

Introduction: Major Issues of Feeding Motor Control in Vertebrates¹

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INTRODUCTION TO THE SYMPOSIUM

The study of motor control is one of the most active areas of research in feeding functional morphology. As many of the muscles responsible for controlling feeding behavior are large and superficial, it has proved relatively easy to record muscle activity during feeding using electromyographic techniques. As a result, feeding muscle activity patterns have been quantified for representatives of all the major vertebrate groups, although sampling intensity varies from relatively good in groups like fishes and amphibians to poor in sharks, turtles and snakes (see Schwenk, 2000; this volume for an overview).

AQUATIC FEEDING MOTOR PATTERNS

Conservation as a theme has shaped inquiry into feeding motor control. Ideas of motor pattern conservation in fish and other aquatic vertebrates grew out of early experiments on rapidly feeding fishes which were found to have stereotypical kinematic and muscle activity patterns (*e.g.*, Osse, 1969; Liem, 1970; Nyberg, 1971; Lauder, 1980). Central pattern generators (CPGs) were hypothesized to control rapid suction feeding, a behavior thought to occur so rapidly that it precluded sensory modulation (Osse, 1969; Liem, 1978; Groeberker and Pietsch, 1979; Groeberker, 1983; Liem, 1984). Although subsequent studies demonstrated that muscle activity patterns could vary in response to prey differences (*e.g.*, Wainwright and Lauder, 1986; Friel and

Wainwright, 1998), the general hypothesis of motor pattern conservation was strengthened by a number of quantitative studies of muscle activity which showed that, at low phylogenetic levels, species motor patterns were statistically indistinguishable (*e.g.*, Sanderson, 1988; Wainwright *et al.*, 1989). The central pattern generator hypothesis provided a mechanism to explain both patterns of stereotypy (*e.g.*, Liem, 1978; Lauder, 1980) and conservation (see Smith, 1994).

Observations of motor pattern conservation were congruent with the identification of many conserved features of biomechanical design in suction feeding fishes (*e.g.*, Lauder, 1985). However, in an important study of motor pattern evolution, Wainwright *et al.* (1989) showed that muscle activity patterns were not conserved across suction feeding species at high phylogenetic levels. Instead, taxa were found to have evolved significantly different suction feeding motor patterns. A few general features, such as muscle recruitment and relative timing, did characterize suction feeders even at high phylogenetic levels. Despite this result, suction feeding motor patterns have been widely regarded as showing a conserved pattern and have led some authors to suggest that this conservation is the result of intrinsic or extrinsic constraint (*e.g.*, Lauder and Shaffer, 1993; Smith, 1994).

TERRESTRIAL FEEDING MOTOR PATTERNS

Similarly, ideas about terrestrial vertebrate feeding have been strongly influenced by notions of conservation and constraint. In 1985, Bramble and Wake proposed the Generalized Feeding Cycle (GFC) model for lower tetrapods. On the basis of similarities between mammalian and reptilian feeding cycles they hypothesized that the

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evolution of the complex mammalian masticatory system could have been accomplished through minimal change in the associated neuromotor mechanisms. The central prediction of the GFC model was thus that neural control of intraoral transport was central pattern generator-based and that this mechanism has been conserved across major tetrapod groups. The most basic implication of the Bramble and Wake (1985) model was that all trophic mechanisms in modern tetrapods represented departures from the generalized ancestral system. One of the strengths of the model was that it predicted that certain kinematic and muscular characters, marking distinct phases of intraoral transport, would be conserved across lineages, thus making it possible to test the validity of the GFC hypothesis.

One key element to both aquatic and terrestrial hypothesis of feeding conservation is the concept of a central pattern generator. Although the idea of central pattern generators was initially controversial, subsequent studies supported the existence of CPG circuits (Thexton, 1974, 1976; Grillner and Wallen, 1985; Lund and Enomoto, 1988; Szekely, 1989; Smith, 1994) and the hypothesis gained general acceptance. These demonstrations of the CPG served to strengthen both aquatic and terrestrial hypotheses of feeding conservation. Furthermore, CPG studies contributed to the evolution of motor conservation hypotheses into largely untested proposals of neuro-motor constraint on the feeding mechanism (Smith, 1994). Liem (1984), for example, suggested that the large degree of feeding specialization observed in tetrapod vertebrates might be an evolutionary consequence of the relative conservatism in the preprogrammed jaw movements. Roth and Wake (1989) used this observation as an example to point out how constraint (on the motor control) can lead to evolutionary diversification at different levels of organization. In the aquatic realm, Lauder and Shaffer (1993) suggested that the conservation of biomechanical patterns of aquatic prey capture represented a major theme of vertebrate functional morphology, and suggested intrinsic and extrinsic mechanisms

that might produce muscle activity pattern conservation in aquatic vertebrates.

In short, the theme of motor pattern conservation across vertebrates continued to develop with the publishing of *Functional Vertebrate Morphology* (Hildebrand *et al.*, 1985). Less than ten years after the GFC model was proposed, the conservation of neuro-motor control hypothesis was widely accepted and used to explain evolutionary patterns of feeding mechanics in diverse groups of vertebrates. Only Smith (1994) cautioned against the broad use of this paradigm, as tests of the hypothesis of conservation of neural control were largely lacking. Still, rigorous testing did support the idea of conservation of neuromuscular control in some cases (Jenkins and Goslow, 1983; Goslow *et al.*, 1989; Dial *et al.*, 1991).

