The Pattern of Respiratory Nerve Activity in the Bullfrog

Yoshikazu Sakakibara

Department of Physiology, Chiba University School of Medicine, Chiba, Chiba, 280 Japan

Abstract The electrical activity of the cranial nerves innervating the muscles which contract and dilate the buccal cavity (defined BCcont and BCdil, respectively) was explored in the bullfrog, Rana catesbeiana. The sternohyoid branch of the hypoglossal nerve innervating BCdil showed electrical activity in two consecutive phases: buccal inhalation and lung expiration as well as in the last phase of the pulmonary ventilatory cycle. The last phasic activity was apparently identical to the first one of the succeeding cycle when the cycles were repeated consecutively. The nerves innervating BCcont, consisting of the Vth, VIIth, IXth, Xth, and XIIth cranial nerves, generally showed two consecutive phasic activities in the period of lung expiration and lung inspiration. Thus the present result indicated that during three consecutive phases of the pulmonary ventilatory cycle, the nerve for BCdil was active in the first two phases, and the nerves for BCcont in the last two phases. In both nerve activities the magnitude of the integrated peak activity was smaller in the preceding than in the later phase. In the buccal oscillation cycle, the nerve for BCdil was active during pressure depression while the nerves for BCcont were active during pressure elevation in the buccal cavity. The nerves for both mouth closing and that for tongue retraction had phasic activity during respiratory cycles.

Key Words: bullfrog respiration, cranial nerve, phasic electrical activity, buccal cavity contractor, buccal cavity dilator.

Due to the lack of a rigid thoracic cage, ventilatory movement in the frog is achieved by the buccal, pharyngeal, and laryngeal muscle groups. These respiratory musculatures are divided into three groups according to their functions (Oka, 1957); the first is related to the dilating or closing of the glottis, the second is a dilator of the buccal cavity (BCdil) governed by the M. sternohyoideus (Oka, 1957; de Jongh and Gans, 1969; Brett and Shelton, 1979), and the third group is a contractor of the buccal cavity (BCcont), composed of the M. mylohyoideus, M. submentalis, M. subhyoideus, Mm. petrohyoidei posterior and anterior, and M.
geniohyoideus (Shinkai and Narita, 1956; Oka, 1957; De Jongh and Gans, 1969; West and Jones, 1975). It is well established that the members of the BCcont contract synchronously as a pump to generate buccal force for lung inspiration (De Jongh and Gans, 1969; West and Jones, 1975).

The pattern of the electromyogram activities (EMGs) of both BCdil and BCcont in the lung expiration phase is complicated. Firstly, the observations by the above-mentioned authors on BCdil EMG in the expiratory phase are not in good agreement. Secondly, the EMGs of BCcont have been reported to be silent in this phase by many investigators. But the M. submaxillaris (M. mylohyoideus according to Minkoff, 1975) is reported to be active therein (Ito and Watanabe, 1962). Therefore, the initial purpose of this study is to explore the electrical activities of BCcont and BCdil in the expiratory phase.

In the frog, during the interval between two pulmonary ventilatory cycles (pulmonary cycles), the cycles of buccal pressure oscillation (buccal cycles) usually intervene. During this cycle, the glottis is kept closed and the nostrils are open, and buccal pressure oscillates to a small extent around the ambient pressure level. There have been, however, contradictory observations made as to the phasic EMG activities of BCcont and BCdil during the buccal cycle. Therefore the second aim of this study is to re-examine thoroughly all the BCcont and BCdil activities in the phase of buccal pressure elevation, as well as that of depression, during the buccal cycle.

For these purposes, electroneurograms (ENGs) of the nerves responsible for BCcont and BCdil were investigated, rather than EMGs themselves. This is because it is generally believed that whole electrical activities are obtainable more easily from nerves than from muscles, and because in the frog, the ENGs of the cranial nerves which innervate the respiratory muscles have never been recorded systematically in combination with respiratory movement. The ENGs of the nerve trunk of the trigeminal (V), facial (VII), glossopharyngeal (IX), vagal (X), and hypoglossal (XII) nerves were first investigated in order to determine each efferent activity in phase with respiration. Individual nerve branch or muscle activities were then recorded. Each of these nerve activities was recorded together with buccal and pulmonary pressure changes.

