

**Reprint**

Publisher: S. Karger AG, Basel  
Printed in Switzerland

**Original Paper**

Brain Behav Evol 1994;43:293-305

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# Are Neuromotor Systems Conserved in Evolution?

**Key Words**

Neuromotor evolution  
Neuromuscular function  
Homology  
Feeding mechanisms  
Vertebrate

**Abstract**

Hypotheses that neuromotor systems are conserved during evolution are examined. Focus is on the fundamental assumption underlying such hypotheses, that neuromotor patterns are homologous. The criteria for testing hypotheses of homology are briefly reviewed and applied to several cases in which neuromotor conservatism has been proposed. It is concluded that few studies of neuromotor conservatism are complete enough to convincingly corroborate a hypothesis of homology. Particular problems include an absence of specific definitions of the parameters designating the conserved neuromotor pattern and the lack of sufficiently broad and detailed phylogenetic tests. The hypothesis that terrestrially feeding vertebrates exhibit a conservative feeding program, which has acted as a constraint in evolution, receives particular attention and it is concluded that existing data do not support this hypothesis.

**Introduction**

During the evolution of skeletal and muscular systems, modification of peripheral structures must be coordinated with changes in their neural control. Studies of the evolution of vertebrate systems have traditionally focused on musculoskeletal alterations and have assumed that changes in neuromotor patterns follow. Recently a number of authors have pointed out that transformations of the patterns of musculoskeletal activity and function during phylogeny or ontogeny may be produced by changes in peripheral structures, changes in motor pattern, or both [e.g. Bramble, 1980; Bramble and Wake, 1985; Dial et al., 1991; Goslow et al., 1989; Hiiemae et al., 1978; Jenkins and Goslow, 1983; Lauder and Shaffer, 1988; Liem, 1984, 1990; Peters and Goslow, 1983; Reilly and Lauder, 1990; Roth and Wake, 1989; Schwenk and Throckmorton, 1989; Wainwright et al., 1989]. Several investigators have observed that in many cases peripheral systems such as muscles,

bones and teeth seem to undergo marked change, but the motor pattern, as reflected in kinematics or electromyography, appears to remain relatively unchanged. These observations have led to a proposal that neuromotor patterns are conserved in evolution and may produce constraints on the evolution of musculoskeletal systems [e.g. Liem, 1984, 1990; Bramble and Wake, 1985; Lauder and Shaffer, 1988; Roth and Wake, 1989].

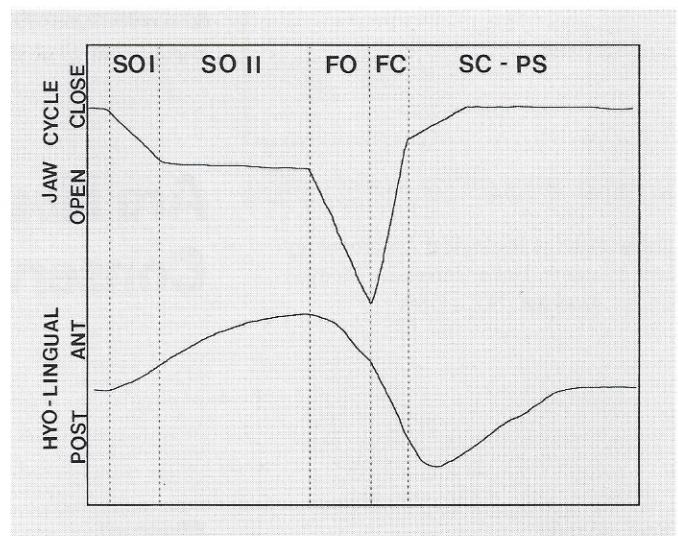
Two examples demonstrate the emergence of these hypotheses of neuromotor conservatism. In the first, Lauder and Shaffer [1988] compare the motor patterns in pre- and post-metamorphic amphibians feeding in water and on land. Although the head and hyobranchial apparatus change in form during metamorphosis (most significantly the gills are lost), the authors point out that the major muscle masses and their lines of action undergo relatively little change. In both pre- and post-metamorphic individuals, suction feeding is used in aquatic prey capture, but the 'design' of the aquatic feeding system differs: flow is unidirectional in pre-



metamorphic animals (i.e., it passes in the mouth and out the gills), whereas it is bidirectional in post-metamorphic animals (passes both in and then out through the mouth). Although the design difference produces a decrease in performance in post-metamorphic animals, the kinematics of prey capture are similar in the two. Lauder and Shaffer analyze electromyographic patterns and find that activity patterns of muscles in aquatic feeding are not significantly different in the pre- and post-metamorphic individuals; thus there is no change in motor pattern associated with metamorphosis per se. Metamorphosed individuals also feed on land using tongue projection for prey capture, and during this behavior both the kinematics and motor patterns change significantly from the larval condition. Lauder and Shaffer conclude that because motor patterns do not change in aquatic feeding across metamorphosis, 'motor patterns are conserved during the origin, either in ontogeny or phylogeny of behavioral novelties' (p. 263).

The second example concerns the similarity in the movement profiles of the jaw, tongue and hyoid during food transport in some reptiles, especially turtles and lizards, and in many mammals [see Bramble and Wake, 1985; Hiiemae and Crompton, 1985; Crompton, 1989, for reviews]. A four-phase jaw cycle, consisting of slow opening, fast opening, fast closing and slow closing, is proposed as a generalized or primitive feeding cycle. In a number of taxa, the tongue and hyoid move forward during the slow opening phase; they move back during fast opening and then begin to move forward again during closing phases [Hiiemae et al., 1978; Smith, 1984; Bramble and Wake, 1985; Hiiemae and Crompton, 1985]. The similarity of jaw, tongue and hyoid movements in these diverse taxa has been interpreted as evidence supporting the existence of an underlying, conservative neuromotor control pattern in vertebrate feeding (fig. 1). Bramble and Wake [1985] speculate that the mammalian masticatory cycle may have evolved from the primitive chewing cycle of reptiles with relatively little change in neuromotor programming and suggest that 'the evolution of the complex mammalian masticatory system was accomplished through minimal change in associated neuromotor mechanisms but relatively enormous alterations in the peripheral feeding structures (bones, muscles, dentition).' (p. 242)

