

MECHANICS AND NEUROMORPHOLOGY OF FEEDING IN AMPHIBIANS

by

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SUMMARY

Salamanders and frogs exhibit strong similarities in their habitats, prey preferences and foraging strategies. Despite these similarities, they differ profoundly in the structure and function of the adult feeding apparatus, and in the participation of cranial and spinal nerves and nuclei in the control of feeding behavior. In frogs, the hyolingual skeleton plays no role in tongue projection. Only the tongue is projected out of the mouth under the control of the nn. trigeminus (tongue protraction) and hypoglossus (tongue protraction and retraction). In all salamanders, feeding is based on forward movement of the hyolingual apparatus, which is folded into a slender, far-reaching projectile in the most highly derived salamanders. Tongue protraction is controlled by nn. glossopharyngeus and vagus, and tongue retraction is controlled by the first and second spinal nerves. All muscles related to feeding are activated sequentially in frogs and simultaneously in salamanders.

While the descending pathways to the brainstem and cervical spinal motor nuclei are similar in frogs and salamanders, differences in muscle function and activation pattern imply that the premotor reticular formation is also different.

In frog tadpoles and salamander larvae, the hyobranchial apparatus plays different roles in feeding and breathing. This has led to differential loss, acquisition and change of function of musculoskeletal elements during the ontogeny and phylogeny of the adult feeding apparatus in frogs and salamanders. These differences in the musculoskeletal periphery imply that a reorganization at or above the level of the reticular formation is likely to have occurred in frogs, but not in salamanders.

KEY WORDS: Frogs, salamanders, feeding, tongue, kinematics, neuromotor control, ontogeny.

INTRODUCTION

The structures associated with food capture and mastication in vertebrates show both a high degree of evolutionary plasticity and great conservatism (BRAMBLE & WAKE, 1985; ROTH & WAKE, 1989). The structures and physiology of these activities are highly integrated,

so two important questions are: Where, and by what means, do novelties arise in this system, so that it can evolve while remaining functional? What remains unchanged? The answers to these questions may provide insight into how different subsystems that are functionally integrated, such as skeletal elements, muscles and the nervous system, interact with each other to induce or inhibit evolutionary changes in the other subsystems (see ROTH & WAKE, 1989; WAKE & ROTH, 1989, for a more general discussion). In this article we explore these topics, using the feeding system of frogs and salamanders as an example of the evolution of structural and functional alternatives in a monophyletic group, the Lissamphibia. We will not discuss the third amphibian order, Gymnophiona, because almost nothing is known about the neuroanatomy of the brainstem and cervical spinal cord or about neural control of feeding in this group. The present paper is an up-dated and extended version of a German-language review article (ROTH *et al.*, 1988b).

Many species of frogs and salamanders are similar in their ecology, life history, feeding behavior, and prey preferences (cf. ROTH, 1987), despite impressive differences in their external appearance. In addition, their nervous systems, despite some differences in gross morphology, are generally similar (as compared with all other vertebrates) with respect to brain and spinal cord centers and nuclei, major pathways inside the brain, and peripheral innervation patterns (ROTH, 1987; ROTH *et al.*, 1990; NAUJOKS-MANTEUFFEL & MANTEUFFEL, 1988).

Furthermore, some frogs and salamanders may be more similar to each other in terms of their feeding strategies and prey preferences than either are to other members of their own order. This is also true for the response properties of the retinal and central neurons involved in visual guidance of feeding behavior (for an overview see ROTH, 1986, 1987).

However, if one compares the feeding apparatus of salamanders and frogs, one finds profound differences in the morphology of the apparatus, the muscles and nerves involved in feeding, the biomechanics, kinematics, and neuromotor control of feeding. Initially, this seems surprising, because the set of skeletal elements, muscles, nerves and motor nuclei is generally homologous in both groups. Thus, frogs and salamanders make very different use of this same set, or, seen from the perspective of feeding, they do the same thing by very different means.

Here we present and discuss these differences in morphology, kinematics and neuromotor control of feeding, and examine their possible origins. Major questions are: what processes and events have

induced the different phylogenetic and ontogenetic pathways of the amphibian feeding system? and, to what degree do functions of the hyobranchial system in larvae determine differences in feeding between adult frogs and salamanders?

FUNCTIONAL MORPHOLOGY AND NEUROMOTOR CONTROL OF FEEDING IN FROGS

At least four different mechanisms of feeding can be found within the order Anura. The most primitive families of frogs (superfamily Discoglossoidea) have tongues that are broadly attached to the floor of the mouth with no free flap posteriorly (REGAL & GANS, 1976; MAGIMEL-PELONNIER, 1924; HORTON, 1982). In these species, the tongue is not flipped, as in most species from more derived families (GAUPP, 1896), but is protruded over the mandible for a distance of only a few millimeters (NISHIKAWA & CANNATELLA, 1988; NISHIKAWA *et al.*, 1989). A flipping tongue is also absent in at least two species from more derived frog lineages, e.g. *Telmatobius* (Leptodactylidae) and *Cyclorana* (Hylidae) (REGAL & GANS, 1976). A unique mechanism of feeding is found in *Rhinophrynus*, in which the tongue is stiffened hydrostatically, and hyoid protraction drives the tongue out of the mouth (TRUEB & GANS, 1983).

Most frogs and toads (i.e., the family Pelobatidae and the superfamily Neobatrachia, with the exceptions noted above) have tongues that are rotated (i.e., flipped) over the mandible during feeding (GAUPP, 1896). The tongue consists of a large fleshy pad that lies on the floor of the mouth and rests on the hyoid plate. Unlike more primitive frogs, the tongues of these species also possess a less massive, relatively thin and elastic posterior flap (figs. 1C, 3). The hyoid consists of a cartilaginous plate and a pair of slender anterolateral cornua. These cornua arise from the anterolateral corners of the hyoid plate, curve posterodorsally and attach by ligaments to the ventral surface of the otic capsule. The hyoid plate bears paired posterolateral and posteromedial processes. The plate is attached to the mandibles near the symphysis by the m. geniohyoideus and to the pectoral girdle by the m. sternohyoideus. The two to four pairs of mm. petrohyoidei arise from the outer extremity of the prootic bone and attach to the ventral surface of the hyoid (fig. 1D).