MATERIALS AND METHODS

The experiments were performed on 52 male and female bullfrogs, Rana catesbeiana, weighing 160–430 g at 20–30°C. The spinal cord at the third and fourth vertebrae as well as the bilateral brachial nerves were dissected and a taper metal-rod was inserted through the orbits to fix the head under anaesthesia with ether and xylocaine. These procedures were necessary to reduce artifacts in the recording of nerve activity. The tests were performed in the prone position after the effect of anaesthesia had sufficiently worn off. In the later period of the study,
an electrode holder was fixed to the experimental animal to approximate closely to the recording site, no metal-rod insertion then being necessary to eliminate artifacts. The results obtained in both experiments with and without metal-rod insertion were apparently the same.

A lung cannula was inserted from the dorsal side around the Vth vertebra and connected to a differential pressure transducer (DLPU 0.05, Nihon Kohden) to record lung pressure and also to a three-way stopcock, so as either to apply a gas mixture of 49.7% CO₂ in N₂ into the lungs, or to close the tubing. Buccal pressure was recorded with a buccal cannula inserted through the eustachian tube and connected to a similar transducer.

The cranial nerves were unilaterally exposed in the following way: for the branches and main trunk of the IXth and Xth nerves, as well as for the XIIth trunk, the scapula and its circumferential muscles were excised; for the XIIth branches, the M. mylohyoideus was excised; for the submandibular branch of the Vth nerve, the M. temporaris and M. pterygoideus were dissected or pulled aside; for the smaller branch which derived from the submandibular branch, the skin was cut along the edge of the lower jaw and a small part of the caudal end of the upper jaw was trimmed away; and for the hyomandibular branch of the VIIth nerve, the mid-ear bone was trimmed away. Its hyoid and subhyoid branches were exposed caudally to the skull. Sites of recording along these nerves are shown schematically in Fig. 1.

The terminal of the individual nerve branch was identified by the description of GAUPP (1899) and confirmed by direct observation under binoculars, as well as by electrical stimulation of the efferent pathway (0.5 msec duration; 50 Hz; 6 V).

Recording nerve and muscle activities and ventilatory pressure. From one frog, one cranial nerve activity, or two at most, was recorded. For each cranial nerve, eight to fifteen frogs were used. ENGs recorded during air breathing were
analyzed. But we also examined the possible appearance of new phasic activity when ventilatory drives were augmented. In response to strong hypoxic (Bouutilier and Toews, 1977) and hypercapnic stimulation (MacIntyre and Toews, 1976) the peak buccal pressure of the pulmonary cycle begins to rise steeply breath after breath, and then declines in a reverse fashion. Such serial pulmonary cycles are called inflation and deflation sequences. In order to induce these sequences, the above-mentioned gas mixture was continuously passed into the lung for less than 30 sec with a moderate rate of flow. Otherwise, animals were allowed to breath pure N₂ through the nares for several minutes. The nostrils were also sealed with a paper strip immersed in water, in some cases in order to enhance respiratory activity.

Nerve activity was picked up via a bipolar silver electrode from the central strand of the cranial nerve. After filtering the noise signals (100-2,000 Hz), nerve activities were integrated by a rectifier and RC circuits (time constant: 120, 100, 70 msec). Electromyograms (EMGs) were picked up via a bipolar silver electrode. The integrated ENG, buccal and pulmonary pressure changes were simultaneously recorded by an ink-writing recorder (Sanei Instrument, 8S12-1-1111), or an oscillograph (Sanei Instrument, visigraph 5L16, or Nihon Kohden, PC-1B). Nerve activity always preceded pressure deflection in the buccal cavity or in the lung. The mean time delay (mean±S.D.) between peak integrated activity of the Vth, VIIth, IXth (R. pharyngeus anterior inferior), Xth (R. laryngeus longus), Xth (R. pharyngeus posterior superior), and XIIth nerves and peak buccal pressure were 159.0±34.0 (n=51, 8 frogs), 169.3±33.0 (n=51, 6 frogs), 143.5±16.9 (n=37, 3 frogs), 159.4±17.9 (n=34, 3 frogs), 140.0±23.8 (n=41, 5 frogs), and 158.0±24.1 msec (n=37, 5 frogs), respectively. Such a time delay is demonstrated in the figures but not in the summarized figure (Fig. 9).

