The evolution of feeding motor patterns in vertebrates

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Despite considerable skepticism, researchers have found that the patterns of muscle activation that control feeding behaviors of lower vertebrates have been surprisingly conserved during evolution. This tendency for conservation among taxa appears in the face of marked flexibility of motor patterns within individuals. One interpretation of these apparently conflicting trends is that the most effective motor pattern for any given feeding situation is the same across substantial phylogenetic distances and morphological differences. The novel evolutionary insight provided by this research is that historical changes to motor patterns are a relatively infrequent source of trophic innovation. The spectacular diversity of feeding abilities and feeding ecology in lower vertebrates is based mostly on axes of variation, and on the innovations in the organization of muscles and the skeletal linkage systems that they drive.

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Abbreviations

emg	electromyograph
MP	motor pattern

Introduction

Vertebrate trophic biology is characterized by staggering diversity. The waterways of the world are filled with fish that feed on nearly every conceivable food source, and tetrapods show an almost equal range of dietary specialization. It is apparent that this diversity is associated with variation in musculo-skeletal morphology and in the mechanical properties of feeding systems; but how have changes in the motor patterns (MPs) that drive feeding behaviors contributed to this diversity?

Vertebrate feeding systems are complex networks of muscles and skeletal elements. Teleost fishes are especially complex, having more than 30 moving bones and 50 muscles in the head [1]. Feeding behaviors can be thought of as emergent phenomena that are formed by the integration of several factors including: the sequence and intensity of muscular contractions, the structural organization of the musculo-skeletal system, and the contractile properties of the muscles driving the system [2–4]. It would appear that modifications to the MP — that is changes in the sequences and timing of muscular contraction or more subtle changes in the proportion of motor units recruited — represent a fertile ground for evolutionary innovation in feeding systems [5–9]. In this review I summarize recent literature on the role of MP changes in the evolution of vertebrate feeding systems. My aim is to emphasize the most common patterns seen in this body of research and to illuminate the persistent challenges that remain.

Motor flexibility provides versatility

The effects of a variety of factors on MPs have been investigated experimentally. The results reveal that most vertebrate species show an extensive capacity to modulate MPs in response to prey type [10–12,13••,14], prey position [15,16], predator satiation [17], prey toughness [18,19], and prey size [20]. This motor flexibility applies across all of the major vertebrate clades that have been studied. The picture that emerges is that vertebrates can integrate feedback from visual, tactile, olfactory, gustatory, vomeronasal and other sensory modalities into the motor control of feeding behaviors [15,21–24]. Vertebrates adjust the motor control of their feeding system to match the demands that are presented by different prey and different conditions. This motor flexibility has been repeatedly identified as a major factor in promoting the versatility of vertebrate feeding behaviors [8,12,25–28].

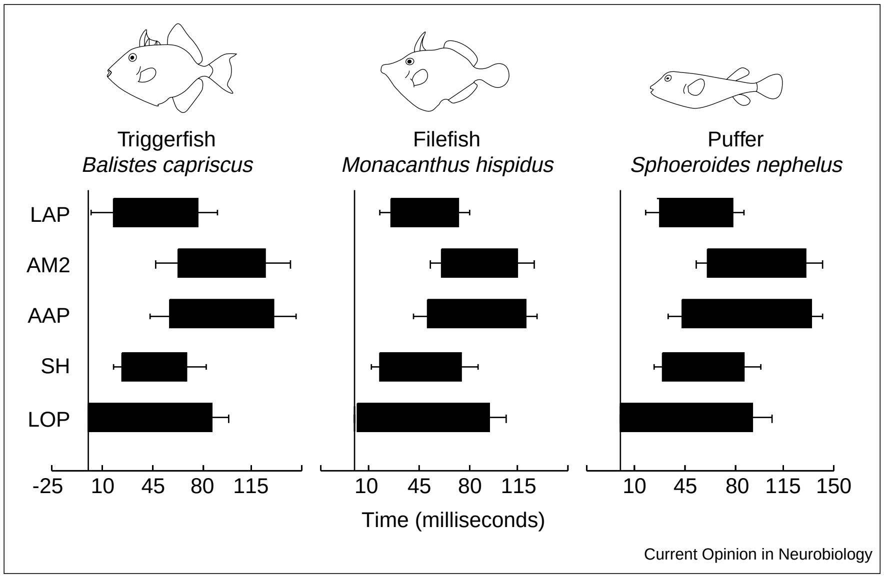
The implication of high variability in quantified characteristics of MPs, and the control that vertebrates show in response to a variety of stimuli, indicates that the neural control of feeding behaviors has an extensive capacity for flexibility [13••,26]. Intrinsic constraints on alterations in MPs have therefore not been identified.

