ELECTROMYOGRAPHIC PATTERN OF THE GULAR PUMP IN MONITOR LIZARDS

TOMASZ OWERKOWICZ,1 ELIZABETH L. BRAINERD,2 AND DAVID R. CARRIER3

ABSTRACT. Gular pumping in monitor lizards is known to play an important role in lung ventilation, but its evolutionary origin has not yet been addressed. To determine whether the gular pump derives from the buccal pump of basal tetrapods or is a novel invention, we investigated the electromyographic activity associated with gular pumping in savannah monitor lizards (Varanus exanthematicus). Electrodes were implanted in hyobranchial muscles, and their activity patterns were recorded synchronously with hyoid kinematics, respiratory airflow, and gular pressure. Movement of the highly mobile hyoid apparatus effects large-volume airflows in and out of the gular cavity. The sternohyoideus and branchiohyoideus depress, retract, and abduct the hyoid, thus expanding the gular cavity. The omohyoideus, constrictor colli, intermandibularis, and mandibulohyoideus elevate, protract, and adduct the hyoid, thus compressing the gular cavity. Closure of the choanae by the sublingual plicae precedes gular compression, allowing positive pressure to be generated in the gular cavity to force air into the lungs.

The gular pump of monitor lizards is found to exhibit a neuromotor pattern similar to the buccal pump of extant amphibians, and both mechanisms involve homologous muscles. This suggests that the gular pump may have been retained from the ancestral buccal pump. This hypothesis remains to be tested by a broad comparative analysis of gular pumping among the amniotes.

INTRODUCTION

Monitor lizards (genus Varanus) have recently been found to supplement their lung ventilation with gular pumping during locomotion (Brainerd and Owerkowicz, 1996). In a gular pump cycle, a monitor lizard first draws fresh air into its large pharyngeal (gular) cavity and then contracts its throat muscles to create positive pressure, thus forcing air into the lungs. Multiple gular pumps may occur in succession between costal breaths. Gular pumping has been shown to significantly increase both minute ventilation and aerobic capacity of savannah monitor lizards (Varanus exanthematicus) during exercise (Owerkowicz et al., 1999). Little is known about the actual mechanism of gular pumping and its evolution. A highly expandable pharynx, supported by an elaborate hyobranchial basket, is a characteristic feature of monitor lizards. The large size and compressibility of the pharynx make it ideally suited for pumping large volumes of air. Smith (1986) studied the function of throat musculature in V. exanthematicus during feeding, and recorded hyobranchial muscle activity and hyoid movements. Bels et al. (1995: 99) provided a kinematic analysis of the throat threat display in Varanus griseus, “a ventilatory bucco-pharyngeal breathing pump (VBPBP),” consisting of alternating expansions and compressions of the gular cavity. These studies have documented the extreme excursions of the hyoid apparatus during a wide repertoire of monitor behaviors. However, the electromyographic (EMG) signature of the gular pump, as a ventilatory mechanism, has not been reported.

This study aims to determine how throat muscle activity is coordinated during gular pumping in V. exanthematicus.
muscles are responsible for gular expansion, and which ones are responsible for compression? How is pressure generated in the gular cavity? What controls the airflow pattern?

The evolutionary origin of the gular pump also presents an interesting dilemma. Squamates have been presumed to ventilate their lungs solely by means of costal aspiration (Gans, 1970; Carrier, 1987; but see Deban et al., 1994); they rely on contraction of intercostal muscles to create negative pressure in the pleural cavity to suck air into the lungs. The use of a pressure pump was thought to be reserved for air-breathing fish and amphibians (Liem, 1985; Brainard et al., 1993). In this mechanism, air is gulped into the buccal (mouth) cavity, and subsequently the hyoid apparatus generates positive pressure, forcing air into the lungs. The gular pump of monitor lizards clearly qualifies as a pressure pump and therefore breaks with this traditional phylogenetic separation of breathing mechanisms. However, the gular pump differs from the buccal pump because the hyoid apparatus of monitor lizards is positioned posteriorly in the throat, whereas the hyoid apparatus of amphibians resides in the mouth cavity between mandibular rami. The presence of gular pumping behavior has not been rigorously investigated in other lizard genera, and it is unclear whether gular pumping is a uniquely derived trait of monitor lizards or whether its ancestry can be traced back to buccal pumping of basal tetrapods.