Two muscles constitute the body of the tongue, the m. genioglossus medialis which arises near the mandibular symphysis and fans out into the tongue pad, and the m. hyoglossus which arises from the ventral surface of the posteromedial process of the hyoid plate and extends for-

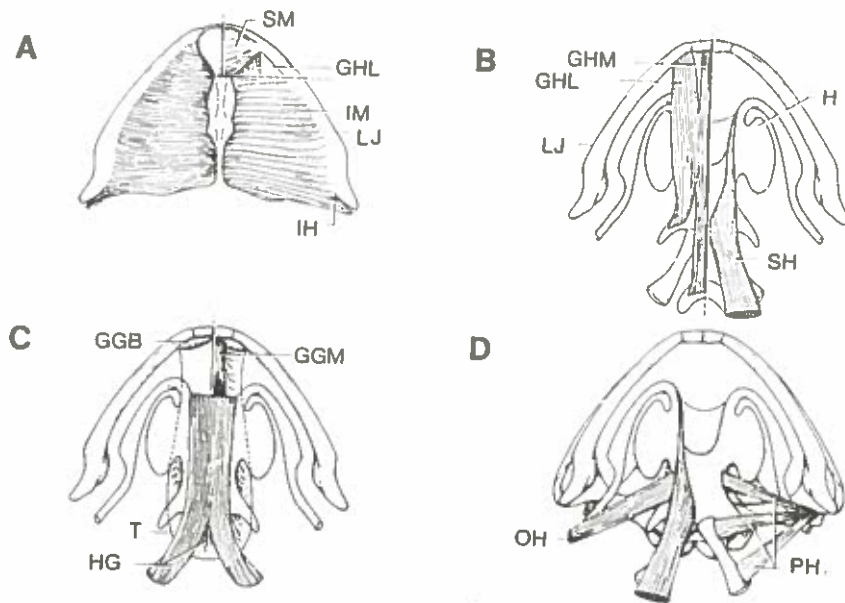


Fig. 1. Lower jaw and hyoid apparatus of *Bufo marinus*. A: Ventral view of the lower jaw with superficial musculature. B: Superficial (right) and deeper (left) hyoid musculature. C: Tongue musculature. D: Deep hyoid musculature. For further explanations see text. For abbreviations see list. After DUELLMAN & TRUEB (1986), modified.

ward, curving around the anterior end of the plate to fan out dorsally into the tongue, where its fibers intermingle with those of the m. genioglossus medialis (figs. 1C, 3). Caudal to the origin of the m. genioglossus medialis lies the rod-like m. genioglossus basalis, which is attached laterally to the anterior tip of the mandible and medially to its contralateral counterpart. Under this muscle lies the unpaired m. submentalis, a short, stout muscle that extends between the mandibles near their anterior tips.

Motor control of feeding in anurans involves brainstem (medulla oblongata) and cervical spinal nerves and nuclei (SZÉKELY, 1976; MATESZ & SZÉKELY, 1978; STUESSE *et al.*, 1983, 1984; OKA *et al.*, 1987a, b) (figs. 2, 6). The trigeminal (fifth cranial) nerve innervates the m. submentalis (involved in tongue protraction), the mm. adductor mandibulae system (closes the mouth), and the m. intermandibularis (elevates the floor of the mouth). The motor nucleus of this nerve lies between the entrances of the fifth and seventh nerves. The neurons controlling the m. submentalis are found mainly in the

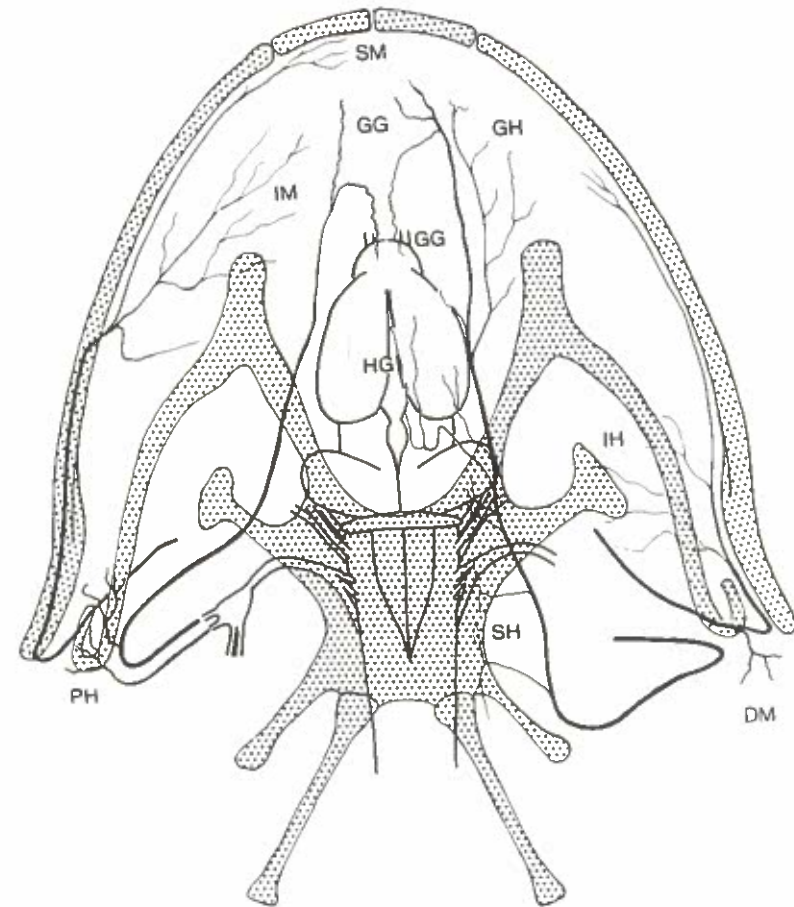


Fig. 2. Innervation pattern of the muscles related to feeding in the toad *Bufo bufo*. The lower jaw and the hyoid (stippled) and the outlines of the brain are shown. To the left, the branches of the nn. trigeminus, glossopharyngeus and vagus, to the right those of the nn. hypoglossus and facialis are shown. For abbreviations see list.

