The Evolution of Feeding Motor Patterns in Lizards: Modulatory Complexity and Possible Constraints[1]

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SYNOPSIS. Previous research indicated that the evolution of feeding motor patterns across major taxonomic groups might have occurred without large modifications of the control of the jaw and hyolingual muscles. However, the proposal of this evolutionary scheme was hampered by the lack of data for some key taxa such as lizards. Recent data on jaw and hyolingual feeding motor patterns of a number of lizard families suggest extensive variability within and among species. Although most lizards respond to changes in the structural properties of food items by modulating the activation of the jaw and hyolingual muscles, some food specialists might have lost this ability. Whereas the overall similarity in motor patterns across different lineages of lizards is large for the hyolingual muscles, jaw muscle activation patterns seem to be more flexible. Nevertheless, all data suggest that both the jaw and hyolingual system are complexly integrated. The elimination of feedback pathways from the hyolingual system through nerve transection experiments clearly shows that feeding cycles are largely shaped by feedback interactions. Yet, novel motor patterns including unilateral control seem to have emerged in the evolution from lizards to snakes.

INTRODUCTION

The vertebrate head is a textbook example of a complex integrated system, where one function cannot be optimised without potentially compromising others (Lauder, 1989). In addition to being a major information gathering and processing centre, immensly diverse functions such as feeding, breathing, drinking, display, and in many tetrapods also vocalisation, have to be performed by the same elements. Yet, these diverse functions can only be performed through the interplay between the jaw and hyolingual systems. Both these systems are complex units composed of a large number of muscles attached to bony or cartilagenous elements. Moreover, as the hyolingual apparatus is a musculoskeletal system suspended between the jaws and the pectoral girdle, the potential number of degrees of freedom is enormous. To add to this complexity, both systems are largely innervated through different pathways. Whereas the jaw adductor system in lizards is mainly innervated by the trigeminal and facial nerves (providing both motor input and sensory afferents), the hyolingual system is mainly supplied by the glossopharyngeal (largely sensory), hypoglossal (predominantly motor input) and first spinal nerves (motor input into the hyoid retractors; Willard, 1915; Oelrich, 1956; Meyers and Nishikawa, 2000). Direct connections between the two systems exist, as the mandibular ramus of the n. trigeminus provides motor input into the m. intermandibularis (running inbetween the two rami of the lower jaw) and branches out into the tongue functioning as sensory afferent and physically connecting to the *N.* hypoglossus. Feedback from the visual, olfactory, gustatory, vomeronasal and somatosensory (*e.g.,* muscle spindles, joint receptors) systems are also important in assuring optimal feeding.

Given this structural complexity, the control of the feeding apparatus is a complex task which appears to require continuous on-line control. Yet, for cyclical systems in

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general, a simple neuromotor steering based on a centralised pattern generator (or a set of coupled CPG's) is thought to exist, thus largely simplifying control (*e.g.,* Grillner and Wallén, 1985; Székely, 1989). Although this paradigm is largely based on studies on the locomotor apparatus, a similar control paradigm is usually put forward for mammalian chewing cycles (Thexton, 1974, 1976; Dellow, 1976). In accordance with this theoretical framework, it has been suggested that in lower tetrapods too, the feeding cycles might be driven by fairly simple motor pattern generators or neural oscillators (Bramble and Wake, 1985).

Based on the large similarities between lower tetrapod and mammalian feeding cycles, it was hypothesized that the evolution of feeding motor patterns across major taxonomic groups might have occurred without large modifications of the central pattern generator(s) controlling the jaw and hyolingual muscles (Bramble and Wake, 1985). The basic elements of the lower tetrapod feeding cycle were summarised in a theoretical model feeding cycle which was hypothesised to represent the primitive tetrapod condition. In analogy to the mammalian feeding cycle, the model feeding cycle was subdivided into five distinct phases: the slow opening of the jaws (I and II), fast opening, fast closing and a slow closing/ power stroke. Muscle activation patterns associated with these kinematic units were proposed as well. Whereas the slow opening phase was thought to be caused by an activation of the jaw opener, intrinsic tongue muscles, the intermandibularis group and the tongue and hyoid protractors, during fast opening coactivation of the cervical epaxial musculature, the jaw opener and hyoid retractors was expected to occur. Jaw closing on the other hand was thought to be associated with activity in the hyoid retractors (fast closing), jaw adductors and potentially the jaw opener (Bramble and Wake, 1985).