RESULTS

Phase division of respiratory cycles

According to buccal and pulmonary pressure changes as well as the opened or closed state of the glottis and the nostrils (De Jongh and Gans, 1969), one pulmonary cycle was divided into six phases, defined as P-I, P-II, P-III, P-IV, P-V, and P-VI, respectively (Fig. 2). In P-I, pulmonary pressure increased to the peak level nearly as the end of this phase. On the other hand, buccal pressure first deflected negatively to a small extent and was restored to the ambient level in the latter half of the phase. The beginning of this pulmonary pressure elevation coincided well with the point where the buccal pressure curve crossed the ambient pressure level in the process of decrease. This usual pattern of buccal pressure changes was modified by the state of the nostrils. When the latter were closed, the negative deflection was intensified. This phase can be termed the buccal inhalation phase. In P-II, the glottis opened and lung expiration occurred. Pulmonary pressure decreas-
nerve activity of frog respiration

ed and buccal pressure increased, becoming equilibrated with each other at the end of this phase. In P-III, lung expiration continued. Pressures nearly equilibrated decreased, remained constant, or increased depending on the intensity of ventilatory activity. In P-IV, the nostrils are closed. When the pulmonary and buccal pressures were almost equilibrated or when the latter slightly exceeded the former, both pressures increased. P-IV was termed the lung inspiration phase. At the end of this phase the glottis is shut. P-V is characterized by a rapid decrease in buccal pressure and by sustained lung pressure with a slight drop. In P-VI, buccal pressure dropped fairly well below the atmospheric level and was restored to the atmospheric level at the end of this phase. Pulmonary pressure fluctuated upward slightly. Phase division of P-II, P-III, and P-IV was made in the same way as in De Jongh and Gans (1969). Based on the ENG activity of the XIIth sternohyoid branch, P-I and P-VI are newly proposed in the present study. If the pulmonary cycles were generated consecutively, P-VI of the preceding cycle corresponded to P-I of the next. During the buccal cycle, pulmonary and buccal pressure oscillations were observed. When pulmonary pressure reached a maximum, buccal pressure rose to about ambient pressure, which roughly coincided to the midpont in its cycle of increasing pressure. On the other hand, the lowest pulmonary pressure was attained when buccal pressure fell approximately to the ambient pressure in its cycle of decreasing pressure.

Trigeminal nerve activity

Figure 3 shows the activity of the submandibular branch of the Vth nerve (recorded from point a in Fig. 1) and pulmonary and buccal pressure changes during air breathing (A) and N₂ breathing (B). Four phasic nerve activities can be distinguished in the pulmonary cycle under both conditions. The first one, a low integrated peak activity, appeared in P-I (Fig. 3c). The second one continued from P-II to III(d). The third one was the greatest and is seen in P-IV(e). In P-V, the fourth activity was detected (f). Two phasic activities were obtained in the
A small nerve activity (a) corresponding to the phase of buccal pressure depression did not appear as consistently as that (b) seen in buccal pressure elevation.

Two different kinds of motor nerve branches responsible for mouth contracting (BCcont) and for mouth closing were considered to be responsible for the above-described Vth nerve activities. Therefore, the attempt was made to take ENGs from many Vth nerve branches innervating the muscles for mouth closing in six frogs. Most of them showed activity in phase with respiration. In Fig. 4 is an example showing electrical activity of the nerve innervating the M. masseter minor (ENGv-M) (from the point b in Fig. 1) and that for BCcont (ENGv-C). The ENGv-C was recorded just proximally to the site of the nerve branching off to the two respiratory muscles, the M. submentalis and M. mylohyoideus (at the point c in Fig. 1). ENGv-C had activities corresponding to buccal pressure elevation (b) in the buccal cycle, P-II and III and P-IV(d), which represent a certain part of the Vth trunk activities (b, d, and e in Fig. 3). On the other hand, ENGv-M showed the activities corresponding to buccal pressure depression (a) in the buccal cycle, P-I(c), P-V(e), which represent the other part of the Vth trunk activities (a, c, and f in Fig. 3). These ENGv-M activities were always obtained in the three frogs examined. The oscillatory activity was consistently detected in this preparation. Electrical stimulation of the peripheral nerve strand innervating the masseter muscles closed the mouth, but had no influence on the buccal pressure when nostrils had been sealed to prevent leakage.

