

## Intrinsic Mechanics and Control of Fast Cranio-Cervical Movements in Aquatic Feeding Turtles<sup>1</sup>

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**SYNOPSIS.** Aquatic feeding strikes on agile prey in snake-necked turtles involve fast neck extension, bucco-pharyngo-oesophageal expansion, and head retraction. The ultimate, rectilinear acceleration of the head towards the prey requires complex vertebral rotations, that vary widely from strike to strike. This poses complex motor control issues for the numerous intrinsic neck-muscles, which are the sole neck extensors. Mathematical modelling reveals that extensor activity might be superfluous for this phase of the strike. The ultimate acceleration of the head at the end of the strike always coincides with forceful oropharyngeal expansion. The momentum of the induced flow of water is sufficient to pull the head (and the neck) straight towards the prey. This buccal expansion proceeds identically to that observed in primary aquatic feeders: a rostro-caudal expansion sequence characterized by an optimal timing of the functional components supporting the expansion wave. Yet distinct structural solutions, both at the skeletal, and muscular level, are involved. This points towards prominent hydrodynamic constraints. Head and neck are retracted by extrinsic neck muscles. Given the high number of degrees of freedom, this musculo-skeletal system is obviously under-determined, which compromises control. We propose that erroneous folding of the neck (*i.e.*, diverging from the highly persistent retracted configuration) might be avoided through the presence of a subtle click system at the level of the joint between cervical vertebrae 5 and 6.

### INTRODUCTION

Despite the recent debate on the phylogeny of turtles (for a comprehensive synopsis see Pough *et al.*, 2001), there is little doubt that the characteristic 'shell' was present in the earliest representatives of this taxon (Benton, 1996; Pough *et al.*, 2001). According to Lee (1997), the evolutionary development of the shell, and the broad flattened body are linked to the herbivorous diet of the ancestral forms. This led (through a network of self-consolidating selective interactions; see Lee, 1997) to the slow, clumsy, and heavily armoured recent turtles. At first glance, such a design seems to lock turtles into herbivory or a scavenging diet. In the best case only non-elusive prey could be taken.

This holds true for most terrestrial turtles

(Pritchard, 1979), but in the aquatic environment many species show adaptations allowing them to exploit another feeding niche: active predation. In most cases (except, for instance luring by the alligator snapper), active predation requires a certain amount of compensatory and/or inertial suction (Van Damme and Aerts, 1997). In this way, even elusive prey like fishes can be captured (*e.g.*, mata mata, snapping turtles, snake necked turtles, etc.; see for instance Pough *et al.*, 2001; Lauder and Prendergast, 1992; Summers *et al.*, 1998; Van Damme and Aerts, 1997). (For an extended bibliography on turtle feeding we refer to Schwenk, 2000).

Long necked turtles further compensate for their reduced mobility (imposed by the rigid, heavy shell) by combining suction feeding with a sudden fast dart of the head towards the prey. In snake necked turtles (*e.g.*, *Chelodina longicollis*), a feeding bout typically consists of a slow approach of the prey through head/neck as well as body movements; a fast strike of the head/neck

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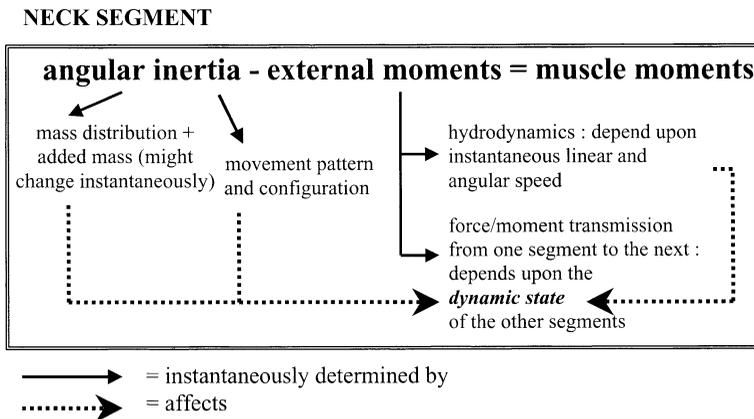


FIG. 1. Scheme illustrating the dynamic equilibrium condition (involving muscle moments) for a neck segment (box). Muscle moments must at all times be in equilibrium with the instantaneously changing external moments and inertial effects.

during which the prey is taken; and subsequent head retraction (Van Damme and Aerts, 1997; Van Damme *et al.*, submitted). During the first stage, the prey is targeted and the long axis of the head is aligned with it. The fast strike always shows a quasi linear displacement of the head (irrespective the position of the prey with respect to the body) and goes along with oropharyngeal expansion for suction. Afterwards the head is retracted.