However, the support for this evolutionary scheme was substantially weakened by the lack of data for some key taxa such as lepidosaurians. At the time data on motor patterns were available for only six out of over 7,000 species of lepidosaurians:

Sphenodon punctatus (Gorniak *et al.*, 1982), *Uromastix aegyptius* and *Iguana iguana* (Throckmorton, 1976, 1978, 1980), *Ctenosaura similis* and *Tupinambis nigropunctatus* (Smith, 1984), and *Varanus exanthematicus* (Smith, 1982). The importance of the model can be best appreciated by looking at the rapid increase in the number of studies investigating feeding in previously largely unstudied groups such as lizards (Fig. 1).

In the current paper we evaluate the Bramble and Wake (1985) model based on recent literature dealing with feeding motor patterns in lizards, and will discuss which components thereof appear evolutionarily conserved and which not. The results of nerve transection experiments and their importance to the theory of motor pattern evolution will be discussed as well.

Discussion

Feeding is a complex behaviour consisting of several distinct stages. It is initiated by an exploratory phase where a food item has to be located. The capture or ingestion of a food item is the first step where the jaw and hyolingual apparatuses come into play (although the chemosensory location of prey by many scleroglossans also involves both the jaw and hyolingual apparatuses, see Cooper, 1994; Schwenk, 1995). Next, a series of reduction (crushing) cycles, interspersed with repositioning and transport cycles occurs (together comprising the intraoral transport stage, Bramble and Wake, 1985). Once the food has been adequately reduced, it is transported to the back of the oral cavity and the swallowing can start. Subsequently, the bolus is transferred to the digestive tract where it is chemically reduced.