Therefore, this study attempts to address the origin of gular pumping from a functional perspective. How similar is the EMG pattern of the gular pump to that of the amphibian buccal pump? Is the gular pump a case of neuromotor conservatism in evolution, or has it evolved de novo in monitor lizards?

MATERIALS AND METHODS

Animals

Experiments were performed on four savannah monitor lizards (230–2,400 g) during and immediately after locomotion on a motorized treadmill at speeds of 1–5 km/h. The animals were maintained at 25–40°C on a 14:10 hour light:dark photoperiod and were fed a diet of mice.

Terminology

This study follows the terminology of Smith (1986) in her description of the osteology and myology of the varanid gular region.

Videoradiography

Videos of the lizards were taken with a Sony DCR VX1000 digital camcorder (60 fields/s at 1/250 s shutter speed) and the Siemens X-ray fluoroscope at the Museum of Comparative Zoology Laboratories at Harvard University. Video recordings were made separately in lateral and dorsoventral projections. Select video fields were imported into Adobe Photoshop on a Power Macintosh computer.

To better visualize movements of the floor of the mouth relative to the skull and hyoid, lead markers (1.6 × 0.5 mm) were placed unilaterally in the left sublingual plica and in the anterior epithelial border of the left choana. Marker implantation was performed percutaneously with a 20-gauge needle and plunger while the animals were under 1–2% halothane anesthesia.

Pneumotachography

Two animals were used to measure airflow during gular pumping. A lightweight mask, fashioned from clear acetate and epoxy, was custom-fitted and taped over the lizard’s snout to enclose the mouth and nostrils. A bias flow of humidified air (1,200 ml/min) was drawn through the mask. A pneumotachograph (8421 series 0-5 LPM, H. Rudolph, Kansas City, Missouri), connected to a differential pressure transducer (MP 45-1-871, Validyne, Northridge, California) downstream from the animal, measured airflow through the mask. The system was calibrated against
repeated injections of measured aliquots of air into the mask.

**Pressure Recordings**

Two animals (not used for airflow recordings) were instrumented to measure gular pressure during gular pumping. With the animal under 1–2% halothane gas anesthesia, a skin incision was made between the ceratohyal and ceratobranchial. The underlying muscles were carefully blunt-dissected and a 13-gauge needle was inserted through the pharyngeal epithelium into the gular cavity. A 20- to 30-cm-long polyethylene cannula (1.14-mm inner diameter, 1.57-mm outer diameter), previously sterilized and heat-flared at the distal end, was threaded through the hole and securely sutured to the lateral wall of the gular cavity. Before each recording session, the cannula was cleared of mucus to prevent capillarity artefacts and connected to a differential pressure transducer (PX138-0.3D5V, Omega Engineering, Inc., Stamford, Connecticut). The pressure transducer was calibrated against 10 cm H₂O after each recording session.

**Electromyography**

Electromyographic activity was recorded in the following muscles: constrictor colli, intermandibularis, mandibulohyoidaeus, omohyoideus, sternohyoideus, and branchiohyoideus. Patch and sew-through bipolar electrodes, as detailed by Loeb and Gans (1986) and Carrier (1996), respectively, were constructed of 0.28-mm-diameter Teflon-coated stainless steel wire (Cooner Wire Co., Chatsworth, California) and silastic-reinforced sheeting (Specialty Manufacturing, Inc., Saginaw, Michigan). In each electrode, the exposed portions of wires were 2 mm long and 1 mm apart. With the animal anesthetized, electrodes were surgically implanted and firmly anchored in the desired muscles. The electrode wires were then passed subcutaneously under the pectoral girdle to a single exit on the trunk's dorsum and soldered to connectors (Microtech, Inc., Boothwyn, Pennsylvania). The signals were amplified 5,000–20,000 times (as appropriate for each channel) with Grass P511J amplifiers (Quincy, Massachusetts), with a bandpass of 100–1,000 Hz (with the 60-Hz notch filter in). The signals were acquired at 5,000 Hz and analyzed on a Power Macintosh computer using AcqKnowledge (BioPac Systems, Santa Barbara, California) and Igor Pro (WaveMetrics, Inc., Lake Oswego, Oregon) software. Electromyographic and pressure signals were temporally synchronized with video recordings by means of a light-emitting diode trigger (Thexton Unlimited, London, United Kingdom).