Feeding in this way might be associated with (at least) three control-problems posed to the musculo-skeletal system of head and neck. (1) Many joints must be moved simultaneously, and in a highly coordinated way, by a multitude of intrinsic neck muscles to obtain the fast, precisely directed final dart towards the prey. (2) Oropharyngeal expansion must generate a proper suction flow. (3) After the strike, the flexible neck must be folded in a particular configuration by a limited number of extrinsic neck muscles.

In the next sections we will focus on each of the above mentioned issues. Special attention will be paid to the manner in which the intrinsic properties of the head-neck system can influence (simplify?) its muscular control. We will argue how the hydrodynamics of suction can play a role in both neck extension and retraction.

#### FAST STRIKE

The head-neck-body system of *Chelodina* (turtles in general), is an open kinematic chain of 10 links (body + eight neck vertebra + head), in extension controlled by a multitude of small mono- and multi-articular muscles (more than 50; for a morphological description of the neck muscles of *Chelodina* see Shah, 1963). This implies a redundancy problem at both the kinematic and kinetic level (*cf.*, Van den Berg, 2000). Theoretically, an indefinite number of combinations of intervertebral rotations, each potentially driven by several alternative muscle activation patterns, is available to strike a target (at any position) by means of a linear head displacement. If it is further taken into account that at any instant the net muscle moments on each vertebral segment (also those showing no rotation) must equal the angular inertia (*i.e.*, moment of inertia times angular acceleration) minus the external moments acting on the segment (see Fig. 1; dynamic equilibrium; see for instance Enoka, 1994; Nigg and Herzog, 1999) it is obvious that the motor programs to apply for fast, accurate strikes are inevitably extremely variable and highly unpredictable. In other words, it is doubtful that these fast ballistic neck movements can be the expression of fixed or general motor patterns, or that these movements could rely on feed-forward information gained during

the pre-strike only. If true, this implies that the fast neck extension during the strike should be steered by instantaneous feedback. But, given the complexity of the dynamic interactions, the redundancy of the system and the high speed of the neck motion (accelerations up to  $44 \text{ m/sec}^2$  are recorded for *Chelodina longicollis*; Van Damme and Aerts, 1997), this seems a rather troublesome task.

Control of the fast strike in *Chelodina*, in which the head accelerates along a linear path towards the prey, can be compared with the problem of unfolding a folding-ruler of ten elements, whereby the next boundary conditions must be satisfied: the proximal element (the body) is fixed; the distal element (the head) has to move (accelerate) along a linear path; and only torques (no linear forces!) can be applied to the joints between elements can be applied (the way muscles act across joints). Obviously, unfolding the ruler under these constraints is no easy task. Nevertheless, this is the problem faced by the intrinsic neck muscles of the turtle during feeding.

The control-problem of the folding-ruler paradigm can be solved in a simple and elegant way by violating one of the boundary conditions (*i.e.*, the sole torque condition). Pull the distal element of the ruler (the head) along a straight line towards the goal and the intermediate elements (the neck segments) will follow one way or another, regardless of their initial configuration. The actual movement pattern will be determined by the intrinsic dynamics of the system (*e.g.*, inertial effects, local frictional forces, etc.).

At first glance, it seems fatuous to propose that the turtle's head is pulled towards the prey, but in fact this is exactly what might happen! In a system on which no external forces and/or moments apply, the total momentum (mass times velocity) cannot change (momentum conservation principle). Considering the turtle and the water as such a closed system, any flow of water must immediately and automatically be compensated for by an opposite momentum somewhere else in the system. Assuming that *Chelodina* uses inertial suction to capture prey, oropharyngeal expansion gener-

ates a backwards flow in the earth bound frame of reference. In that case, an equal and opposite impulse (equal to the change in momentum) acts on the head, representing a pulling force as required to apply the ruler paradigm to neck extension in *Chelodina*. Similarly, Muller *et al.* (1982) and Muller and Osse (1984) argued that (at least part of) the forward displacement of the body of suction feeding fishes relies upon this principle. Jaw protrusion in fishes would add independently to this body translation in reducing the prey distance.