The aim of the above proposals of conservative neuromotor patterns is not to describe similar behavioral patterns in different taxa, but instead is to define a character, the neuromotor pattern, that has an independent evolutionary history and can provide a source of constraint or directionality in evolution. 'In contrasting terrestrial vertebrates with aquatic feeding of fishes, Liem [1984] has commented that



**Fig. 1.** The model of the preprogrammed feeding system redrawn from Bramble and Wake [1985]. The upper tracing shows the hypothesized jaw cycle and the lower tracing illustrates the predicted movement of the hyo-lingual apparatus during this cycle. Vertical dotted lines indicate phases. Abbreviations: SO I and SO II, slow open I and II; FO, fast open; FC, fast close; SC-PS, slow close – power stroke. Note the hypothesized correlation between the anterior-most extent of hyo-lingual movement and the transition between SO and FO.

tetrapods rely on a very restricted neuromuscular 'software', while jaws, teeth, skulls, and muscles have evolved as specialization proceeded... This has led to the evolution of much higher degrees of feeding specialization (by which we mean restriction in diet in terms of taxa, size, quality, etc.) in tetrapods than seen in fishes. Perhaps this specialization arises as an evolutionary consequence of the relative constancy of the preprogrammed oscillations and jaw movements found in tetrapods [Liem, 1984]. This example shows that a constraint at one level can lead to evolutionary diversification at other levels of organization within a major lineage.' [Roth and Wake, 1989, p. 10].

Observations of similarities in movement patterns thus have passed from descriptions, to hypotheses of neuromotor conservatism, to assertions of evolutionary constraints. However, few studies have discussed how these hypotheses of neuromotor conservatism may be corroborated or refuted. In this review I discuss the evaluation of such hypotheses. The argument centers on the fact that a hypothesis of a conservative neuromotor pattern during evolution is first a hypothesis that the neuromotor patterns are homologous. My discussion focuses on the evaluation of such hypotheses of homology and I discuss three general issues: the testing of the hypothesis of homology through the criteria of



similarity and phylogenetic congruence; the particular difficulties in defining a character such as a 'neuromotor program'; and finally, the evaluation of alternative hypotheses to explain similarity across taxa.

### The Hypothesis of Homology

The definition of homology and the criteria necessary for its testing have received renewed attention in the past decade [e.g. Cracraft, 1981; Patterson, 1982; Van Valen, 1982; Roth, 1984, 1988, 1991; Kluge and Strauss, 1985; Striedter and Northcutt, 1991; Wake, 1991, and references therein]. Behavioral and neurobiological approaches to homology have also received attention in a number of papers [e.g. Hodos, 1976; Lauder, 1986; Baker, 1991; Bass and Baker, 1991; Paul, 1991; Wenzel, 1992]. Although many aspects about the identification and assessment of homologous characters remain controversial, most authors agree that homology applies to a character with some degree of genetic or developmental autonomy and reflects a common inheritance from an ancestral condition. Likewise, it is commonly accepted that the testing of hypotheses of homology involve, first, the recognition of similarity (be it similar form, position or ontogeny) and, second, congruence of the hypothesis of homology with a phylogenetic hypothesis.

#### *Similarity*

The use of similarity in assessment of morphological homology is generally regarded as an initial test and usually relies on shape, connections, developmental pattern or mechanism, and so on. The aim of the similarity test is the recognition of possible homologies, and the development of information on character complexity and detail so that spurious and superficial similarities can be eliminated before further analysis proceeds. For example, it is not sufficient to claim that bony foramina found in two taxa are homologous because they look the same. Details such as the bones in which the foramina lie, the structures passing through the foramina, and the ontogeny of the foramina and surrounding structures provide data with which to assess the hypothesis of homology. Such details are critical in order to be confident that a unique character has been defined, and that this character possesses some degree of developmental and evolutionary independence.

Bass and Baker [1991] provide a model for studying the homology of neuromotor traits in their study of vocal control systems in fish. This study not only is placed within a well-defined phylogenetic context (see below), but also

focuses on a complex, well defined coadapted suite of traits in order to formulate hypotheses regarding the extent to which phylogenetic factors contribute to the neural design of motor systems. Bass and Baker map nine characters including peripheral organs (e.g. the sound producing organ and its muscles), nervous pathways (e.g. peripheral nerves and central nuclei), neurophysiological traits (e.g. firing pattern), and patterns of variability. In this study the homology of vocal sonic motor systems is assessed by careful and detailed study; the extent to which it is constrained or patterned by evolution is examined in a phylogenetic context. Neither the homology nor the phylogenetic constraint is assumed. Other examples of assessments of homology of neurobiological traits are found in the same volume including Baker [1991] and Paul [1991].

In most of the examples discussed in the introduction, the hypothesis that neuromotor patterns are homologous has arisen out of observations that kinematics or electromyographic activity appear similar in two or more taxa or developmental stages. Few of these studies either define the character in sufficient depth and detail to make it clear that a unique character is being considered, or provide sufficient criteria to objectively confirm or refute the hypothesis that the characters are homologous across taxa.

One way in which similarity of motor pattern can be rigorously and objectively assessed is to test the statistical similarity of either kinematics or muscle activity patterns. Such tests provide specific, unambiguous criteria. Wainwright et al. [1989] quantitatively compare neuromotor patterns during underwater suction feeding in four ray-finned fishes and *Ambystoma*, a salamander. Previous studies had demonstrated that in many fish a consistent neuromotor pattern occurs during feeding on a given prey type, although variations occur when different prey types are consumed [Sanderson, 1988]. Despite controlling for prey type, Wainwright et al. find that although general features of the suction feeding motor pattern are the same, any tendency toward conservation within genera and families breaks down in a broader phylogenetic context. In this case the neuromotor patterns hypothesized to be conservative were specifically and quantitatively defined so that the hypothesis of similarity could be rigorously tested. Reilly and Lauder [1992] also compare kinematic patterns in feeding across salamander families and show that morphological differentiation is generally accompanied by novelties in feeding pattern. These authors establish an explicit model for evaluating patterns of change in morphology, kinematics and motor pattern in a phylogenetic context.