In the fifteen years since the publication of *Functional Vertebrate Morphology* (Hildebrand *et al.*, 1985), there has been an explosion of research on vertebrate feeding. The purpose of this symposium was to synthesize recent studies across phylogenetic groups in order to re-evaluate our current understanding of motor pattern evolution. Central questions within the scope of the symposium were: "are muscle activity patterns conserved within and across aquatic vertebrates" and "is the generalized model feeding cycle as proposed by Bramble and Wake (1985) supported by a comprehensive survey of terrestrial amniote feeding systems." We were also interested in functional diversity within and across clades, and in groups where the feeding system would appear to place novel, and extreme demands on the control system. We asked participants to identify central issues of the control of feeding specific to their group, and to suggest directions for future study.

CURRENT PERSPECTIVES

The papers in this volume cover motor control in all the major vertebrate groups and represent some of the diversity in perspective and research goals present in the field today. One conclusion evident from these studies is that motor control of feeding is complex: it may involve integration of sensory input from a number of modal-

ities, and usually requires precise coordination of discrete functional systems (such as coordination between oral and hyolingual system). Furthermore, muscle activity patterns show ontogenetic variation (Mallett *et al.*, 2001), complicating the quantification of the motor pattern of an individual, much less a species. As a result, it is not surprising that general hypotheses of motor pattern conservation do a poor job of explaining the variation in muscle activity pattern seen across vertebrates. Instead, motor patterns, like most other levels of organismal design, seem to fit a mosaic pattern of evolution. Within certain groups, particular elements may appear highly conserved, yet these conserved elements may differ among groups. At broad phylogenetic levels, it is unclear which elements of the motor pattern, if any, are conserved.

One key issue, raised by Deban and co-workers was the general lack of a good definition of the concept of "motor pattern" (see also Smith, 1994). Clearly, this lack of a semantic consensus among different researchers complicates broad comparative analyses of motor pattern evolution. Motor patterns are generally thought to originate in a CPG-like system that is located in the central motor systems at the level of the brain stem (Lund and Enomoto, 1988). As the CPG is nothing more than populations of rhythmically active neurons whose activity is dependent on both peripheral input (*i.e.*, feedback, see Davis and Kovac, 1981; Rossignol *et al.*, 1988) and central, higher level control systems (Lund and Enomoto, 1988), the definition of a motor pattern is inherently vague. Ewert and co-workers (1994) for example, defined a motor pattern as the spatiotemporal pattern of excitation and inhibition in motoneurons necessary to activate and coordinate muscle contractions. Clearly such a definition is of little practical use, and until generally accepted, very specific operational definitions of the concept of motor patterns emerge, no rigorous tests of hypotheses of constraint can be undertaken (but see Deban *et al.*, 2001).

The roundtable saw spirited discussion on the issue of intrinsic constraint. Most participants agreed that there was little evidence of the kind of rampant conservation

of muscle activity pattern in any groups that would suggest that the neural circuits were acting as a constraint on the evolution of feeding behavior. Furthermore, the notion of the nervous system as a constraining agent appears to enjoy greater currency with functional morphologists than neurobiologists as was pointed out so convincingly by Joe Fetcho. He suggested that neural circuitry might be expected to show even greater evolutionary plasticity than other levels of design in order to accommodate the striking changes in morphology and function present during ontogeny and evolution.

FUTURE TRENDS

The symposium suggested a number of possible avenues for future study. These suggestions can be divided into three broad categories. The first involves using new techniques to study the neural control and function in greater detail. One of the most critical deficits in the field of feeding motor pattern evolution is the lack of studies on the activity of motor neurons during feeding. Visualization techniques currently used to study escape response behavior in fishes hold great promise for applications in feeding. Similarly, nerve transection, which has been shown to strongly complement EMG studies of amphibian and lizard feeding, could potentially be used to address many hypotheses of muscle function and sensory control in other vertebrate groups.

The second focuses on theoretical issues of complex system control. Questions such as "what are the limits of motor control during predatory behavior" and "can the intrinsic properties of the system (*sensu* Kugler and Turvey, 1987; Holt *et al.*, 1990) help simplify control issues" have been examined in relatively few vertebrates. As Aerts *et al.* (2001) and Van der Leeuw *et al.* (2001) show birds and aquatic feeding turtles both appear to reduce the complexity of axial system control, though by unrelated mechanisms. Do other organisms with similarly complex, underdetermined prey capture systems, such as snakes, also employ mechanisms to reduce the burden of system control?

Finally, the function and causes of mus-

cle activity pattern variation and evolution remain poorly studied. Although nearly every study of muscle pattern finds a high degree of within and among individual variation, the implications for feeding performance of this variation are poorly understood. Grubich's (2001) study of kinematic correlates of EMG variation represents one of the first attempts to understand the significance of the characteristically high levels of motor pattern variation within individuals. At the species level, the implications of high versus low amounts of EMG variation are unknown, but might reflect differential capacities for modulation. Finally, the hypothesis that novel muscle activity patterns should accompany functional shifts (articulated by Peter Wainwright in his talk and during the round table discussion) represents a potentially important change in our thinking of motor pattern evolution. Functional shifts can be identified at many different levels within most vertebrate groups. Future studies focusing explicitly on the correlates of muscle activity with behavior should lead to a more thorough understanding of feeding motor control and offer the best opportunity for identifying the causes, and discerning the limits of motor pattern evolution.

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