**RESULTS**

**Kinematics**

Four stages of hyobranchial movement characterize each gular pumping cycle (Fig. 1): resting, active expansion, early closure, and compression. The cycle usually begins with the expansion of the hyobranchial basket. From its resting position (Fig. 1A), the basihyoid and the lingual process are drawn slightly ventrad and caudad. The anterior processes are abducted and, pivoting on the basihyoid, swung laterad. The ceratohyals and ceratobranchials rotate to assume a more vertical orientation (Fig. 1B).

The compressive phase of the pump cycle begins with the elevation of the buccal floor to abut the palate, thereby closing off the mouth and nostrils. As highlighted by radiopaque markers, each choana is occluded by its ipsilateral sublingual plica. The glottis is located in the gular cavity, while the hyoid remains in a retracted and expanded configuration (Fig. 1C). Finally, the basihyoid is protracted and elevated, while the trachea slides rostrad in the gular cavity. The anterior processes are abducted, and the ceratohyals and ceratobranchials fold horizontally (Fig. 1D). The hyobranchium then relaxes and passively returns to its resting state (Fig. 1A); another pumping cycle may follow.
Figure 1. Still frames from an X-ray positive video (shutter speed 1/250 s) showing one gular pump cycle in *Varanus exanthematicus* (body mass = 600 g). The left column shows the animal in lateral projection, the right column in dorsoventral projection. Although not recorded simultaneously, frames in each row portray corresponding stages of a pump cycle. (A) Gular cavity relaxed. (B) Gular cavity expanded. (C) Buccal floor elevated. (D) Gular cavity compressed. Radiopaque markers (arrows) are placed at the choana (Ch), the sublingual plica (SP), and the glottis (G). Note the closure of the mouth and nares, which seals the gular cavity, as demonstrated by proximity of markers Ch and SP in (C).
Active expansion was not observed in every pump cycle. The animals often chose to proceed to closure and compression directly from the resting stage, in which case the volume of air pumped was not as great as when preceded by active expansion. Furthermore, resting gular volume was dependent on the positioning of the hyobranchial apparatus in the neck of the animal, which varied with the animal’s posture and muscle tone of associated pectoral musculature (sternohyoideus and omohyoideus—see below).

Airflow

The airflow pattern at the animal’s mouth and nostrils (Fig. 2A) is consistent with a biphasic nature of each gular pump, whereby a filling (expansive) phase is immediately followed by an emptying (compressive) phase. Average filling volumes ranged from 6 to 15 ml, but individual gular inspirations up to 33 ml were also recorded. Early in the pump cycle, animals were observed to rely on passive filling of the gular cavity by gravitational drop of the hyoid (correspondent to the return of the hyoid from compressed to resting stage). Passive filling was followed by active expansion, as indicated by concomitant activity in the branchiohyoideus and sternohyoideus, which resulted in faster (more negative) airflow and greater filling volumes.

Early in the filling phase, airflow into the gular cavity was rapid, as shown by the steep descent of the airflow trace to its minimum value. Late in the filling phase, inspiratory airflow gradually diminished to
A slight overshoot of the zero-flow line (N in Fig. 2A) marked early closure of the mouth and nostrils, and the beginning of the emptying phase. A zero-flow plateau was recorded for the duration of the emptying phase, as air was forced from the gular cavity into the lungs. The emptying phase terminated in a small expiratory spike (0.5–1.0 ml), after the inferred closure of the glottis (G in Fig. 2A) and opening of the mouth and nares. Unless another pumping cycle occurred immediately afterwards, passive filling followed and a longer apnoeic period ensued.

Pressure

Each costal breath was followed by as many as five gular pumps, with successive pump cycles generating increasingly positive gular pressures (Fig. 2B). Peak pressures up to 15 cm H₂O were recorded. With the onset of each compressive phase, gular pressure climbed steeply and reached peak pressure within 200 milliseconds. For most pumping cycles, gular pressure hovered within 5% of peak value for less than 100 milliseconds, although gular pressure would sometimes remain elevated at peak for up to 400 milliseconds. Thereafter, gular pressure dropped rapidly (within 100 milliseconds), often dipping to subatmospheric levels, and then equilibrated with the atmospheric pressure.