Similarly, Westneat and Hall [1992] use analysis of variance and principal component analysis of electromyo-



grams to examine the ontogeny of feeding patterns in rats and to test the hypothesis of the homology of neuromotor patterns during suckling and chewing. They found that the electromyographic pattern of the masseter, digastric, sternohyoideus and genioglossus muscles present during rhythmic suckling is significantly different from the electromyographic patterns during chewing. However, nipple attachment is indistinguishable from chewing, and a fourth behavior, the 'stretch response', resembled these latter two behaviors in some aspects. These authors discuss the complex interactions of external factors, sensory integration, deprivation state, peripheral maturation with developing neuromotor patterns and conclude that no simple model of conservation or innovation can account for the ontogeny of feeding behaviors in these animals.

In most other cases, character definitions are not rigorous and it is difficult to define the conditions under which the hypothesis of similarity might be independently corroborated or refuted. For instance, tongue projection in tetrapods has been studied in a number of taxa including salamanders, frogs and lizards, with particular focus on the highly specialized chameleon [e.g. Lombard and Wake, 1976; Thexton et al., 1977; Gans and Gorniak, 1982a, b; Gorniak et al., 1982; Smith, 1984, 1986; Schwenk and Bell, 1988; Schwenk and Throckmorton, 1989; Wainwright et al., 1991; So et al., 1992; Wainwright and Bennett, 1992a, b]. Although each of these taxa use very different muscles, mechanisms and motor patterns to project the tongue, it has been observed that prior to and during tongue projection the jaws are opened. After projection, and during prey withdrawal, the mouth is further opened and then closed. Several authors have attempted to homologize movements occurring during specialized projection cycles with components of the primitive tetrapod feeding cycle [e.g. Bramble and Wake, 1985; Schwenk and Throckmorton, 1989]. Specifically it has been proposed that tongue projection is an alteration of the slow opening stage of the generalized feeding program. Bramble and Wake [1985] have predicted that modifications of the feeding cycle for prey capture will be ordinarily expected during the slow opening stage. However, testing this hypothesis is made difficult, because the criteria that would distinguish 'slow opening' as a unique character, which is homologous across taxa and in different behaviors, from simply opening the jaws slightly, have not yet been defined. This is a particular problem in Schwenk and Throckmorton [1989], who attempt to corroborate the above hypothesis of the role of slow opening. Their illustration of slow opening contains up to three distinct profiles of jaw opening in the phase preceding tongue projection in *Iguana iguana* and *Uromastix aegyptius* (fig. 2). However,

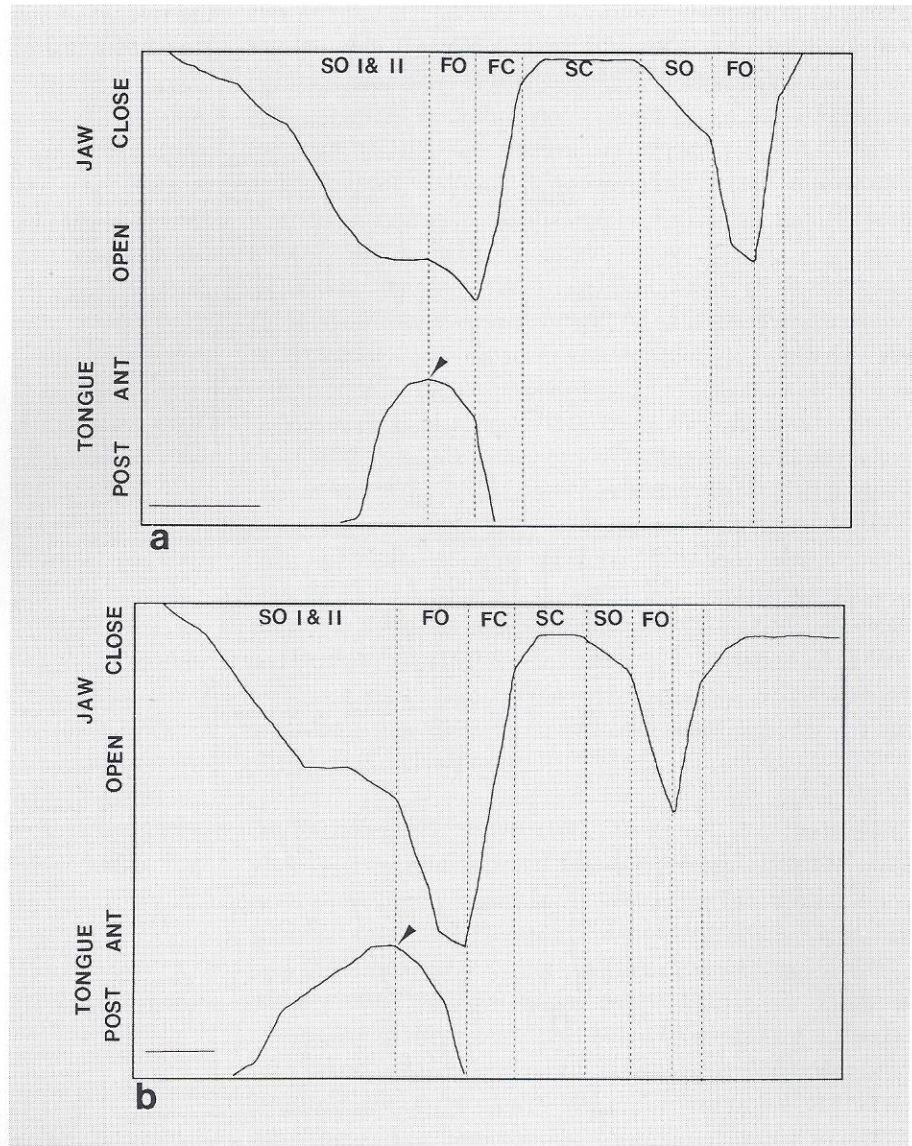
the rate and total amount of jaw movement in portions of slow opening are similar to (and in some cases greater than) that of fast opening in the same sequence. 'Slow opening' in this study actually is defined not on the basis of jaw movement, but as the period of anterior tongue movement. 'Fast opening' begins after maximum tongue projection and contact with the prey just before the tongue is withdrawn. Because anterior tongue movement is used to define the phase 'slow opening', the subsequent claim that these observations support the hypothesis that specialized feeding mechanisms such as tongue projection represent modifications of slow opening is true by definition and could never be refuted.