Clearly, it is essential in any comparative study to compare similar events across different taxa. As the model feeding cycle was proposed for chewing and transport, and as sufficient evidence exists that these cycles differ from capture and swallowing cycles (Schwenk and Throckmorton, 1989; Kraklau, 1991; Delheusy and Bels, 1992; So *et al.*, 1992; Urbani and Bels, 1995; Herrel *et al.*, 1996; Delheusy and Bels, 1999; Schwenk, 2000), and might even be gov-
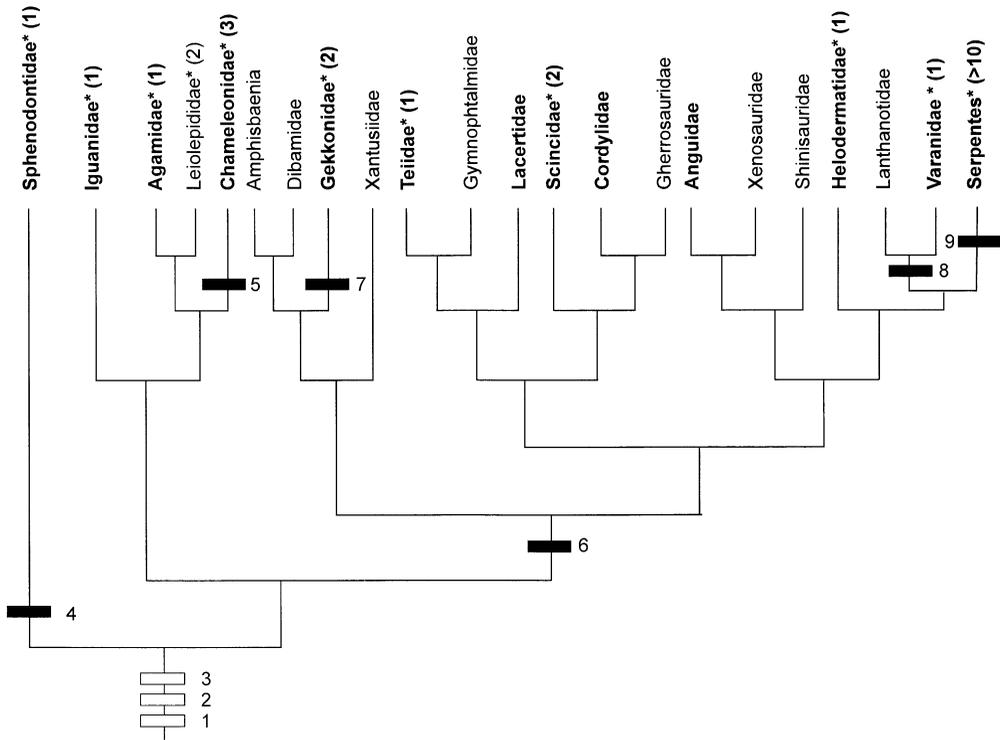
FIG. 1. Cladogram showing the relationships of extant lizard groups (modified after Estes *et al.*, 1988; Lee, 1998; Macey *et al.*, 1999; Donnellan *et al.*, 1999). Taxa for which kinematic data are available are indicated in bold; taxa for which electromyographic data are available are indicated by an asterisk. The numbers in between brackets indicate the number of species for which electromyographic data are available. Primitive features of the lizard feeding system are indicated by white bars, and evolutionary novelties in control are indicated by black bars. 1, extensive intraoral processing and transport; 2, the use of the hyolingual apparatus in prey transport; 3, bilaterally simultaneous activation of the jaw and hyolingual muscles; 4, a mammal-like power stroke presumably arose within the rhynchocephalian lineage; 5, the development of ballistic tongue projection and the modification of the tongue protraction system; 6, the specialisation of the tongue for chemoreceptive purposes; 7, the origin of a highly kinetic skull; 8, the aquisition of a kinetic inertial transport mode; 9, unilateral control of the jaw musculature.

erened by a differing descending control (Smith, 1984; Herrel *et al.*, 1997a), we consider here only the characteristics of chewing and transport cycles.

One of the essential steps in a comparative analysis of feeding motor control is to determine the amount of within-group variance (*e.g.,* Shaffer and Lauder, 1985a, b). Consequently, the investigation of variability in feeding motor patterns has been an essential part of most recent studies (*e.g.,* Herrel *et al.*, 1996, 1997a, 1999a; Herrel and De Vree, 1999; Delheusy *et al.*, 1999; see Schwenk, 2000 for an overview). By examining the kinematic and muscular activation patterns for the jaw and hyolingual systems in response to different food items,

the amount of variability and the modulatory capacities of the organisms under study can be quantified. So far extensive modulatory capacities have been demonstrated in members of both the Iguania (Throckmorton, 1980; Schwenk and Throckmorton, 1989; Herrel *et al.*, 1996, 1997a) and Scleroglossa (Bels and Baltus, 1988; Goosse and Bels, 1992; Delheusy *et al.*, 1995; Urbani and Bels, 1995; Herrel *et al.*, 1997b, 1999a; Herrel and De Vree, 1999; Delheusy and Bels, 1999). Variation in movement patterns has been shown to be fairly extensive in most species, and usually affects both jaw and hyolingual systems (although few quantitative data on hyolingual movement patterns exist due to lack of
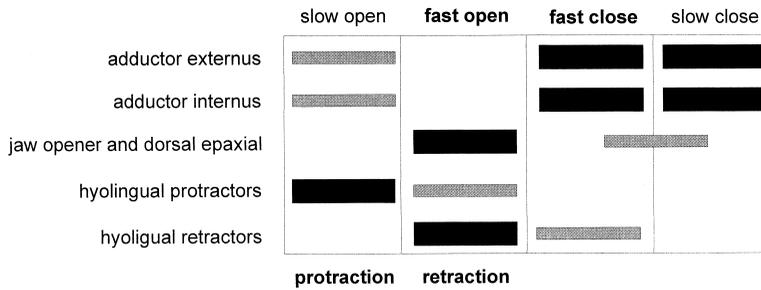
FIG. 2. Summarizing block diagram showing the components of the jaw and hyolingual activation patterns that appear "conserved" across major lizard groups. Elements in black or bold face have been observed throughout all intraoral transport cycles in all species studied. Grey bars represent activity that has been observed in all species studied, but for which a lot of cycle-to-cycle variation exists, and which may be absent in some intraoral transport cycles.