Gular pressure varied little from atmospheric pressure during the filling phase of a pump cycle. Active gular expansion generated only slightly subatmospheric pressures (−0.2 to −0.4 cm H₂O).

Electromyographic Activity

Recordings from hyobranchial muscles produced a consistent activity pattern during gular pumping (Fig. 2A, B). Although they remained quiescent during passive filling, branchiohyoideus (both cerato- and cornuhyoidei heads), sternohyoideus, and mandibulohyoideus III were turned on during active gular expansion. Onset of the branchiohyoideus was followed in 50–200 milliseconds by almost simultaneous activation of the sternohyoideus and mandibulohyoideus III. The intensity of their firing remained roughly constant while these muscles were active. All three muscles were turned off before the end of the filling phase, with activity in the branchiohyoideus persisting for up to 150 milliseconds after the offset of the sternohyoideus and mandibulohyoideus III.

Gular compression began with a burst of activity in the intermandibularis anterior, which was followed within 100 milliseconds by contraction of the constrictor colli, intermandibularis posterior, and all three heads of mandibulohyoideus. The intensity of their firing generally increased from onset to offset. Activity ceased in all muscles together, once gular pressure had peaked.

The activity of the mandibulohyoideus III was biphasic; it contracted during gular expansion and compression, but not continuously (Fig. 2B). It was briefly (50–100 milliseconds) silent between the two phases of the pumping cycle.

The omohyoideus was usually quiescent during gular pumping. When participating in gular pumping, the omohyoideus was predominantly active during gular compression. However, it might occasionally fire during gular expansion (in Fig. 2A), which tended to decrease the gular filling volume. In such instances, activity of the omohyoideus was correlated with changes in posture and/or neck bending by the animal.

During locomotion, regular phasic activity was observed in most hyobranchial muscles, but was especially prominent in the sternohyoideus and omohyoideus. The rate of discharge was the same as the footfall frequency, and in the latter two muscles the signal amplitude was greater than in stationary animals.

DISCUSSION

Hyobranchial Muscle Function

The role of individual muscles involved in the gular pump can be inferred by con-
Figure 3. The hyobranchial apparatus of Varanus exanthematicus, in ventral (top row) and lateral (bottom row) views. Force vectors (gray arrows) show the sites of insertion and lines of action of the hyobranchial muscles, as measured in dissected specimens. (A) The hyoid in its expanded configuration; contraction of musculi (mm.) mandibulohyoideus and omohyoideus will result in hyoid compression. Constrictor colli and intermandibularis are not shown, because they do not insert directly on the hyoid. (B) The hyoid in its compressed configuration; contraction of the branchiohyoideus, sternohyoideus, and mandibulohyoideus III will result in hyoid expansion. Abbreviations: ap, anterior process; bh, basihyoid; cb, ceratobranchial; ch, ceratohyal; clav, clavicular; lp, lingual process; scap, scapular; others as in Figure 2.

Considering their insertion sites on the hyoid apparatus (Fig. 3), the patterns of their EMG activity, and the kinematics of the hyoid elements during each gular pump cycle.

Gular expansion results from the coordinated activity of the sternohyoideus, branchiohyoideus, and mandibulohyoideus III. The sternohyoideus pulls the ceratobranchial in a caudoventrad direction, giving it a more vertical orientation. This action tends to retract and depress the basihyoid, while pointing the lingual process ventrad. With the ceratobranchial stabilized by the sternohyoideus, the branchiohyoideus tends to abduct the anterior process and retract the ceratohyal. However, the proximal end of the anterior process pivots about the basihyoid, and the ceratohyal has its distal end anchored to the lower jaw by the mandibulohyoideus III. The broad, loose nature of articulation between the ceratohyal and the anterior process allows sliding to occur between these two elements. Thus, as the anterior process swings laterad, it pushes against the ceratohyal, the angle between these two elements increases, and the ceratohyal assumes a more vertical orientation. Altogether, these muscles tend to expand the gular cavity in the lateral and dorsoventral dimensions.