anterior part of the nucleus (TAKEI *et al.*, 1987). The facialis (seventh cranial) nerve innervates the m. depressor mandibulae (mouth opener) and the m. interhyoideus (raises the floor of the mouth). The motor nucleus of this nerve lies caudal to both the trigeminal nucleus and the entrance of the seventh nerve.

The glossopharyngeal (ninth cranial) nerve innervates the most anterior of the mm. petrohyoidei. The round nucleus of this nerve is

situated at the level of the entrance of the first root of the IX-XI root complex. Activity of the mm. petrohyoidei raises the hyoid during calling and breathing, but the muscles are not involved in feeding (GANS & GORNIK, 1982a, b). The vagus (tenth cranial) nerve innervates the more posterior mm. petrohyoidei. This narrow and elongate nucleus arises caudal to the glossopharyngeal nucleus and ends slightly caudal to the hypoglossal root.

The hypoglossal nerve serves the mm. geniohyoideus, sternohyoideus, genioglossus and hyoglossus. It possesses dorsomedial and ventrolateral subnuclei (SZÉKELY, 1976; STUESSE *et al.*, 1983; OKA *et al.*, 1987a, b). Motor neurons innervating the m. hyoglossus are found in the more anterior, while those innervating the m. genioglossus are found in the more posterior part of the dorsomedial nucleus, but there is substantial overlap between these groups of neurons. Motor neurons innervating the m. geniohyoideus are found in both the dorsomedial (anterior part) and ventrolateral (anterior three quarters) nuclei; neurons innervating the m. sternohyoideus are found throughout the ventrolateral nucleus (WEERASURIYA & EWERT, 1981; STUESSE *et al.*, 1983; OKA *et al.*, 1987a, b; TAKEI *et al.*, 1987).

Electromyographic and kinematic data on anuran feeding are available only for *Bufo marinus* and *Bufo japonicus* (GANS & GORNIK, 1982a, b; MATSUSHIMA *et al.*, 1985). The first observable behavioral event during feeding is the opening of the mouth by contraction of the m. depressor mandibulae. This muscle shows its first activity about 50 ms before mouth opening (MATSUSHIMA *et al.*, 1985).

Tongue protraction is accomplished by contraction of the mm. genioglossus basalis and medialis and the m. submentalis (fig. 3). These muscles apparently form a coupled rod-and-wedge system that is raised and rotated over the region of the mandibular symphysis. A major component of the system is the contraction of the m. submentalis, which bends the mandibles downward and rotates them outward (GANS & GORNIK, 1982a, b). The mm. geniohyoideus and sternohyoideus contract slightly during tongue protrusion to stabilize the hyoid plate. The long posterior flap of the tongue follows the stiffened rod-like base, formed by the m. genioglossus medialis, and travels out of the mouth. The mm. genioglossus medialis and basalis relax, and the tongue is extended to its full length by its own inertia.

The tongue is retracted by contraction of the m. hyoglossus, which becomes active 400 ms before peak activity of the mm. genioglossus medialis and basalis, and remains active long after these muscles have relaxed. At maximum activity of the mm. genioglossus, the activity of the m. hyoglossus is temporarily suppressed. The m. submentalis and the mm. genioglossus basalis and medialis abruptly cease to contract

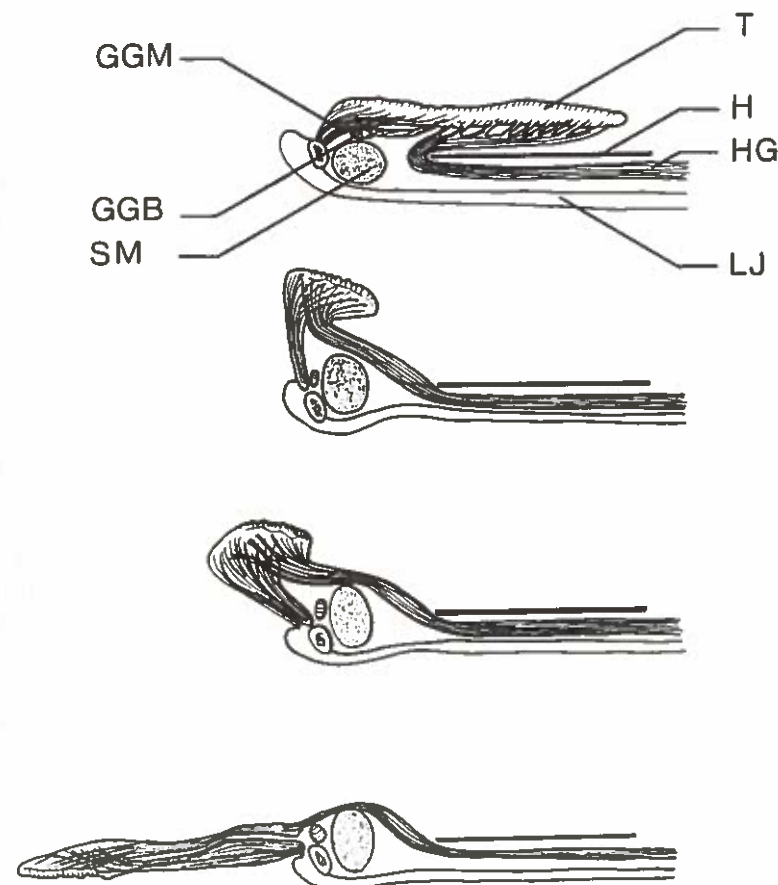


Fig. 3. Sequence of tongue projection in the toad *Bufo marinus*. For abbreviations see list. After GANS & GORNIK (1982b), modified.

as the m. hyoglossus reaches its maximum activity. As the m. hyoglossus gains mechanical advantage, the tongue pad is returned to the mouth, and the mm. adductor mandibulae close the mouth on average 250 ms after opening (MATSUSHIMA *et al.*, 1985).