Fig. 3. Fifth nerve activities and respiratory pressure changes. A, during air breathing; B, the last cycles of inflation sequence induced by N₂ breathing. a and b, phase of buccal pressure decreasing and increasing, respectively; c, P-I activity; d, beginning of P-II; e, peak activity in P-IV; f, P-V activity.
Figure 5 illustrates the relation between pulmonary and buccal pressure changes and integrated VIIth nerve activity. The VIIth nerve activity was obtained from the R. hyomandibularis and R. hyoideus (d and e in Fig. 1) as well as from the R. subhyoideus (f in Fig. 1). The former (d) involves two muscle nerves for the M. depressor mandibulae and M. subhyoideus. The latter two (e and f) have the

Facial nerve activity

Figure 5 illustrates the relation between pulmonary and buccal pressure changes and integrated VIIth nerve activity. The VIIth nerve activity was obtained from the R. hyomandibularis and R. hyoideus (d and e in Fig. 1) as well as from the R. subhyoideus (f in Fig. 1). The former (d) involves two muscle nerves for the M. depressor mandibulae and M. subhyoideus. The latter two (e and f) have the
motor nerve only for the M. subhyoideus (Gaupp, 1899), which is known to fire in the pulmonary cycle (Shinkai and Narita, 1956). The ENGs of these nerves appeared to be principally the same. But the former branch activities appeared somewhat irregular (Fig. 5). This might be due to the activity of the nerve innervating the M. depressor mandibulae. Although the EMG from this muscle could not be obtained in the normal respiratory cycles, it tended to fire in phase with respiration when the nostrils were artificially sealed. The VIIth nerve showed two peaks in the pulmonary cycle, one in P-II and III (Fig. 5, b to c) and the other in P-IV(d). A small amount of activity in the buccal cycle clearly coincided with the phase of pressure depression (a).

**Glossopharyngeal nerve activity**

The IXth nerve was subdivided into the R. communicans and the other main trunk (see Fig. 1). No respiratory activity was recorded from the R. communicans. The other IXth trunk gives off the R. pharyngeus anterior inferior which was observed to further ramify into several branches innervating the M. petrohyoideus anterior. The ENG of the IXth trunk (g in Fig. 1) exhibited P-IV activity with low spike amplitude and neither P-II and III activity, nor oscillatory activity in all the five frogs examined even during inflation sequences. In another three frogs, the ENG of the R. pharyngeus anterior inferior was taken during air breathing. In two frogs, the activity corresponding to the pressure-increasing phase of the buccal cycle appeared infrequently (9.4% of 840 buccal cycles analyzed). But in the third frog this oscillatory activity was always detected (340 buccal cycles analyzed). This difference might be due to the different nerve branch used for recording. In all three frogs, clear P-IV activity, but no P-II and III activity, was observed (1,159 pulmonary cycles analyzed) (Fig. 6, bottom panel).

---

**Fig. 6.** Relationships of ENGs of Xth and IXth nerve branches to buccal pressure curve. From top to bottom traces in each recording, direct recording of the ENG was made after passage through a band pass filter; integrated ENG; buccal pressure curve.

*Japanese Journal of Physiology*
Vagal nerve activity

The Xth nerve emerges from the ganglion jugulare and consists of two nerves: the R. auricularis and main trunk. Not far from the ganglion in the efferent pathways, two important respiratory branches ramify from the trunk, the R. pharyngeus posterior superior (i in Fig. 1) which innervates respiratory muscles, the Mm. petrohyoidei posterior I and II, and R. laryngeus longus (k in Fig. 1) to innervate the laryngeal dilator and constrictors, as well as M. petrohyoideus posterior III. The rest of the nerve trunk involves many motor branches, including the M. petrohyoideus posterior III, and sensory ones to the laryngeal area and other organs in the thoracic and abdominal cavity. The electrical activity from this vagal trunk (at the point j in Fig. 1) was recorded first in four frogs. Its ENG showed three phasic activities in the pulmonary cycle (P-II and III, P-IV and P-V) and showed no apparent activity during the buccal cycle.

The R. laryngeus longus displayed diphasic activities (Fig. 6, upper panel). The first one started at the beginning of P-II and usually exhibited a plateau. It lasted until the end of P-IV. The second phase of the activity became evident shortly after the termination of the plateau in the former phase. Continuous discharges were observed between two pulmonary cycles in some frogs examined. But no phasic oscillatory activity appeared in this branch in any of seven frogs examined. Electrical stimulation of this nerve at the site of recording had revealed that this part of the nerve involved the R. petrohyoideus posterior III (GAUPP, 1899). From these results, the petrohyoideus posterior III may not have stable oscillatory activity.

The ENG of the ramified part of the R. pharyngeus posterior superior was obtained in five frogs. One typical example is demonstrated in Fig. 6 (middle panel). The ENGS always showed clear buccal cycle activity corresponding to pressure elevation. P-IV activity appeared as the biggest burst, but P-II and III activity appeared rather rarely (16.5% of 925 pulmonary cycles in four frogs analyzed). These results were observed during air breathing and were changed little even by N₂ breathing. At near the end of P-V, a small amount of activity was always detected (Fig. 6, middle panel).