This specific example merely illustrates the general problem in testing the model of the generalized or the pre-programmed tetrapod feeding pattern. As discussed above, this pattern was originally defined by observations of consistent patterns of jaw and tongue movement in several relatively primitive mammals [reviewed in Hiiemae, 1976, 1978; Bramble and Wake, 1985; Hiiemae and Crompton, 1985; Oron and Crompton, 1985]. Similar movements have been observed in additional taxa that transport food through the oral cavity with their tongue [e.g. Bramble, 1980; Throckmorton, 1980; Smith, 1984; Bramble and Wake, 1985; Schwenk and Throckmorton, 1989], and a hypothetical model of the primitive tetrapod feeding cycle was defined [Bramble and Wake, 1985] (fig. 1). This hypothetical model soon metamorphosed into a 'preprogrammed pattern' and evolutionary constraint [Liem, 1984, 1990; Bramble and Wake, 1985; Roth and Wake, 1989]. However, the specific features that must be present for behaviors to be congruent with the generalized pattern have never been specified. Therefore it is impossible to assess what observations would constitute a refutation of the hypothesis that the preprogrammed pattern is present.

This problem can be illustrated by a brief review of feeding in terrestrial vertebrates. Mammals comprise the best studied and most taxonomically confined case; however, enormous behavioral plasticity is present (fig. 3). In most taxa the correlation between jaw movement and hyoid movement is approximate (fig. 3A, B). In many mammals during the chewing of most food items, the four phase cycle is unrecognizable (fig. 3C-F). Phase one transport and the 'puncture crushing' cycles of mammals are especially variable [Hiiemae and Crompton, 1985]. In addition, the masticatory stroke (power stroke) exhibits great neuromotor variability among mammals. The primitive mammalian power stroke is a labial to lingual movement of the lower jaw and occurs on alternate sides, with asymmetrical jaw muscle activity [Hiiemae, 1976; Crompton et al., 1977]. In



**Fig. 2.** Diagram of tongue protrusion during capture in (a) *Iguana iguana* and (b) *Uromastyx aegyptius*, redrawn from Schwenk and Throckmorton [1989]. The transition between SO and FO is defined on the basis of tongue movement, e.g. the anterior-most extent of tongue movement (contact with the prey), and not by intrinsic parameters of jaw movement. The scale bars represent approximately 100 milliseconds; arrows indicate point of contact with the prey. All other abbreviations as in figure 1.

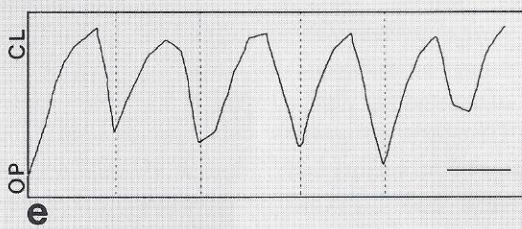
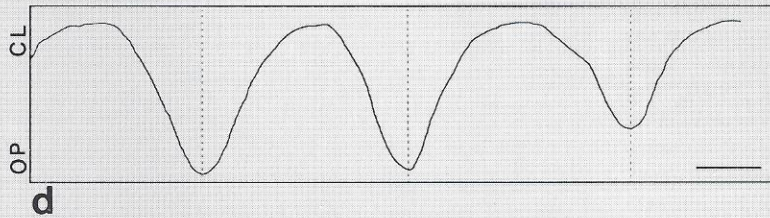
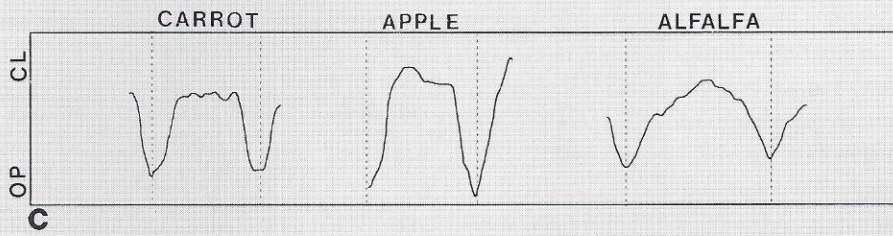
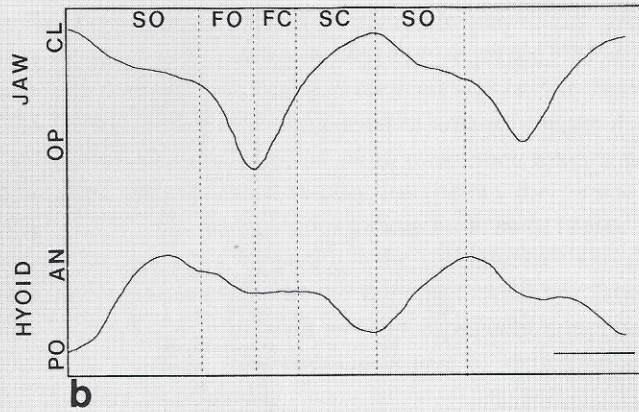
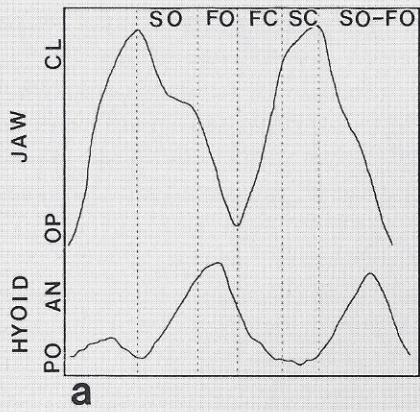


rats the power stroke is propalinal (anterior-posterior) with symmetrical jaw muscle activity [Weijs and Dantuma, 1975]. In golden hamsters, the power stroke combines lateral translation and propalinal movement [Gorniak, 1977]. Herring [1976] described consecutive bilateral grinding in pigs, in which the direction of chewing was reversed within each stroke. A similar pattern was observed in the armadillo, *Euphractus* [Smith and Redford, 1990]. Kallen and Gans [1972] observed reversals in lingual-labial movements in bats. Thus even within mammals there are numerous departures from the primitive or generalized pattern, but because the character, the preprogrammed feeding cycle has not been sufficiently defined, it is impossible to

know if this variation constitutes a refutation of the hypothesis that a preprogrammed cycle exists.