The sequence of onset of electrical activity in muscles is the following: (1) mm. hyoglossus-geniohyoideus (which are almost simultaneously activated), (2), m. depressor mandibulae, (3) m. sternohyoideus, (4) m. submentalis, (5) m. genioglossus, (6) mm. adductor mandibulae (MATSUSHIMA *et al.*, 1985). It is surprising that the main tongue-retractor muscle, m. hyoglossus, is the one that is

activated first, and the main tongue-protractor muscle, m. genioglossus, is one of the last to be activated. However, the onset time of activity in these muscles is not correlated with the time of their peak activity. The muscles reach their maximum activity at times that are determined by their anatomical and physiological properties, and possibly by inhibitory input from interneurons onto the motor neurons that innervate them.

FUNCTIONAL MORPHOLOGY AND NEURAL CONTROL OF FEEDING IN SALAMANDERS

All terrestrial salamanders use their tongues to apprehend prey, as do frogs, but in contrast to frogs, movement of the hyolingual skeleton is essential for tongue protraction (fig. 4). The hyolingual apparatus of salamanders consists of a pair of flattened ceratohyals and a series of articulated elements including an unpaired basibranchial (first basibranchial of some authors), two pairs of ceratobranchials (hypobranchials of some authors) and one or two pairs of epibranchials (ceratobranchials of some authors). The basibranchial, typically bearing one or two pairs of relatively small radii (or cornua) near its anterior end, supports the fleshy tongue pad (fig. 4).

The main muscles associated with feeding are: (i) M. subarcualis rectus (main tongue protractor) which extends from the caudal end of the epibranchial to the ventral surface of the anterior part of the ceratohyal (fig. 4B). (ii) M. rectus cervicis profundus (main tongue retractor), which originates on the sternum and extends anteriorly to wrap around the end of the basibranchial and insert into the base of the tongue (fig. 4A). In bolitoglossine salamanders, it is folded in the gular region and becomes continuous with the m. rectus abdominis profundus, which originates on the ventral surface of the mandible and inserts on the urohyal. (iii) M. geniohyoideus medialis which arises from the ventral surface of the mandible and inserts on the urohyal. (iv) M. geniohyoideus lateralis, present in the Plethodontidae and some other groups, which arises lateral to the m. geniohyoideus medialis and extends to the anterior part of the ceratohyal. (v) M. genioglossus (tongue retractor, when present), which extends posteriorly from the ventral surface of the mandible and inserts dorsally into the rostral part of the tongue. (vi) Tongue pad muscles (e.g., m. hyoglossus, m. basiradialis and m. interradialis), which are responsible for flipping the tongue pad and for shaping the tongue. The mm. depressor and levator mandibulae connect the lower jaw to the cranium and are responsible for opening and closing the jaw, respectively.