Hypoglossal nerve activity

The ENG of the XIIth nerve trunk (1 in Fig. 1), which included the activity of the nerve responsible for either BCont, or BCDil, is shown in Fig. 7. In the buccal cycle, two peaks, small and large in peak height, were usually distinguished. The small and large peaks corresponded to the phase of buccal pressure elevation and depression, respectively. In the pulmonary cycle, the phasic activities were noticed in P-I (a to b), P-II and III(c), P-IV(d), and P-VI (arrow). The P-II and III activity was not clearly distinguished from the preceding activity, especially when ventilatory activity was low.

Electrical activities of both the sternohyoid muscle and the intact XIIth nerve
were recorded ipsilaterally and simultaneously in the prone position (Fig. 7, inserted figure). In the buccal cycle, the EMG appeared synchronously with the XIIth nerve activity. In the pulmonary cycle, both showed activities in the period between two vertical bars corresponds to P-I through to P-III activities.

Fig. 7. Twelfth trunk activities and respiratory pressure curves. a, beginning of P-I; b, peak P-I activity; c, peak P-II and III activity; d, peak P-IV activity; arrow, peak P-VI activity. Inserted figure: intact XIIth trunk ENG and ipsilateral sternohyoid EMG. The period between two vertical bars corresponds to P-I through to P-III activities.

Fig. 8. Relationships of the ENGs of two XIIth nerve branches to buccal pressure curve. ENGXII-R, ENG of XIIth nerve branch involving R. geniohyoideus; ENGXII-SH, ENG of R. sternothyroides. a, peak activity corresponding to the highest buccal pressure in buccal cycle; b, peak P-I activity; c, P-II and III activity; d, P-IV activity; f to g, P-VI activity.

were recorded ipsilaterally and simultaneously in the prone position (Fig. 7, inserted figure). In the buccal cycle, the EMG appeared synchronously with the XIIth nerve activity. In the pulmonary cycle, both showed activities in the period
NERVE ACTIVITY OF FROG RESPIRATION

of P-I, P-II and III, and P-VI. The XIIth ENG (ENGxII-R), after giving off the R. sternohyoideus (the point m in Fig. 1), R. omohyoideus and R. posterior M. hyoglossi, and containing the nerves for the M. geniohyoideus, a BCcont, was recorded in the supine position together with the sternohyoid ENG (ENGxII-SH) (Fig. 8). ENGxII-R represented activities in the phase of buccal pressure elevation (a), in P-II and III (c), and in P-IV(d). ENGxII-SH showed a similar pattern of activity to the sternohyoid EMG: in the phase of buccal pressure depression during the buccal cycle (e), and P-I(b), P-II and III(c), and P-VI (f to g) during the pulmonary cycle. It was confirmed that ENGxII-R was similar to the geniohyoid ENG. ENGxII-SH was repeatedly taken together with buccal pressure from five animals to confirm the above description. The R. omohyoideus was too short to obtain electrical activity. Accordingly, the omohyoid EMG was recorded which showed the biggest burst in P-IV, in agreement with the observation by De Jongh and Gans (1969) and West and Jones (1975). However, this result was at variance with the view of Oka (1957) who claimed that this muscle serves as a BCdir.

Figure 8 also shows that when pulmonary cycles occur consecutively, P-VI activity (f to g in Fig. 8) of ENGxII-SH in the preceding cycle is the same as P-I activity of the succeeding cycle.

It was further revealed that the R. posterior M. hyoglossi, innervating the M. hyoglossus, had P-II and III as well as P-IV activities, but little activity during the buccal cycle. Electrical stimulation of the peripheral strand of this nerve caused tongue retraction on the buccal floor, with little change in position of the floor itself.

DISCUSSION

Electromyographic studies of frog respiratory musculatures have been repeatedly conducted for more than the last three decades. There is still disagreement among investigators on the major pattern of the electrical activity of the respiratory muscle. This is the first study where the electroneurographic method has been applied to investigate this problem.

It was found that there is a common pattern of electrical activity in cranial nerves innervating either BCcont or BCdir, and that there is an interrelationship between the two systems. These common features are summarized in Fig. 9.