Gular compression begins with the early closure of mouth and nostrils. The intermandibularis anterior, positioned under the sublingual plicae, contracts to elevate
Figure 4. Cross section of the snout of Varanus exanthematicus at the anterior border of the choanae. Each nasal passage connects to its ipsilateral choana just posterior to this plane. Elevation of the mouth floor allows the sublingual plica to plug the choana above. The congruent outlines of the lower and upper jaws allow an airtight closure of the mouth, sealed with saliva from labial and sublingual glands. Abbreviations: Ch, choana; LG, labial gland; U, lower jaw; N, nasal passage; SG, sublingual gland; SP, sublingual plica; UJ, upper jaw.

the buccal floor and push the plicae against the choanae (SP → Ch in Fig. 4), thus blocking airflow through the nasal passages. Although no recordings were taken from the adductor mandibulæ, this muscle is most likely to be responsible for keeping the mouth closed, while the thick, fleshy gums (Auffenberg, 1981) seal the oral margins with secretion of salivary glands lining both lingual and labial aspects of the lower jaw. The gular cavity is effectively made airtight for the duration of gular compression.

Muscles responsible for gular compression include the omohyoides, constrictor colli, intermandibularis posterior, and mandibulohyoides. The clavicular and scapular heads of the omohyoides attach the ceratobranchials to the respective parts of the pectoral girdle, and their contraction retracts and elevates the basihyoid. The constrictor colli encircles the floor and sides of the gular cavity, forming a sleeve in which the hyobranchial basket is suspended. Together with its anterior extension, the intermandibularis posterior, this superficial transverse muscle elevates the hyoid apparatus. On the other hand, the mandibulohyoides connects the hyoid to the lower jaw and, along with the sternohyoides and omohyoides, controls its anteroposterior position in the neck. As the basihyoid is protracted, the ceratohyals and ceratobranchials assume a more horizontal orientation, in effect folding the hyobranchial basket. The orthogonal orientation of muscle fibres in the constrictor colli and intermandibularis to the mandibulohyoides means that their synchronous activity will squeeze the air out of the gular cavity.

With the onset of locomotion, most hyobranchial muscles show bursts of activity in phase with the footfall pattern. This is particularly pronounced in the sternohyoides and omohyoides; their firing intensity during locomotion is several times greater than at rest. Yet it is hard to imagine their acting as locomotor muscles. It is more likely that with every retraction of the forelimb these muscles are stretched and fire reflexively to stabilize the hyoid, keeping it in position for pumping. Low-intensity phasic activity detected in other hyobranchial muscles is probably an artefact of cross-talk from the underlying axial muscles of the neck, participating in the lateral bending of the neck during locomotion.

Airflow and Pressure Changes

The pneumotachograph and the pressure transducer provide complementary information about the patterns of airflow and pressure generation outside and inside the gular cavity. During gular expansion, pressure drops only slightly below the atmospheric level. The lizard's mouth and nares are wide open (Fig. 1B) and provide little resistance to airflow into the gular cavity. Gular expansion, whether passive or active, is too slow for gular pressure to turn more negative; instead, it quickly equilibrates with atmospheric pressure.

Inspiratory airflow ceases when the mouth and nares are shut (see above). The "corking" of the choanae by the sublingual
plicae expels an aliquot of air from the nar­
ial passages (N in Fig. 2A). The gular pres­
sure increases from this point on and air is pressed through the open glottis into the 
trachea and lungs. The plateau at zero­
flow indicates the efficacy of the oral seal.

Only at the very end of compression does a puff of air leak out of the mouth 
and nares at a high flow rate (G in Fig. 
2A). The hyobranchial muscles have al­
ready turned off by this time, yet their 
contraction clearly persists for approxi­
mately 120 milliseconds (a reasonable time 
period for slow-twitch fibers in isometric 
contraction) and gular pressure remains 
reduced. This expiratory “gular leakage” 
possibly represents excess air, which was 
not pressed into the lungs. The fact that 
this occurs at the end of every pumping 
cycle indicates that the glottis always closes 
before the nares open. Such carefully co­
ordinated timing suggests that this may be 
a hard-wired mechanism designed to pre­
vent air escaping from the lungs, which 
have been pressurized by gular pumping.

