central nervous system in order to adjust lung volume changes during postural changes. Although it was suggested that group I afferents are mediating the reflex that was associated with an increase in diaphragm operating length [13], the role in the voluntary muscle activation was still unclear. The influence on modulating respiratory muscle activation was not so large, because the diaphragm has few muscle spindles [18].

A wide range of contractile properties has been reported for the diaphragm muscle units which were classified as slow-twitch fatigue-resistant (S), fast-twitch fatigue-resistant (FR), fast-twitch fatigue-intermediate (FI), or fast-twitch fatigable (FF) types [19]. In normal ventilatory requirements, adequate force could be generated by the recruitment of type S and FR units [20], whereas type FI and FF units were recruited during non-ventilatory activity [20]. Taken together, diaphragmatic activities during trunk movement in the present study may recruit type FI and FF units. The descending postural and respiratory pathways may act separately on different motor units of the diaphragm. Our diaphragm recordings were limited to the costal portions, although previous studies have shown that larger increases in activity occur in the crural than in the costal diaphragm during nose-up tilts from a supine position [1]. In the crural region, the pronounced effects in the diaphragm activity could have been observed, but at least the diaphragm contributes actively to the postural control of the trunk in addition to its role in respiration.

In the present study, there was clear modulation of the diaphragmatic activity during voluntary trunk movements. These results suggest that the diaphragm plays a role of adjusting mechanism for changes in body position. It has been documented that contraction of the diaphragm, EO and RA increases intra-abdominal pressure and contributes trunk stability [15]. Contraction of LD also seems to stabilize the spine [21]. In the present study, we observed that the diaphragm on the left and right sides was synchronously recruited during the standing-up and reaching movements. Therefore, this synchronous recruitment of the diaphragm on both sides could be assumed to stabilize the trunk. During the standing-up movement, not only the diaphragm but also all the trunk muscles examined were recruited coincidently. These activities would play the role in the stabilization of trunk and spine as was suggested. On the other hand, during reaching movement by the left forelimb, when the diaphragm was recruited, the amplitude of left EO activity was small and RA activity was essentially mostly silent. An interpretation could be that the rigid stabilization of the trunk is unnecessary and that recruitment of the diaphragm is enough to control stability. Further studies are needed to clarify the neuronal mechanism of adjustment and co-ordination of the diaphragmatic activities and the voluntary trunk movements.

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