Motor patterns are conserved

In the face of an almost universal capacity for modulation of MPs, there is a remarkably strong tendency for closely related species to show little or no difference in the MPs that they exhibit when feeding on the same prey under the same conditions [29–31]. Thus, only one of 11 variables characterizing the MP used by suction feeding sunfishes differed among species feeding on the same prey [10]. This is in spite of the fact that the species studied differed ecologically, from piscivores to planktivores, and had large differences in the size and shape of mouth parts and the linkage mechanics of the jaws [32]. Triggerfishes, filefishes and pufferfishes, which feed by directly biting their prey, exhibit indistinguishable MPs when feeding on a common prey ([33]; Figure 1). A common MP of the hyolingual muscles has been found to characterize prey capture in major lizard groups [7,34•]. Similarly, mammals from different Orders exhibit a common MP that is associated with chewing [28,35,36].

The pattern is striking. Species that differ in feeding ecology, feeding abilities and feeding kinematics often drive their feeding behavior with muscle activity patterns that differ only slightly or are indistinguishable from each

Figure 1



Bar diagrams showing the average timing of activity of five cranial muscles in three species of tetraodontiform fish during biting behavior while feeding on pieces of squid. A nested analysis of variance found no differences among species in mean burst duration or onset of movement time. This conserved pattern exists in the face of marked morphological and ecological differences among these taxa, and despite the passing of about 50 million years since the time of their last common ancestor. Muscle abbreviations: AAP, adductor arcus palatini; AM2, section 2 of the adductor mandibulae; LAP, levator arcus palatini; LOP, levator operculi; SH, sternohyoideus. Values represent mean and standard error (SE) across five individuals of each species. Data taken from [12].

other ([32,37,38]; Figure 2). The pattern is so common in closely related groups of species that, to date, very little of the variation among species in feeding performance can be attributed to evolutionary modifications to the MPs that drive the behaviors. In contrast, species vary markedly in the mechanics of their jaw linkage systems and the contractile and metabolic properties of their muscles. Changes at these levels of design appear to account for most of the variation among closely related species in feeding ability [39,40].

Why are motor patterns conserved?

How are we to reconcile the apparent paradox produced by the extensive flexibility in the motor control of vertebrate feeding behaviors and the lack of inter-specific differences in the MPs for a common behavior when feeding under similar conditions? Clearly, the conservation of feeding MPs among close relatives does not reflect constraints on the ability of the nervous system to change its output. One explanation for these different patterns of variation is the tendency for conservation across species to reflect a common solution that is the most effective MP for the task. Thus, it may be that although vertebrates can modify feeding MPs in response to several stimuli, when executing the same behavior under the same conditions the most effective MP remains nearly constant across closely related species. This interpretation is strongly supported by the extensive flexibility in motor output seen among vertebrates. If vertebrates are invariably able to modulate their MP in response to environmental factors, this would imply that sensory feedback is being used to fine-tune the MP. We can therefore assume that most species of vertebrate have a wide range of MPs. Different species utilize indistinguishable patterns under similar conditions, implying active convergence on a common choice of MP. In the future, one approach to testing this hypothesis would be to establish the performance consequences of MP variation within species, and to ask whether each species tends to use the optimal pattern from the repertoire that it possesses.

The flexibility in MPs across species argues strongly against the possibility that the conservation of MPs among closely related species is attributable to constraints on neural output [41,42]. Mammalian MPs for chewing are thought to be driven by relatively simple central pattern generators that can be modified by peripheral feedback [42]. However, the presence of a central pattern generator, although giving an anatomical basis for homologous behaviors in different species, does not argue for narrow constraints on the specific form that the MP can take.

Challenges to the conservation paradigm

Several points have been raised that challenge the conclusion that feeding MPs tend to be strongly conserved in vertebrate evolution.