One of the reasons that the hypothesis of the preprogrammed pattern of vertebrate feeding has been readily adopted is that the hypothesis is often tied to data suggesting that a central pattern generator (CPG), which produces rhythmic jaw opening and closing, exists in mammals [e.g. Dellow and Lund, 1971; Thexton, 1976; Thexton and Crompton, 1989; Hiiemae et al., 1978; Hiiemae and Crompton, 1985; Lund and Enomoto, 1988; Crompton, 1989]. The idea of a CPG relies on the presence of discrete neural circuits, located in the central nervous system that induce rhythmic behaviors. Although initially controver-





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sial, the existence of such circuits is now generally accepted [Delcomyn, 1980; Andersson et al., 1981; Grillner and Wallen, 1985; Selverston and Moulins, 1985; Pearson, 1987; Cohen, 1988; Getting, 1988; Lund and Enomoto, 1988; Harris-Warrick and Johnson, 1989]. Lund and Enomoto [1988] summarize much recent work on CPGs in mammalian mastication. It is true that in mammals distinct populations of rhythmically active neurons exist in the hypoglossal (cranial nerve XII) and trigeminal (cranial nerve V) motor systems. However, the output and cycle time of these neural systems is dependent on peripheral input as well as central control mechanisms, and activity can be generated by a number of stimuli. Further, the coordination of the hypoglossal and trigeminal systems is not rigidly linked but varies in different rhythmic activities such as mastication, suckling and lapping [e.g. Kawamura, 1974; Iriki et al., 1988]. Thus, the oscillations of the CPG may be modified to produce a variety of movements, rhythms, and combinations of muscle activity patterns.

The concept of the CPG is important in generating the hypothesis of a homologous feeding cycle across terrestrial vertebrates, because it is the means by which peripheral output may become a character with developmental or evolutionary autonomy. However, despite its attractiveness as a concept, no data on CPGs indicate that the output of a CPG

is as precise and specific as that required by this hypothesis. Further, thus far, a CPG such as that documented for mammals has not been demonstrated in non-mammalian tetrapods. There is, therefore, no evidence that a pattern generator with 'pervasive' distribution among terrestrial vertebrates insures 'the precise coordination of jaw movements with the kinematics of the hyoid apparatus and tongue' [Liem, 1990, p. 211].

Despite the fact that most hypotheses of neuromotor conservatism rely on assessment of similarity, similarity in itself does not provide a convincing case for homology. As pointed out by Striedter and Northcutt [1991], similarity is neither a necessary nor a sufficient criterion of homology. Divergent evolution may produce homologous characters that are quite dissimilar, therefore similarity is clearly not a necessary criterion. It is also not a sufficient criterion, because parallel or convergent evolution may produce non-homologous characters that are strikingly similar to one another. As Striedter and Northcutt discuss [1991], the similarity of characters does not serve as a 'criterion of homology' but rather defines the set of possible hypotheses of homology that must be tested by further analysis of the phylogenetic distribution.

#### Phylogeny

It is generally accepted that congruence with the most parsimonious phylogeny is the best arbitrator of homology, although this principle relies on the fundamental assumption that homoplasy is not common [e.g. Cartmill, 1981; Wake, 1991]. As will be discussed below, the issue of homoplasy in the evolution of behavioral patterns might be considered independently, but there is no doubt that a fine-grained view of the phylogenetic distribution of characters considered to be homologous is important in corroborating the hypothesis of homology. The detailed phylogenetic context is one of the strong points of the analyses of Bass and Baker [1991] and of Lauder and colleagues [e.g. Lauder, 1986; Wainwright et al., 1989; Reilly and Lauder, 1990, 1992].

Thus far, studies of neuromotor conservatism in amniotes have relied on scattered comparisons or incidental observations. Reilly and Lauder [1990] provide virtually the only comprehensive view of feeding behaviors in tetrapods, but focus is on anamniotes. They demonstrate significant differences between amniote and anamniote tetrapods and therefore refute, in some measure, the hypothesis of a conservative pattern in tetrapods. Their study is hampered, however, by the lack of sufficient data on a wide variety of non-mammalian amniote taxa. Smith [1992] also considers the evolution of the feeding apparatus broadly, however,

**Fig. 3.** Composite of illustrations of mammalian masticatory cycles, demonstrating patterns of variation. **a** and **b** Jaw and hyoid cycles of *Didelphis virginiana* (opossum) and *Procavia syriacus* (hyrax). Although both taxa exhibit relatively distinct SO-FO transitions on the basis of gape profile, note that the relation between this transition and the transition between anterior and posterior movement of the tongue is variable. [**a** redrawn from Crompton et al., 1977; **b** from Franks et al., 1985]. **c** Jaw profile of *Capra hircus* (pygmy goat) feeding on three distinct food types [redrawn from De Vree and Gans, 1975]. **d-f** Jaw profiles during normal mastication in *Macaca fascicularis* (macaque monkey), *Myotis lucifugus* (little brown bat), and *Felis catus* (domestic cat), respectively [**d** redrawn from Hylander and Crompton, 1986; **e** from Kallan and Gans, 1972; **f** from Gorniak and Gans, 1980]. In **a** and **b** vertical lines represent the phases of the jaw cycle with abbreviations as in figure 1. In **c-f**, vertical lines designate one complete jaw cycle from maximum gape to maximum gape. Division of these cycles beyond opening and closing is difficult. In the figures in which scale bars are indicated, the bars represent 100 milliseconds (in others, scale was not present in originals). All drawings are redrawn to the same proportion as the original, however, the scaling of time and gape varies from drawing to drawing. Note that these drawings represent movement only in the vertical plane; far more variability exists with regard to movement in the horizontal plane. Abbreviations: PO, posterior hyoid movement; AN, anterior hyoid movement; OP, jaw open; CL, jaw close.