cineradiographic studies). In general, both the maximal excursions of different elements of the jaw and hyolingual systems as well as the duration of kinematic phases are modulated (Urbani and Bels, 1995; Herrel et al., 1996; Delheusy and Bels, 1999; Herrel et al., 1999a). Unfortunately, hardly any data are available on the effect of food type on the activation patterns of the jaw and hyolingual muscles. Only Herrel et al. (1999a) have explicitly investigated this in a quantitative way. Their results show that whereas differences in the intensity of muscular contraction are large, the timing of activation of the jaw muscles does not seem to change markedly. Similarly, data on muscle activation patterns in H. horridum (Herrel et al., 1997b) show distinct modulation of the activation pattern of the jaw adductors for different types of transport and crushing bites (for a single food item). Again, differences are largely situated in the intensity of the activation rather than affecting the temporal characteristics.

One interesting exception on the general observation that modulatory capacities are extensive, was noted for the herbivorous lizard Uromastix acanthinurus (Herrel and De Vree, 1999). Statistic analysis of both kinematic (Herrel and De Vree, 1999) and electromyographic (unpublished) data indicated no differences between grasshopper and endive intraoral transport cycles, despite the large differences in prey characteristics (mechanical properties, weight, moveability, etc. . . .) which readily result in differences in movement and motor patterns

in other species of lizards (Herrel et al., 1999a). The extreme dietary specialisation of U. acanthinurus might thus have led to a reduced functional versatility and flexibility (sensu Ralston and Wainwright, 1997) in this species. Further research on species with an extensive dietary specialisation should be conducted to test the generality of this finding for lizards.

Despite the large variability observed within and among species, some elements of the feeding cycle in lizards do appear to be conserved and corroborate parts of the Bramble and Wake (1985) model (Fig. 2). In all species examined slow opening phases are present, but this is clearly food type dependent and SO phases do not always occur in every cycle (e.g., see Delheusy and Bels, 1992, 2000; Herrel et al., 1999a; Herrel and De Vree, 1999; Schwenk, 2000). During this phase the fitting of the tongue to the prey occurs (ensuring an effective subsequent backward prey transport), hence this phase is related to, and might even be determined by, anterio-dorsad tongue movements (see Bramble and Wake, 1985; Herrel et al., 1997a). Consequently, heavier or larger food items result in more pronounced slow open phases, and inertial transport cycles generally show a lack of slow open phases altogether (Smith, 1982, 1986; Elias et al., 2000). The delimitation of the slow open phase is thus largely based on tongue, rather than jaw movements. Correspondingly, it is characterised by distinct activity in the hyolingual protractors (including the m. hyoglossus in iguanians) and