Limited behavioral and taxon sampling

The first objection is that only a few behaviors have been studied well enough to permit general statements about interspecific patterns [30••]. In fact, the conservation of MPs has been reported in several behaviors and several major vertebrate groups. These reports describe conserved MPs in teleost fishes for suction feeding [10], biting behaviors [12,30••], pharyngeal jaw chewing behaviors [43], and pharyngeal jaw crushing behavior [44•]. MPs have been conserved for suction feeding in amphibians [31], and for prey prehension and prey transport in lizards [34•]. In mammals, suckling and chewing have also provided evidence of conserved patterns [28]. Whereas there are clearly groups and behaviors that have not yet been evaluated, enough research has been conducted to permit general conclusions to be drawn.

Consequences of small changes in motor patterns

An important point is that small changes in the MP may have large functional consequences. An analogy can be made to recent analyses of morphological systems in the skull that have shown that the mechanical properties of skeletal linkages do not map linearly onto morphological variation [45,46]. Loeb and Gans [47] conclude that it is possible to only make limited connections between electromyographic (emg) variation and the mechanics of the associated muscle contraction. Future tests of this hypothesis will require a combination of emg recordings with details of muscle strain and skeletal kinematics. This would permit mapping of the variation in MPs onto variation in the mechanical output of the muscle and the motion of the feeding structures. It is possible that the conserved nature of MPs reflects, in part, the crude relationship between emg data and the mechanical output of muscles. Indirect support for this point comes from the observation that the MPs associated with different behaviors may be similar. The biting and suction-feeding behaviors of teleost fish involve surprisingly similar MP patterns, in spite of their obvious differences [30••,48,49].

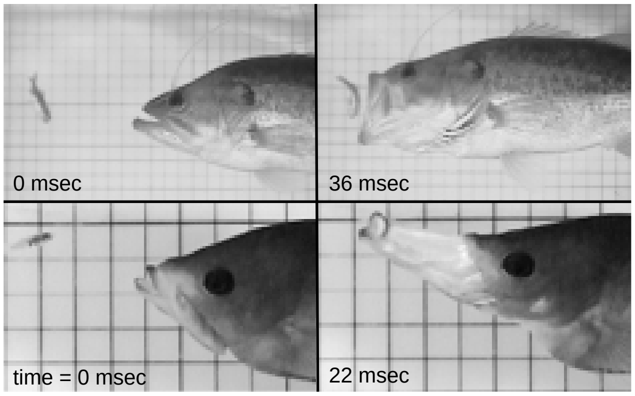
Motor pattern innovation

There are many examples of innovations in MPs being associated with changes in trophic biology [6,26,50,51,52••,53]. However, this does not negate the fact that when comparisons are made among closely related species, or even across broad phylogenetic stretches, relatively little of the variation in trophic biology can be attributed to changes in MPs. MP innovations appear periodically within vertebrate evolution. In some cases major trophic shifts can be partly attributed to changes in muscle activation patterns. For example, crushing of mollusks by centrarchid sunfishes involves a novel pattern of muscle activation that is found only in the mollusk-eating taxa [40,51]. Up to four distinct innovations in chewing MPs are known across different Orders of mammals [28]. Thus, distinct MP innovations have periodically allowed vertebrate groups to invade novel feeding niches. These innovations are frequently substantial enough that they define previously unknown behaviors.

Conclusions

A central goal in evolutionary neurobiology is to understand the role of nervous system outputs in generating the diversity of behaviors and ecotypes that are seen in nature. With respect to the evolutionary history of vertebrate feeding systems, innovations in MPs have occurred periodically and can play a key role in facilitating the invasion of novel trophic niches. However, the surprising general pattern is that trophic diversity does not usually have a basis in MP variation. Vertebrate feeding MPs are characterized by being readily modified in response to a variety of feedback systems. When feeding under similar conditions, however, different species typically exhibit muscle-activation patterns that are indistinguishable, or have only minor differences. The capacity for fine-tuning MPs, together with their conserved nature, suggests that the uniformity of MPs is brought about by an active convergence. This implies that the most appropriate MP for the job is largely the same among taxa, in spite of the variation in morphology and muscle physiology seen among even close relatives.

Figure 2



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Images taken from high-speed videos of prey capture in two teleost fishes. Remarkably, the jaw mechanics and prey capture kinematics have diverged radically in these fish, whereas the MPs driving these behaviors show only minor differences [38]. The top two images show the largemouth bass, *Micropterus salmoides* (Centrarchidae), a freshwater teleost from North America. The bottom sequence shows the sling-jaw wrasse, *Epibulus insidiator* (Labridae), an inhabitant of Indo-Pacific coral reefs. Both species feed predominantly on other fishes.

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