this study primarily discusses swallowing and not transport and mastication, the focus of most hypothesis of conservatism. Jenkins and colleagues [Jenkins and Weijs, 1979; Jenkins and Goslow, 1983; Goslow et al., 1989; Dial et al., 1991] examine comparative patterns in the shoulder girdle of tetrapods and Wainwright et al. [1989] study comparative patterns of underwater feeding. Few studies hypothesizing homologous neuromotor patterns test the hypothesis in a formal phylogeny.

A return to the example of the programmed tetrapod feeding hypothesis makes clear the necessity of a phylogenetic treatment. The variation in feeding profiles in mammals was discussed above and it was concluded that even in this relatively uniform group, it is difficult to generalize beyond the fact that the jaws open and close in a more or less rhythmic fashion [e.g. Kallen and Gans, 1972; De Vree and Gans, 1975; Herring, 1976; Weijs and Dantuma, 1975, 1981; Gorniak, 1977; Gans et al., 1978; Gorniak and Gans, 1980; Hylander and Crompton, 1986]. When the feeding cycle is placed in a broader phylogenetic context, the hypothesis of a conservative pattern is not corroborated. In non-mammalian tetrapods the labial-lingual power stroke is absent, and is replaced by vertical or propalinal biting that require quite different detailed patterns of jaw muscle activity. In many tetrapods fast closing is followed by a stationary phase in which there is virtually no activity of jaw muscles [Smith, 1982, 1984; Gans et al., 1985; Schwenk and Throckmorton, 1989]. There is little reason to believe that a stationary phase, in which no motor activity occurs, is a neuromotor pattern homologous with the complex labial-lingual power stroke of primitive mammals, or with any of the mammalian departures from this primitive condition. More significantly, the following patterns of terrestrial feeding represent even greater departures from the generalized model, because they lack any hint of the four phase jaw cycle, exhibit different sequences of jaw muscle activity, and differ in the coordination of tongue and hyoid movement with jaw movement: (1) inertial feeding [Gans, 1969; Smith, 1982; Busbey, 1989; Cleuren and De Vree, 1992]; (2) lapping – either liquids or whole particles in mammals or lizards [Smith, 1984; Hiemae and Crompton, 1985; Thexton and Crompton, 1989]; (3) suckling in infant mammals [Gordon and Herring, 1987; Westneat and Hall, 1992]; (4) food transport in snakes involving independent mobility of upper jaws [e.g. Kardong, 1974, 1977; Cundall, 1983]; (5) straining in ducks [Zweers, 1974]; (6) the 'peck throw' or slide and glue transport mechanisms of pigeons and other birds [Zweers, 1982, 1985], and (7) other upper and lower jaw manipulations by birds [e.g. Beecher, 1962; Bock, 1964; Burton, 1974; Buhler, 1981; Dubbeldam,

1984]. Thus far no amphibian, including terrestrially feeding forms, has been shown to possess the 'primitive tetrapod' pattern [Reilly and Lauder, 1990]. Figure 4 briefly summarizes some current data on the distribution of various kinds of feeding behaviors on a phylogeny of tetrapods; these feeding types are listed in table 1. A critical view of this phylogeny leads to one of two conclusions: either the preprogrammed pattern does not exist in tetrapods, or it does not provide a significant constraint on the evolution of feeding patterns.

### The Evaluation of Alternative Hypotheses

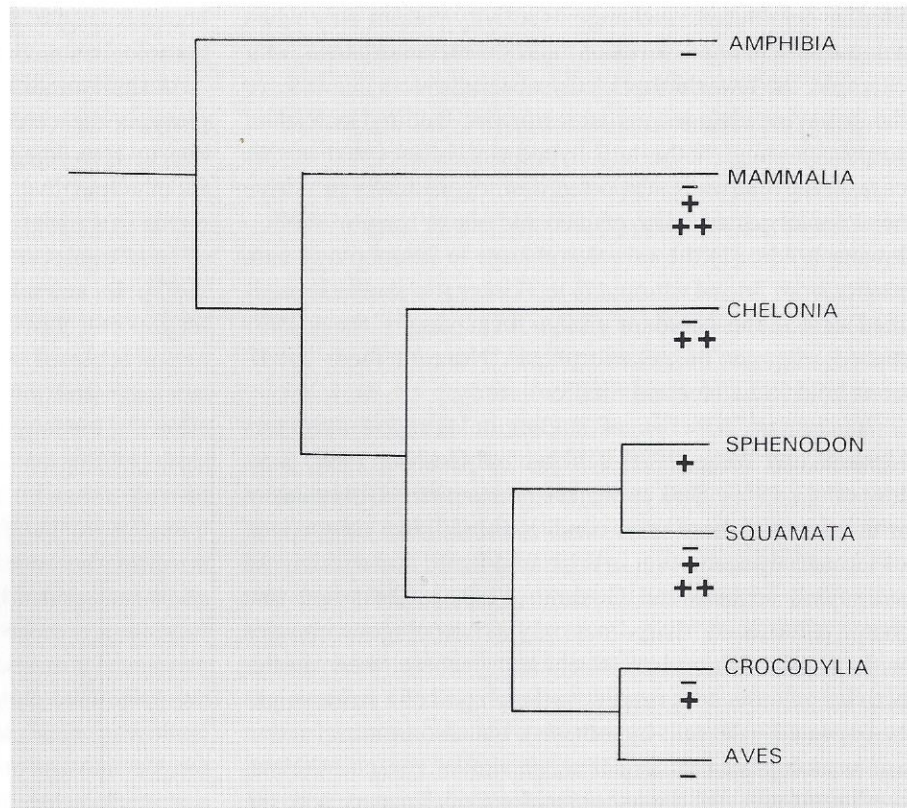
As stated above, the use of a parsimonious fit to a phylogeny as the arbitrator of homology relies on the assumption that homoplasies (convergence or parallelism) are not common [e.g. Cartmill, 1981; Wake, 1991]. While it may be generally difficult to assess the relative merit of a hypothesis of homoplasy independent of the phylogenetic hypothesis, there are three conditions that would make similarity of neuromotor pattern or kinematic output likely. The first source of similarity is when only one condition can be reasonably expected, as in the case where only one condition or neuromotor pattern is physically likely or possible. For example, the tongue will not be protruded when the mouth is closed. It is likely that physical necessity accounts for the observation that a slight amount of jaw opening immediately precedes tongue projection in all terrestrial tetrapods that use the tongue in prey capture or sensory behaviors, so that even if such slight movement is 'homologous' there is little significance for questions on the way that neuromotor systems evolve.