a variable, but always low intensity activity in the jaw openers and closers. Similarly, the fast opening phase is most easily characterised as starting at the moment of tongue retraction and ending at maximal mouth opening. A marked increase in mouth opening velocity between slow and fast opening phases is not always evident and is again largely prey type dependent. Still, this phase can be delimited fairly well on the basis of its EMG signature consisting of a distinct high level activity burst in the jaw opener and the dorsal epaxial muscles. Fast closing is probably the only phase that can be consistently defined on the basis of external jaw movements. In all species examined it starts at maximal gape and lasts until the sudden decrease in closing velocity, associated with prey contact. This phase is characterised by distinct bilateral activity in all major jaw closers (both adductor externus and internus groups). The slow closing/power stroke phase is again largely prey type dependent, but when present it is very clearly characterised by a bilaterally simultaneous activity burst in all jaw closer groups. Occasionally distinct jaw opener activity bursts, presumably serving to stabilise the jaw joint, are also present during slow closing (*e.g.,* see Herrel *et al.*, 1997*a*, 1999*a*). Obviously slow closing phases are only present when 1) the food is situated between the tooth rows, and 2) when the animal is actually crushing the food item. For some food items such as leaves which are flat, and ants which are typically small, the slow closing phase cannot be distinguished on the basis of external jaw movements. However, EMG recordings always allow an unambiguous delimitation of this phase when present.

Motor pattern evolution within lepidosaurians

Within lepidosaurians several distinct evolutionary trends can be observed. Although probably a derived rhynchocephalian character, a true mammalian-like power stroke is only present in *Sphenodon punctatus* (Gorniak *et al.*, 1982) and is not present in extant lizards. As mentioned earlier, in lizards a slow closing phase associated with distinct jaw closer activity exists, but

consists of bringing the toothrows together in the vertical plane. Although no horizontal grinding-like movements have been observed, some streptostylic lizards (such as *Uromastix* and geckoes) do show a posterior movement of the lower jaw associated with mouth closing (Herrel *et al.*, 1999*b*; Herrel and De Vree, 1999; Schwenk, 2000). However, the majority of the movement in these animals occurs during fast closing, which is clearly different from the propalineal or transverse power stroke in *Sphenodon* and mammals, respectively (Gorniak *et al.*, 1982; Weijs, 1994). The specialisation of the chameleon tongue for ballistic projection has also clearly affected its intraoral transport mechanism. Due to the reduction or loss of genioglossus muscles (major tongue protractors in iguanians) tongue protraction has to be achieved by other means. The intrinsic musculature (accelerator muscle) specialised for prey capture (Wainwright and Bennett, 1992*a, b*) is used during intraoral transport and pushes the tongue forward (personal observation). In agamids, the homologous muscle also functions to move the tongue forward, assisting the major tongue protractors (Herrel *et al.*, 1997; Meyers and Nishikawa, 2000). Remarkably, the loss of the tongue protractors in chameleons has not affected the external feeding kinematics (So *et al.*, 1992).

One of the striking evolutionary transformations within lizards is the specialisation of the tongue for chemoreceptive purposes. This chemosensory specialisation of the hyolingual apparatus in the more derived scleroglossan lineages has resulted in a decrease of the use of the tongue during transport, among other things (Schwenk, 2000). In some groups such as varanids, kinetic inertial transport (Gans, 1969) becomes the predominant feeding mode. As the importance of the tongue during transport decreases in these animals, the persistence of a slow open phase does too. Remarkably, antero-posterior tongue movements are retained in these highly specialised animals (Smith, 1986; Elias *et al.*, 2000; but see Schwenk, 2000). Although the tongue presumably helps to position the prey for subsequent intraoral transport, the

retention of this pattern might be the result of an intrinsic underlying pattern.