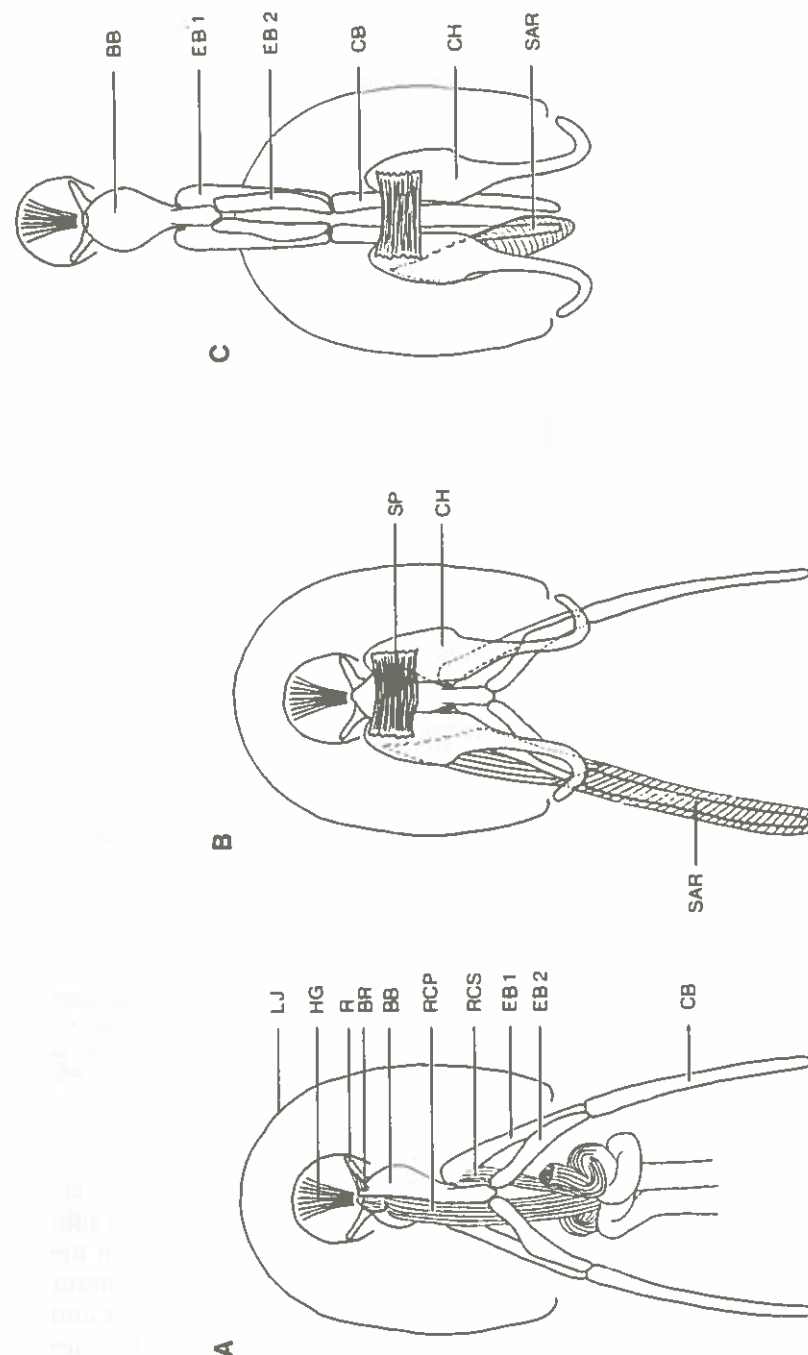


Fig. 4. Tongue skeleton and tongue projection in the plethodontid salamander *Eurycea bislineata* (dorsal views). A: Tongue skeleton at rest, with tongue-retractor muscles mm. rectus cervicis profundus and superficialis. Note coiling of the muscles in the gular region. B: Tongue skeleton at rest, with the tongue-protractor muscle m. subarcualis rectus and the m. suprapeduncularis. C: Folded tongue during protraction phase. Note strongly contracted m. subarcualis rectus. For abbreviations see list.

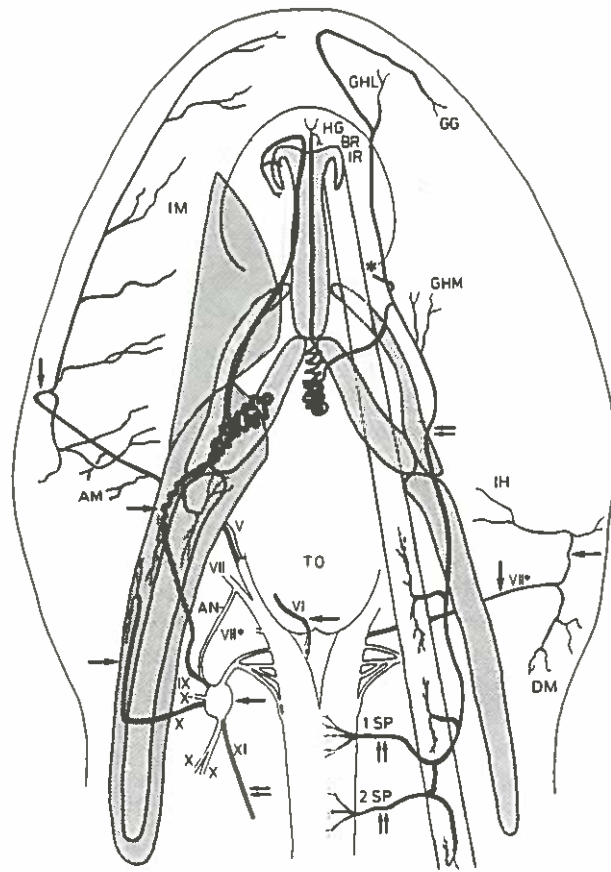
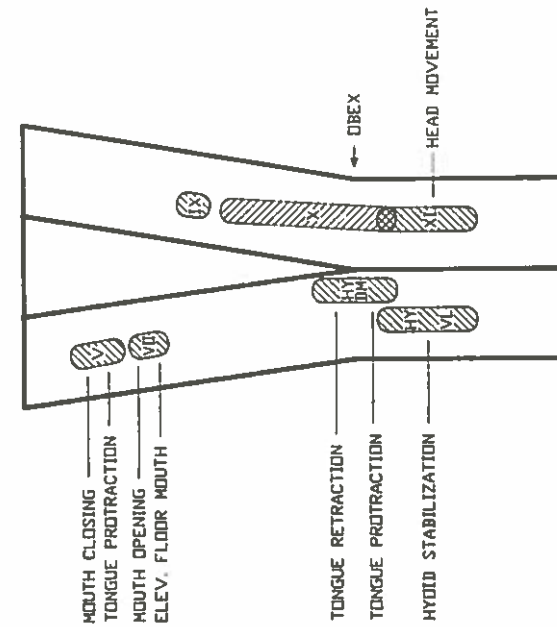


Fig. 5. Innervation pattern of the muscles related to feeding in the tongue-projecting salamander *Batrachoseps attenuatus*. The tongue skeleton (stippled), the tongue-protractor muscle SAR (left, hatched), the outlines of the brainstem and cervical spinal cord and of the tongue pad, the tongue-retractor muscle RCP (right, parallel-lined band), the course of the nn. trigeminus (V), glossopharyngeus (IX), vagus (X), accessorius (XI) (left side) and of the n. facialis (VII), the first and second spinal-nerves (right side) are shown. For abbreviations see list. From ROTH *et al.*, 1988.