A second source for similarity is the null hypothesis, where homologous, unmodified muscles in two related taxa have similar function in similar behaviors (i.e. retain a primitive state). If the behavior is the same, the neuromotor pattern is expected to be the same even if aspects of other peripheral structures may have changed. In these cases, it is true that the neuromotor pattern is conserved, but there is no reason to expect that any change would have occurred. The observation of neuromotor conservatism (similarity) is only significant when other aspects of the function of the musculoskeletal system change, just as the observation of homology is significant in phylogeny reconstruction only when it reflects derived states and not the plesiomorphic condition. Two examples illustrate this point.

As discussed in the introduction, Lauder and Shaffer [1988] study changes in feeding across metamorphosis in amphibians and conclude that neuromotor patterns are con-



**Fig. 4.** Phylogenetic relations of tetrapods based on Reilly and Lauder [1990] and Gauthier et al. [1988] mapped with distribution of the generalized feeding program. Key: + contains taxa in which the four-phase cycle (SO, FO, FC, SC, with or without a masticatory or power stroke) has been observed; ++ contains taxa in which a four-phase cycle with coordinated hyo-lingual movements (anterior movement of hyo-lingual apparatus during SO and reversal at approximately the SO/FO transition) has been observed; - contains taxa in which feeding cycles lacking above characteristics of generalized feeding program have been reported (therefore, - does not indicate absence of data). See text and table 1 for references.



**Table 1.** Examples of the variation in jaw cycles observed in tetrapods

Amphibia	-	Absence of slow open stage; lack of hyolingual coordination with jaw cycle [e.g. Reilly and Lauder, 1990]
Mammalia	-	Rhythmic jaw movements lacking distinct slow opening/fast opening stages [e.g. see references in fig. 3]
	+	Variations in coordination of hyoid and jaw movements [e.g. Hiiemae and Crompton, 1985]
	++	Jaw cycle in primitive mammals [e.g. Crompton et al., 1977]
Chelonia	-	Aquatic feeding [e.g. Bramble and Wake, 1985; Lauder and Prendergast, 1992]
	++	Food transport in terrestrial turtles [e.g. Bramble and Wake, 1985]
Sphenodon	+	May exhibit coordinated tongue cycle, but hyolingual cycles were not reported [Gorniak et al., 1982]
Squamata	-	Food transport in snakes [e.g. Cundall, 1983]
	+	Inertial feeding in <i>Varanus</i> [Smith, 1982]
	++	Food transport in Iguanians [Smith, 1984; Schwenk and Throckmorton, 1989]
Crocodylia	-	Inertial feeding in <i>Alligator</i> [Busbey, 1989]
	+	Feeding in <i>Caiman</i> [Cleuren and De Vree, 1992]
Aves	-	Zweers, 1974, 1982, 1985; Buhler, 1981; Dubbeldam, 1984 (and further references in text)

+ = Observation of the four phase jaw cycle (SO, FO, FC, SC); ++ = observation of the four phase cycle with coordinated hyolingual movements (anterior movement during SO; reversal at the SO/FO transition); - = observation of feeding cycles in which four phase cycle not present. + Category combines taxa with power stroke and taxa with stationary phase following fast closing. For further explanation and references see text.

served during the origin of behavioral novelties in phylogeny and ontogeny. However, their data do not address 'behavioral novelties', because they found conserved motor patterns only when the behaviors were similar (aquatic feeding). When behavioral novelties appear (e.g. terrestrial

feeding), motor patterns change. Even though performance differentiates pre- and post-metamorphic animals, the two groups contract homologous, morphologically unmodified muscles in a similar pattern during similar behaviors. This would be expected by the null hypothesis. Lauder and



Shaffer demonstrate a change in activity pattern only when a muscle changes function across metamorphosis, for example, the branchiohyoideus/subarcalis rectus muscle, or the behavior changes, as in terrestrial feeding instead of aquatic feeding. If the null hypothesis is accepted in this case, conservatism is supported if ontogenetically primitive neuromotor patterns are retained and one or more of the following holds: (1) the muscles change in morphology and, particularly, line of action, (2) the kinematic profile is modified or (3) the behavior (rather than simply the performance) changes in metamorphosis. None of these conditions hold in Lauder and Shaffer's study.