The most striking novelty that occurred in the evolution of lepidosaurian feeding systems is undoubtably the static inertial feeding mode of macrostomatan snakes (Gans, 1969). The evolution from a typical lacertilian tongue-based transport cycle to the highly specialised pterygoid walk associated with static inertial feeding in snakes (*e.g.,* Cundall and Gans, 1979; Kardong, 1986; Cundall and Greene, 2000), has been accompanied by the integration of an entire suite of novel characters (Kardong *et al.*, 1997; Cundall and Greene, 2000). The most drastic change in control is likely the change from a bilaterally simultaneous to a unilateral, alternating activation of the associated musculature. Within lizards, only in varanids (putatively the closest living relatives to snakes; Lee, 1998) are there some indications for unilateral activation of the jaw musculature (Smith, 1982). However, there is the possibility that bilaterally asymmetric control of the jaw muscles is a primitive feature for squamates (Cundall *et al.*, 1987). Although asymmetric activation of the jaw muscles in *Varanus* would nicely reflect a first step in a transformation series leading to the highly specialised snake prey transport system, it is necessary to confirm this finding, as the functional basis for unilateral activation in varanids remains unknown. Whether novel motor patterns including unilateral control emerged in the evolution from lizards to snakes or within the radiation of snakes therefore remains unknown. Information on the use of the feeding system in scolecophidians (basal snakes) and primitive alethinophidian snakes is clearly crucial in this respect (but see Kley and Brainerd, 2000; Cundall and Greene, 2000).

Stereotypy, conservation, and constraint?

Some elements of the feeding cycle appear to be conserved across lizards. Notably, we see hyolingual protractor activity during slow opening, jaw opener and dorsal epaxial muscle activity during fast opening, bilateral contraction of all jaw closer groups during fast closing, and bilaterally simultaneous, co-activation of all jaw closers during the slow close phase (Smith, 1982, 1984, 1986; Gans *et al.*, 1985; Herrel *et al.*, 1997a, b, 1999a, b). The limited amount of information available for jaw and hyolingual muscle activation patterns suggests that the overall amount of variation is larger for the jaw closer muscles compared to the hyolingual muscles. However, as quantitative data on hyolingual muscle activation patterns are scarce (Herrel *et al.*, 1997a, unpublished) this should be confirmed by further research.

Whether the similarities in the feeding cycle of lizards noted above are the expression of an intrinsic pattern is an important question in the debate on motor pattern evolution. As Smith (1994) discussed in her influential paper, similarities in these patterns need not always be the expression of a conserved intrinsic pattern. Simple functional or physical constraints (*e.g.,* the need to open the mouth before it can be closed, or to protract the tongue before it can be retracted) definitely come into play during feeding, and might be important in causing some of the observed similarities. Nonetheless, there is some evidence for the existence of an underlying basic pattern (see also Schwenk, 2000). One line of evidence can be found in the case of dietary specialists. The lack of modulation in jaw and hyolingual movement and motor patterns when confronted with differing prey types points to a (at least partially) centrally controlled pattern. A more convincing case, perhaps, is the retention of the typical antero-posterior movements of the tongue and hyobranchium in inertial feeders such as varanids (Smith, 1986). In this case, a novel behaviour (inertial transport) is associated with a primitive feature (antero-posterior movements of the hyolingual apparatus), without a functional constraint being evident (hyolingual movements are not essential during inertial feeding). This suggests the retention of an intrinsic control pattern. Nerve transection experiments might help to solve this question. By eliminating feedback pathways (through transection of sensory afferents, see below) a basic, stereotyped pattern of jaw and hyolingual movement, regardless of food type, should emerge.

Plotting the apparently conserved elements on a phylogeny (Fig. 1), shows that many of these are primitive characters originated early-on in the evolution of lepidosaurians. If these elements are the expression of a conserved control pattern, then their retention clearly did not constrain the further trophic evolution of squamates. Evolutionary novelties associated with the development of ballistic tongue projection (Herrel *et al.*, 1995; Wainwright and Bennett, 1992*a*, *b*), specialisation of the hyolingual system for chemoreception in anguinomorphs (Schwenk, 2000), the extremely kinetic skulls of geckoes (Herrel *et al.*, 1999*b*, 2000) and the unilateral feeding mechanism of macrostomatan snakes (Cundall and Greene, 2000) have clearly been extremely succesful (Fig. 1).