As in frogs, salamander feeding is controlled by brainstem and cervical spinal nerves and nuclei (ROTH & WAKE, 1985; ROTH *et al.*, 1988; WAKE *et al.*, 1983, 1988) (figs. 5, 6). The trigeminal nerve controls the m. intermandibularis and the m. adductor mandibulae. The motor nucleus is oval in shape and is situated between the trigeminal and facial roots. Motor neurons serving the m. adductor mandibulae are

FROGS (TOAD)



SALAMANDERS (BOLITOGLLOSSINI)

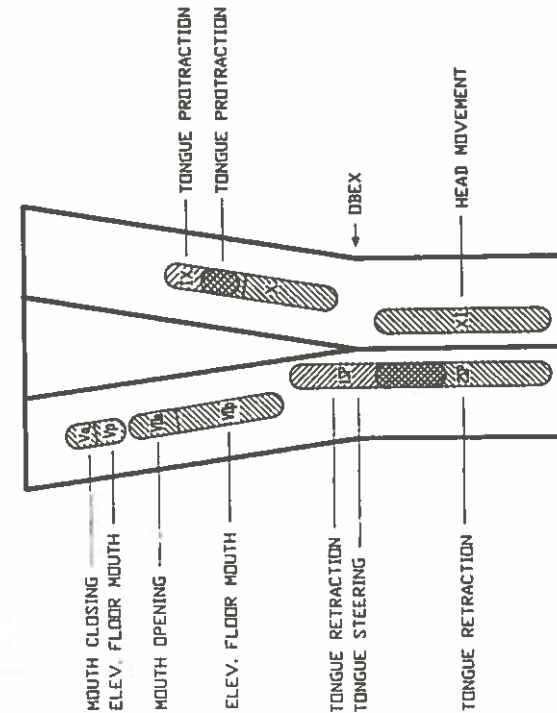


Fig. 6. Diagrammatic comparison of the arrangement of cranial and cervico-spinal motor nuclei related to feeding and their functions in salamanders and frogs.

situated in the rostral part and those innervating the m. intermandibularis are found in the caudal part of the nucleus.

The facial nerve, which innervates the m. interhyoideus and m. depressor mandibulae, has a large, elongate motor nucleus. This nucleus originates caudal to the facial root. Motor neurons innervating the m. depressor mandibulae are situated in the anterior part, and those innervating the m. interhyoideus are found in the posterior part of the nucleus (ROTH *et al.*, 1988a). In contrast to frogs, the nucleus completely overlaps the motor nucleus of the glossopharyngeal nerve and partially that of the vagus nerve. The glossopharyngeal nerve, which innervates the m. subarcualis rectus, has a nucleus that originates at the level of the first root of the IX-XI root complex and extends caudally to the second root of this complex. A small branch of the vagus nerve also innervates the m. subarcualis rectus. The motor nucleus of the vagus nerve is narrow and elongate, extending caudally to the level of the first spinal root. Its anterior subnucleus, which overlaps the glossopharyngeal nucleus, serves the m. subarcualis rectus, while the posterior part is related to parasympathetic functions.

The hypoglossal nerve is constituted either by the motor components of both the first and second spinal nerves or by those of the first alone (ROTH *et al.*, 1984; NISHIKAWA *et al.*, in prep.). The hypoglossal nerve innervates the m. genioglossus (if present), the m. geniohyoideus medialis and lateralis (if present), m. suprapeduncularis (if present), the tongue pad muscles, and the mm. rectus cervicis profundus and superficialis. The motor nucleus of the first spinal (hypoglossal) nerve is elongate in shape. It arises at the second or third root of the IX-XI complex and extends almost to the ventral root of the second spinal nerve. The second spinal nerve, in addition to its contribution to the r. hypoglossus (if any), innervates the mm. rectus cervicis profundus and superficialis and neck musculature. The motor nucleus starts at or behind the root of the first spinal nerve and extends caudally to the midpoint between the ventral roots of the second and third spinal nerves. Thus, there is considerable rostrocaudal overlap between the nuclei of the first and second spinal nerves.

As in frogs, mouth opening and closing in salamanders is controlled by the mm. depressor and adductor mandibulae, respectively. There is no m. submentalis, but the large m. intermandibularis may contract during tongue projection to raise the floor of the mouth.

In the primitive condition, found in at least some members of all families that have terrestrial adults, the tongue is attached to the mandibular symphysis by a stout m. genioglossus. This muscle restricts the distance of tongue projection, except in some species of the family

Salamandridae, e.g., *Chioglossa* and *Salamandrina*, in which the tongue is highly projectile despite the presence of a well-developed m. genioglossus (ÖZETI & WAKE, 1969; MILLER & LARSEN, 1988).

In the family Plethodontidae, three classes of tongue attachment are found (PIATT, 1935; LOMBARD & WAKE, 1977, 1986). The most primitive condition, found in the subfamily Desmognathinae and in the tribe Plethodontini, is a protrusible tongue attached to the mandible by a strong m. genioglossus (LOMBARD & WAKE, 1986). Attached projectile tongues, characterized by a somewhat to greatly elongate and slender m. genioglossus, occur in at least one species in each of the three plethodontine tribes (LOMBARD & WAKE, 1986). Free projectile tongues have evolved independently in the plethodontine tribes Hemidactyliini and Bolitoglossini. In these species there is no anterior attachment because the m. genioglossus is lost. About one-half of the living species of salamanders have free projectile tongues.

Tongue protraction of plethodontids is based on the m. subarcualis rectus which arises from the ceratohyals and extends posteriorly to wrap around the epibranchials. When this muscle contracts, the epibranchials are both pulled forward and squeezed out, and the hyolingual skeleton forms a compact projectile that is forced through a cylinder formed by the m. suprapeduncularis, which extends between the ceratohyal blades over the dorsal surface of the projectile (LOMBARD & WAKE, 1976, 1977) (fig. 4C). The m. hyoglossus protracts the tongue pad. In the more primitive condition for plethodontid salamanders, the tongue is returned to the mouth by a combination of m. genioglossus and m. rectus cervicis, but in the free-tongued salamanders (LOMBARD & WAKE, 1977, 1986) the m. genioglossus is lost and the m. rectus cervicis/abdominis complex is the sole tongue retractor.

In most tongue-projecting salamanders of the families Hynobiidae and Plethodontidae, the feeding cycle lasts from 87 to 116 ms (LARSEN *et al.*, 1989; ROTH, 1976). The fastest tongue projection (7.7 ms) occurs in members of the plethodontid genus *Bolitoglossa* (THEXTON *et al.*, 1977; BENESKI *et al.*, 1988; LARSEN *et al.*, 1989).