In contrast, a series of studies on tetrapod shoulders [Jenkins and Weijs, 1979; Jenkins and Goslow, 1983; Goslow et al., 1989; Dial et al., 1991] examines a situation in which some of these latter conditions hold. In a comparison of terrestrial locomotion in a varanid lizard and a didelphid marsupial, Jenkins and Goslow [1983, p. 290] find that motor patterns are shared not only in homologous muscles with 'similar anatomical attachments' where 'their similar activity patterns with respect to the phases of a stride might be expected' (the null hypothesis), but also in muscles that are homologous but do not share similar musculoskeletal configurations (the supracoracoideus of *Varanus* and the supra- and infra-spinatus of *Didelphis*). This case of functional divergence, but similarity of motor pattern, is not consistent with the null hypothesis, and supports a hypothesis of neuromuscular conservatism. Their argument of conservatism is further strengthened in later studies of activity patterns of the same muscles during flight in birds [Goslow et al., 1989; Dial et al., 1991]. These later studies find that in some cases these muscles retain a similar motor pattern even with the functional reorganization associated with flight. The most striking example is the supracoracoideus (or its homologues) which exhibits a conservative biphasic pattern in *Varanus*, *Didelphis* and *Columba*. Functional specialization is achieved despite the conservative neuromotor pattern, because, although the activity is biphasic in all three taxa, a different phase serves as the power stroke in flight vs. walking. "Through a process that we may call 'neuromuscular canalization,' the upstroke (= swing) component of the biphasic activity cycle for the supracoracoideus is most important in birds, whereas the propulsive (= downstroke) component of the homologous supraspinatus and infraspinatus muscles is essential in mammals. Yet in both birds and mammals the primitive organization of the neural control components still persists, for in both groups we find evidence of a biphasic pattern" [Goslow et al., 1989, p. 296]. A strong argument can be made here for a significant hypothesis of neuromuscular conservatism,

because despite changes in morphology and functional role, homologous muscles retain a common activity pattern.

A third condition and the major reason to expect homoplasy, is the convergent evolution of neuromotor patterns due to convergent functional requirements. It is possible, for example, that the coordination of jaw and tongue movements in various tetrapods is similar because the demands of food transport are convergent in these tetrapods [Smith, 1992]. In animals with lingual-based food transport, the tongue will move forward and under the bolus, while the mouth is closed or slightly opened (slow opening), because the teeth and palate hold the food in place at this time, allowing the tongue to slide forward relative to the food. If slow opening occurs, it is because the jaws open slightly to provide room for this tongue movement. The tongue and bolus move back when the jaws are opened wide (fast opening), because at this time the oral cavity is enlarged to allow unimpeded backwards movement of a food item. If a food item is to be chewed, the food is repositioned in this phase and a masticatory stroke or biting occurs once while the jaws have closed to the point of contact with the food (following fast closing). Thus, the similarity in jaw and tongue movement profiles observed between reptiles and mammals using lingual transport could be explained by simple functional requirements. This alternative hypothesis is functionally reasonable and can be refuted by specific data. For example, if animals that do not use the tongue in transport exhibit the four-phase jaw cycle, with the same coordinated tongue movements, then the functional hypothesis would be refuted, and a hypothesis of neuromotor conservatism supported. Likewise, if the slow opening phase with accompanying tongue movements occurs during activities other than transport (i.e. puncture crushing) or was invariant with different food sizes, consistency or position, then the functional hypothesis again would be weakened and the hypothesis of neuromotor conservatism strengthened. While a phylogenetic analysis is generally considered the best arbitrator of homology versus homoplasy, there are instances where arguments can be made for analyzing the likelihood of homoplasy independent of the phylogeny, because there are biological processes that make homoplasy likely [Wake, 1991].

## Conclusions

Questions about the evolution of neuromotor systems are important, and understanding the relative evolutionary plasticity of neural, muscular and skeletal systems will do much to illuminate the sources of constraints on evolution-



ary diversity. However, hypotheses on the ways that neuromotor patterns evolve must be rigorously tested. Testing requires more data than just observations of similar movement patterns. A hypothesis of neuromotor conservatism is fundamentally a hypothesis of homology and requires the depth of analysis necessary to support a hypothesis of homology for morphological data. Because data are behavioral, criteria such as position, development and connections are unavailable and assessment generally relies on overall similarity. But such assessments are generally weak. Most hypotheses of the conservatism of neuromotor pattern have not yet received the vigorous challenge normally given to hypotheses of morphological homology and rely exclusively on observations that patterns appear similar in two or more stages or taxa.

At a minimum, a well supported analysis of neuromuscular conservatism will define the neuromotor pattern and its underlying constituents (e.g. musculoskeletal substrate, innervation, central connections, etc.) with enough specificity and complexity so that it is clear that: (1) a unique character is being defined; (2) this character has developmental and/or evolutionary autonomy, and (3) the character is complex enough so that superficial or spurious resemblance can be eliminated. An example of such a complete definition is that of Bass and Baker [1991]. Further, the hypothesis of conservatism will be enhanced if explicit null hypotheses are addressed and probable sources of homoplasy are examined. Finally, the hypothesis of evolutionary conservatism or homology must be examined in light of a phylogenetic hypothesis. When the elements of a hypothesis of neuromotor conservatism are presented as specific well-defined characters, and sufficient phylogenetic representa-

tion exists to allow phylogenetic tests of homology, then the case for conservative pattern and perhaps accompanying evolutionary constraint or directionality will be strengthened. Further, the critical evaluation of alternative sources of similarity will allow understanding of the complex processes determining the evolution of neuromotor patterns.

With regard to the specific hypotheses discussed here, the most general is the hypothesis of the preprogrammed tetrapod feeding cycle. The interpretation of the tetrapod feeding cycle has passed rapidly in the literature from incidental observations of similarities (based on representative cycles with no quantitative definition or analysis), to an example of an evolutionary constraint that determines the ecological and morphological diversification of terrestrial tetrapods. The intervening stages, of demonstrating that the 'preprogrammed' feeding cycle actually exists and testing its distribution phylogenetically, are missing. The kinematic pattern held in common in tetrapods is little more than generally rhythmic jaw opening and closing. Tetrapods develop a whole series of modifications of feeding including inertial feeding, various kinds of medio-lateral and antero-posterior masticatory strokes, independent upper and lower jaw movements, and lingual feeding (lapping). Some common functional patterns hold, but there is no evidence of pervasive distribution or evolutionary constraint.

### Acknowledgements

I thank W.L. Hylander, W.M. Kier, C.F. Ross, V.L. Roth, J.G.M. Thewissen, and A.D. Yoder for comments on earlier drafts of this manuscript. NSF grant BSR 90-07480 provided support during the preparation of this paper.

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