Origin of Gular Pumping

The gular pump of monitor lizards bears 
striking resemblance to the buccal pump 
of extant amphibians, in function and in 
mechanism. Both pumps generate positive 
pressure to force air from the pharyngeal 
cavity into the lungs. Both employ the 
hyobranchial apparatus to produce volu­
metric changes of the buccal and gular 
cavities. This similarity suggests that buc­
cal pumping and gular pumping may be 
accomplished behaviors. However, the de­
ived morphology of the monitor lizards 
and their deeply nested position in the 
squamate phylogeny (Estes et al., 1988) 
suggest the possibility that gular pumping, 
as ventilatory behavior, may have evolved 
independently in monitor lizards. This al­
ternative hypothesis would be supported 
by finding that the gular and buccal pumps are powered by nonhomologous muscles, 
or that the patterns of their activation are 
markedly different.

Lepidosaurs, especially the highly de­
rived varanids, do not necessarily possess 
the same ensemble of hyobranchial mus­
cles found in Lissamphibia, and even 
among the latter, the muscular organiza­
tion of the throat is highly variable. How­
ever, muscle homologies can be estab­
lished with a fair degree of certainty by 
determining their anatomical relations and 
motor nerve supply (Fürbringer, 1888, in 
Cunningham, 1890). The constrictor colli 
of lizards and the interhyoideus of am­
phibians seem to be homologous, by virtue 
of having a common precursor in the con­
strictor hyoideus, as found among the Dip­
noi (Edgeworth, 1935). Exceeding for its la­
teralmost third head with a disparate motor innervation and therefore origin (Riep­
pec, 1978), the mandibulohyoideus is clearly a highly differentiated version of 
the geniohyoideus, ubiquitous among the vertebrates. The rectus cervicis of caeci­
lians is homologous with the sternohyoideus in both frogs and monitor lizards. 
Lacking a pectoral girdle, caecilians lack 
an omohyoideus.

The branchiohyoideus is found in nei­
ther anurans nor caecilians. Its putative 
endome, subarcualis rectus I (not the larval branchiohyoideus externus; Edge­
worth, 1935, contra Smith, 1920), is pres­
ent in urodeles, but the EMG activity of 
this muscle during buccal pumping is yet 
to be investigated. Nevertheless, EMG ev­
dence from feeding studies in Ambystoma 
(Lauder and Shaffer, 1985; Reilly and Lau­
der, 1991) shows that the subarcualis rec­
tus I is active during buccal expansion in 
aquatic and terrestrial prey capture, and its 
role in generating buccal expansion during 
suction feeding has been deduced from its 
anatomical position and fiber orientation 
in various salamanders (Ermann and Cun­
dall, 1984; Lauder and Shaffer, 1988; Lo­
renz-Elwood and Cundall, 1994). This 
suggests that the subarcualis rectus I func­
tions in much the same way in the buccal 
pump of salamanders as does the bran­
chiohyoideus in the gular pump of lizards.

Having established the homology of hyobranchial muscles of amphibians and
lizards, it is possible to directly compare their activity patterns in the gular pump of *V. exanthematicus* and in the buccal pump of a caecilian (Carrier and Wake, 1995) and an anuran (de Jongh and Gans, 1969; West and Jones, 1974). Differences in pressure profiles aside, all three neuro-motor patterns clearly are similar (Fig. 5). This suggests that homologous hyobranchial muscles function in much the same way in these distantly related clades. Therefore, the homology of the gular and buccal pumping behaviors cannot be rejected.

Nevertheless, analysis of the present data does not allow us to conclude with confidence that the gular and buccal pumps are homologous behaviors. Neuro-motor similarity is not sufficient to claim that a behavioral mechanism has been
with our finding of neuromotor similarity widespread among nonserpentine squamates (Deban et al., 1973), and throat displays (Bels et al., 1995). One or more of these behaviors could have retained the ancestral motor pattern for hyobranchial movement and this pattern could have been co-opted for lung ventilation (with appropriate modification of narial and glottal valving). The next study undertaken to explore the homology of buccal and gular pumping should be a broad comparative analysis to map the character of gular pumping (its presence or absence) on the phylogeny of Amniota. Preliminary investigations within Squamata indicate that gular pumping is widespread among nonserpentine squamates (Deban et al., 1994; Al-Ghamdi et al., 2001; Brainerd and Owerkowicz, personal observation). This result, combined with our finding of neuromotor similarity in the pumping mechanisms of monitor lizards and amphibians, suggests that the gular pump of lizards may have been retained continuously from a buccal pumping ancestor.

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