In all urodeles studied so far, all muscles involved in feeding are activated at the same; this is true for aquatic as well as terrestrial feeding. In both larval and metamorphosed *Ambystoma*, all muscles related to feeding start contracting within a time interval of 0.34-1 ms (LAUDER & SHAFFER, 1985). Near-simultaneity of electrical activity in the main protractor and retractor muscles was also observed in the free-tongued plethodontid *Bolitoglossa occidentalis* (THEXTON *et al.*, 1977). Despite simultaneous onset of electrical activity, the muscles reach their peak activity in a more-or-less rostrocaudal sequence

(WAKE *et al.*, 1986). Retraction (first spinal nerve) actually occurs after protraction (glossopharyngeal and vagus nerves), because the m. subarcualis rectus is under tension when the tongue is at rest, and the m. rectus cervicis must unfold in the floor of the mouth before contraction is effective in shortening the tongue.

DIFFERENCES AND SIMILARITIES BETWEEN FROGS AND SALAMANDERS

In all terrestrial salamanders, tongue projection is based mainly on forward movement of the articulated hyolingual skeleton. In contrast to salamanders, the hyolingual skeleton of most frogs is an unarticulated plate (the hyoid) which does not move during tongue protraction.

Protraction of the tongue mainly or exclusively is achieved in salamanders by contraction of the m. subarcualis rectus, that moves the tongue skeleton forward relative to the ceratohyals which are anchored to the floor of the mouth. In frogs, tongue protraction is accomplished by the joint contraction of the m. submentalis and the mm. genioglossus basalis and medialis. In salamanders, a homologue of the m. submentalis, the m. intermandibularis anterior, is present, but it plays no role in tongue protraction. Furthermore, the mandibles do not bend during feeding in salamanders, as they do in frogs. Thus, tongue protraction is based on completely different mechanisms in frogs and salamanders (tables I, II).

The salamander tongue is retracted by the mm. rectus cervicis and genioglossus, if present. In frogs, the m. sternohyoideus, homologue of the m. rectus cervicis, stabilizes the hyoid during feeding, but is not involved in tongue retraction, which is accomplished by the m. hyoglossus alone. In salamanders, this muscle functions to propel the tongue pad forward, rather than to retract it. Therefore, tongue retraction is also based on entirely different mechanisms in frogs and salamanders (tables I, II).

In salamanders, the nerves involved in feeding are: (i) the n. glossopharyngeus, and (ii) the n. vagus, which together innervate the tongue protractor, m. subarcualis rectus; (iii) the first spinal nerve, which innervates hypobranchial muscles including mm. genioglossus and geniohyoideus, muscles of the tongue tip, and the tongue retractor, m. rectus cervicis; and (iv) the second spinal nerve, which also innervates the m. rectus cervicis. The n. trigeminus is not involved in tongue protraction. In frogs, the glossopharyngeal and vagus nerves play no role in the motor control of feeding. Tongue action is controlled by only two nerves: the hypoglossal nerve, innervating the

TABLE I

Feeding action	Salamanders Muscles (nerves)	Frogs muscles (nerves)
Raising floor of mouth	IMP (V) / IH (VII)	IMP (V) / IH (VII)
Mouth opening	DM (VII)	DM (VII)
Tongue protraction	SAR (IX, X)	SM (V) / GG (XII)
Tongue pad protraction	HG (XII)	—
Tongue retraction	GG / RCP (XII, 2SP)	HG (XII)
Mouth closing	AM (V)	AM (V)

TABLE II

Muscles	Nerves	Function	
		Salamanders	Frogs
Depressor mand.	VII	Mouth opening	Mouth opening
Adductor mand.	V	Mouth closing	Mouth closing
Subarcualis rectus/ Petrohyoideus	IX/X	Tongue protraction	Breathing/Calling
Genioglossus	XII	Tongue retraction	Tongue protraction
Hyoglossus	XII	Tongue pad protr.	Tongue retraction
Intermandib. ant./ Submentalis	V	Raising mouth floor	Tongue protraction
Rectus cervicis/ Sternohyoideus	XII/2SP	Tongue retraction	Hyoid stabilization
Geniohyoideus	XII	Tongue steering	Hyoid stabilization

mm. genioglossus basalis and medialis, and the m. hyoglossus, and the trigeminal nerve, innervating the m. submentalis (tables I, II).

Frogs and salamanders show large differences in the pattern of muscle activation during feeding. In salamanders the onset of activity in muscles innervated by all four nerves involved in feeding, including the protractor and retractor muscles, is virtually simultaneous (THEXTON *et al.*, 1977; LAUDER & SHAFFER, 1985). In contrast, in frogs, even muscles innervated by the same nerve become active at different times (e.g., mm. genioglossus and hyoglossus). These results suggest that differences exist between frogs and salamanders in premotor or higher level centers involved in the neuromotor control of feeding.

ONTOGENY OF THE FEEDING APPARATUS

There remains the question of the origin of the differences reported here. Our hypothesis is that they cannot be understood primarily as the result of adaptive processes acting upon adult feeding, but as a

consequence of differences in larval feeding and breathing mechanisms. In fact, both the hyolingual skeleton of adult salamanders and the hyoid of frogs are derived from the larval hyobranchial apparatus. In amphibian larvae, this apparatus plays an important role in both breathing and feeding. However, frog tadpoles and salamander larvae differ strongly in the role the branchial apparatus plays in these two functions.

In frog embryos, the individual elements of the ancestral branchial skeleton (ceratohyals, basibranchial or copula, hypobranchials, and ceratobranchials) are present. Early in larval development, the branchial apparatus forms a basket-like structure by fusion of the different branchial elements. This fusion proceeds during later stages and finally results in nearly complete absorption of the ceratobranchials. This is accompanied by elongation of the ceratohyals into the anterior cornua of the hyoid (DE JONGH, 1968).