One control strategy emerging from all studies conducted so far is complex and fine-tuned integration of the jaw and hyolingual systems. This implies that changes in one system must be correlated to changes in the other system. This can be achieved in three, not mutually exclusive, ways: (1) Both systems are centrally controlled and coordinated, and changes in the descending control result in a modified, but highly integrated output; (2) Systems influence each other through continuous feedback which also results in a highly integrated output; (3) The system is fine-tuned by its own intrinsic dynamics as has been suggested for locomotor systems (Kugler and Turvey, 1987; Holt *et al.*, 1990).

In order to shed some light on this question we recently performed the first of a series of experiments using nerve transection techniques, involving the elimination of feedback pathways. As noted earlier, the jaw and hyolingual systems are largely controlled through different nervous pathways. However, sensory afferents from the jaw (trigeminal) and hyolingual (mainly glossopharyngeal) systems carry information from a variety of sensory receptors back to the brainstem, where the information can be integrated and used to modulate the next cycle. Although a variety of potential feedback sources is thus present, it has been postulated that an important source of information regarding the food item (position,

state of reduction, taste, . . .) is the tongue, when positioned against the prey during the slow open phase of the jaw cycle (Bramble and Wake, 1985; Herrel *et al.*, 1996, 1997*a*). We thus decided to eliminate feedback pathways from the hyolingual to the jaw system. First step, the mandibular ramus of the trigeminal (which is known to function as a sensory afferent and is physically connected to the hypoglossal system) was transected unilaterally and bilaterally under anaesthesia in three individuals of the agamid lizard *Pogona vitticeps* (see Meyers and Nishikawa, 2000 for technical details on nerve transections in lizards). By comparing feeding bouts (kinematics) of these animals before and after transection we could quantitatively assess the importance of feedback in modulating the feeding cycle. Before transection, the animals were filmed while feeding on prey with largely differing mechanical and behavioural characteristics (ants, crickets, isopods and endive). All individuals clearly responded to the changes in prey type before surgery resulting in large statistical differences in global feeding kinematics (Rao's $R_{12,69}$ = 13.03; $P < 0.0001$). After surgery, all animals readily ate all prey types offered, and again different prey types resulted in large differences in feeding kinematics (Rao's $R_{12,69}$ = 9.57; $P < 0.0001$). Analysis of a unilateral transection revealed no effects of the surgery on feeding kinematics. However, feeding kinematics after bilateral transection differed strongly from normal feeding (Rao's $R_{4,60}$ = 8.48; $P < 0.0001$). The most striking differences were an increase in cycle duration, an increase in the number of intraoral transport cycles, and an increase in the duration of the entire feeding bout for all prey items. Thus, our nerve transection experiment shows that feeding cycles are shaped by feedback interactions from the hyolingual to the jaw system. Further experiments in which both trigeminal and glossopharyngeal sensory afferents are transected are planned, and should enable us to investigate the presence of an intrinsic control pattern (see above).

Although enormous progress in our knowledge of lizard feeding systems has been achieved since the proposal of the

Bramble and Wake model in 1985, many questions still remain unanswered. The Bramble and Wake model seems to be supported by the available data to some degree, indicating a central control of the feeding system. Yet, nearly all lizards studied are capable of, and do modulate feeding cycles to a large degree. Comparative data on many more species of lizards are badly needed to be able to test the generalities of previously proposed hypotheses (see also Schwenk, 2000). Especially groups such as cordylids, lacertids, gymnophtalmids, dibamids and amphisbaenids require more attention. The function and use of the hyolingual system during feeding remains largely unstudied to date and cineradiographic studies on virtually all groups (so far only a few iguanians, varanoids, two geckoes, two scincids and one teiid have been studied) would be extremely valuable for our understanding of evolutionary patterns. We also foresee important insights to be gained from transection studies, and would encourage other workers to use similar approaches to this interesting field of research.

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