All the cranial nerves innervating BCcont showed the biggest burst in the lung inspiration phase (P-IV). This result is well consistent with that for EMGs reported by De Jongh and Gans (1969) and West and Jones (1975). Almost all of these nerves also had a small amount of activity in the lung expiration phase (P-II and III). Ito and Watanabe (1962) have already found that this phenomenon occurs in the electrical activity of the M. mylohyoideus, as well as in the medulla of toads. The present study confirmed that it is a general discharge pattern of
the BCcont in the bullfrog. However, it must be noted that the R. pharyngeus anterior inferior (IX) had no such an activity. It became clear that all the BCcont, possibly except for the R. petrohyoideus posterior III, are active in the phase of pressure elevation during the buccal cycle.

Thus it was demonstrated that the BCcont has one phasic activity in the buccal cycle and two activities in the pulmonary cycle.

The sternohyoid nerve (XII) and muscle, serving as a BCdil, showed an oscillatory activity, which supports the datum of EMG in Rana nigromaculata (Oka, 1957). They had P-I, P-II and III, and P-VI activities during the pulmonary cycle. These ENG and EMG patterns during the pulmonary cycle were not the same as for any sternohyoid EMG reported to date. Shinkai and Narita (1956) reported two activities: one early part in P-I and the next from P-IV through P-VI in toads; Oka (1957) P-I or P-VI in Rana nigromaculata; De Jongh and Gans

*Japanese Journal of Physiology*
(1969) from P-I to early part of P-II and III in Rana catesbeiana. These differences might be due mainly to the difficulties in recording total electrical activities from the muscle. EMG was usually poorer in spike number and sometimes shorter in length of activity than the ENG in the present study.

Figure 9 explains that the two nervous systems responsible for BCcont and BCdil become excited reciprocally during the buccal cycle as well as during the pulmonary cycle. Figure 9 also shows that during the pulmonary cycle, the nervous system for BCdil exhibits small P-I and large P-II and III activities, whereas those for BCcont show small P-II and III and large P-IV activities. Thus, both systems are active in the lung expiration phase. This new finding is inconsistent with the common view that the bucco-pharyngeal musculatures make little contribution to lung expiration. How both systems are organized to achieve lung expiration remains to be solved. The present study revealed that both P-I and P-VI were represented by sternohyoid nerve activities, and that P-VI activity is apparently P-I of the succeeding cycle when pulmonary cycles repeat consecutively. This finding may allow us to take either of them as a phase of the pulmonary cycle. In this study, P-I could be tentatively chosen, because P-I activity was observed to succeed P-II and III activity in the ENG of BCdil. It must be added that P-VI, which is characterized by the deepest negative deflection of buccal pressure, is considered to be included in the pulmonary cycle by many authors (OKA, 1957; DE JONGH and GANS, 1969; WEST and JONES, 1975). Therefore more conclusive evidence should be presented to determine the phase division.

Laryngeal musculatures are innervated both by the short and long laryngeal nerves, each of which is either involved in the vagal trunk or is a separate strand. The activities of these two nerves were principally consistent with EMGs of the laryngeal dilator (SHINKAI and NARITA, 1956; WEST and JONES, 1975), and with those of the laryngeal sphincters (DE JONGH and GANS, 1969). These nerves had no phasic electrical activities in the buccal cycle. This observation is also consistent with those EMGs.

The ENG of the nerve branch innervating the minor masseter muscle was taken either from the submandibular branch (V) (Fig. 3) or from the masseter branch itself (Fig. 4). This ENG pattern was rather similar to the sternohyoid ENG. No study has hitherto been conducted on whether or not this muscle has electrical activity in normal respiratory cycles. The mouth of the frog is well known to be kept closed during normal respiratory cycles. The present result suggests masseter participation in mouth closing during respiratory cycles. In fact, unsealing the mouth was frequently observed at the side where the trigeminal nerve was dissected.

The tongue is situated on the lower jaw in the bullfrog. Its movement during the breathing cycle has not been studied. The present results of the R. posterior M. hyoglossi provided the evidence that the tongue is actively bent on the buccal
floor corresponding to both lung expiration and inspiration. These phasic movements of the tongue may be beneficial for reducing the resistance of flow in the mouth. A similar mechanism is well known to play a vital role in mammals (Sau erland and Harper, 1976; Brou illette and Thach, 1979).

I wish to thank Dr. Yoshiyuki Honda for his criticism of the manuscript as well as for valuable discussions, and Drs. Yasuichiro Fukuda and Jean Charles Massabau for their valuable suggestions. This work was partly supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture of Japan (No. 367016).

REFERENCES