The great majority of anuran tadpoles are suspension feeders. Their lower jaw is relatively undeveloped, and they use the branchial apparatus to trap food particles suspended in the water (WASSERSUG & HOFF, 1979; WASSERSUG & ROSENBERG, 1979). In addition, their gills are covered by a fleshy operculum.

All salamander larvae, in contrast, are carnivorous and use gape-and-suck feeding. They possess well-developed lower jaws and have external gills supported by an articulated system, which is composed of a basibranchial, two ceratobranchials and up to five epibranchials. During metamorphosis, the epibranchials are reduced to one (most families) or two (Hynobiidae) pairs, or disappear completely, as in some salamandrids. The apparatus remains articulated and movable throughout life. All terrestrial salamanders use forward and backward movement of the tongue skeleton against the relatively immobile ceratohyal for protraction and retraction of the tongue. This is possible in salamanders only because the ceratohyals do not fuse with the basibranchial as they do in frogs.

Differences between frog and salamander larvae in the morphology and function of the gill apparatus thus determine the morphology and function of the adult feeding apparatus. In frogs, transformation of the branchial apparatus by fusion of its components into a basket-like structure essential for breathing and filter-feeding prevents this apparatus from being used for tongue protraction and retraction.

The differences between frogs and salamanders in the cranial nerves that control feeding are determined by the developmental fate of the branchial muscles during metamorphosis. At metamorphosis, most of the branchial muscles are lost. In salamanders, the most anterior m. subarcualis rectus is retained through metamorphosis and forms the

adult hyoid protractor, which is innervated by the glossopharyngeal nerve and a small ramus of the vagus nerve. In contrast, in frogs all subarcualis and constrictor muscles disappear at metamorphosis. Two to four of the levators transform into the muscles of the mm. petrohyoidei complex, the most anterior of which is innervated by the glossopharyngeal nerve while all of the more posterior m. petrohyoidei are innervated by the vagus nerve (EDGEWORTH, 1953). Thus, in frogs, the glossopharyngeal and vagus nerves do not control feeding behavior because the mm. petrohyoidei, which are the only branchial muscles that survive metamorphosis, are not hyoid protractors.

The simultaneous rostrocaudal cascade of muscle activation during feeding in adult salamanders is also observed in embryos and larvae of both fishes and amphibians (COGHILL, 1929). In frogs, loss of the subarcualis rectus muscles at metamorphosis occurs in all species. This disrupts the spatial continuity of those motor nuclei related to feeding. Because the nuclei of the glossopharyngeus and vagus nerves are no longer involved in feeding behavior, there is a gap in the "feeding brainstem" which may prevent simultaneous rostrocaudal activation from being an effective mechanism of feeding. Muscles are activated individually in frogs, and the feeding cycle takes approximately twice as long as in salamanders.

CONCLUSION

We have shown that frogs and salamanders, while possessing the same embryonic bauplan with respect to their nervous system and hyobranchial apparatus, differ dramatically in larval and adult morphology, kinematics of tongue projection, and neuromotor control of feeding behavior. Differences also are observed in the ontogenetic fate of embryonic skeletal and muscular elements, and in the biomechanics of these elements. Musculoskeletal differences between adult frogs and salamanders arise at least in part as effects of larval adaptations for feeding and breathing.

Neither the relationships between the nerves and the muscles they innervate, nor the topography of motor nuclei and sensory tracts in the brainstem and spinal cord, have been affected by the diversification in morphology and behavior among the two orders. Brainstem and spinal cord topography have been remarkably conservative during amphibian phylogenesis despite the marked diversification of the musculoskeletal elements.

The remaining question is whether or not brain centers which generate patterns of muscular activity, such as the reticular formation, have been as evolutionarily conservative as the sensory and motor

components of cranial and spinal nerves. The answer seems to be "yes" for salamanders, but "no" for frogs. Available data from salamanders show that a single motor pattern, that of near-simultaneous rostrocaudal activation of muscles, is found, despite substantial differences in the degree of specialization of the hyobranchial apparatus and in some aspects of the degree of complexity of feeding behavior. Frogs, in contrast, deviate both ontogenetically and phylogenetically from this motor pattern by developing patterns of individual activation of different muscles such that no two muscles are fully synchronous. These observations lead to the inference that integrative centers in the brain evolve in response to changes in the musculoskeletal periphery. How the central pattern generators and musculoskeletal periphery are coupled during evolutionary diversification is a fascinating question that merits further investigation.

ACKNOWLEDGEMENTS

Research on which the present paper is based was supported by DFG (to GR) and NSF (to KN and DBW).

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ABBREVIATIONS

AM = m. adductor mandibulae; AN = anastomosis between nerves VII and IX; BB = basibranchial; BR = m. basiradialis; EB = epibranchial; CH = ceratohyal; DM = m. depressor mandibulae; GG = m. genioglossus; GGB = m. genioglossus basalis; GGM = m. genioglossus medialis; GHL = m. geniohyoideus lateralis; GHM = m. geniohyoideus medialis; H = hyoid; HG = m. hyoglossus; IH = m. interhyoideus; IM = m. intermandibularis; IMP = m. intermandibularis posterior; IR = m. interradians; LJ = lower jaw; OH = m. omohyoideus; PH = m. petrohyoideus; R = radii; RCP = m. rectus cervicis profundus; RCS = m. rectus cervicis superficialis; SAR = m. subarcualis rectus; SH = m. sternohyoideus; SM = m. submentalis; SP = m. suprapruncularis; T = tongue muscle; TO = tectum opticum; V = nervus/nucleus trigeminus; VI = nervus abducens; VII = nervus/nucleus facialis; IX = nervus/nucleus glossopharyngeus; X = nervus/nucleus vagus; XI = nervus nucleus accessorius spinalis; XII = nervus/nucleus hypoglossus/1st spinal nerve; 2SP = 2nd spinal nerve.