Two observations from our high speed video recordings of feeding *Chelodina* (NAC1000; 500 fr/sec) support this theory. First, the fast strike is always initiated simultaneously with oropharyngeal expansion. Second, inertial suction is definitely present in aquatic feeding *Chelodina*, as displacements of the food particles are very obvious. Ultimate prey velocities (in the earth bound frame; *i.e.*, speed when the prey passes the gaping mouth) of several meters per second are recorded (Van Damme and Aerts, 1997). It has to be remarked, however, that the absence of any obvious prey displacement (see for instance in the snapper and the terrapin; Lauder and Prendergast, 1992 and Summers *et al.*, 1998 respectively) does not automatically imply that there is no inertial flow. Flow visualisations and calculations in suction feeding fishes show that flow velocities rapidly drop with the distance in front of the mouth (Ferry-Graham and Lauder, 2001; Lauder and Clark, 1984; Muller *et al.*, 1982; Muller and Osse, 1984; Van Leeuwen, 1984; Van Leeuwen and Muller, 1984) and this most likely is true for turtles. As prey transport relies upon frictional forces (which depend upon the flow velocity), sometimes the actual flow is insufficient to carry the prey. Moreover, even if external flows (in the earth bound frame) are not evident it is inevitable that water is displaced internally in the oropharyngeal cavity.

Still, to what extent can momentum conservation contribute to the head/neck displacements observed during fast strikes in snake necked turtles? To assess this we present a mathematical model inspired by that used to analyse suction feeding in fishes by

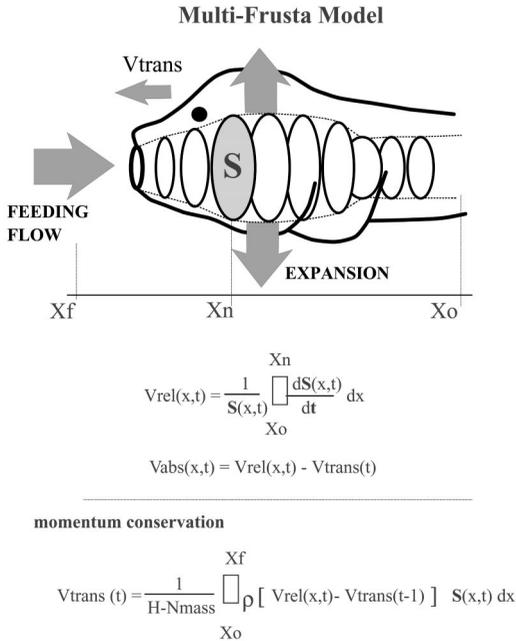


FIG. 2. Schematic representation of the 14 segment multi-frustum model (only some segments are shown).  $V_{rel}(x,t)$  = flow speeds relative to the oropharyngeal cavity;  $V_{abs}(x,t)$  = flow speed in the earth bound frame of reference;  $V_{trans}(t)$  (upper panel) = forward speed of the head/neck;  $V_{trans}(t)$  (lower panel) = forward speed of the head/neck as a result of inertial suction;  $S(x,t)$  = cross sectional surface of oropharynx at location  $x$  at time  $t$ ;  $X_o$  = rostral-most longitudinal position along the neck showing no expansion during feeding;  $X_f$  = position in front of the mouth aperture where the absolute flow speed equals zero;  $X_n$  = any position in between  $X_o$  and  $X_f$ ;  $\rho$  = density of the water;  $H-N_{mass}$  = mass of the head/neck system.

Muller *et al.* (1982) and Muller and Osse (1984). In the turtle model, the expanding oropharyngeal cavity is represented by 14 serially arranged frusta of equal length (*i.e.*, conical segments with a lopped top) of which the instantaneous anterior and posterior radius are determined by the expansion actually observed during the strikes of turtles. The gape coincides with the base of the first frustum, the top of the last frustum is situated well behind the bulging oesophagus. The top radius of each frustum equals the basal radius of the next one (see Fig. 2).

Radial changes were deduced from the high speed movies following the method developed by Drost and Van Den Boogaart

(1986). The profiles of the head/neck of the striking turtle were digitized frame by frame in dorso-ventral and lateral view. Width and height were calculated at 15 equally spaced positions along the mid-line of the head/neck, and elliptical cross-sectional surfaces were calculated for each frame. The ellipses were recalculated to circular cross-sections with equal area. Surface increments from one frame to the next accord to local expansions of the oropharyngeal cavity. The initial volume of the cavity was obtained from dorso-ventral and lateral X-rays of an anaesthetized turtle.

In this way, we can accurately model the internal volume change of the turtle's head and neck throughout the strike. According to the continuity principle any change of this volume must generate a flow *relative* to the turtle's head, that is, any increase in volume must be filled instantaneously with water. The flow involved is constant over any local, instantaneous cross section of the cavity. Indeed, since a gape cycle in *Chelodina* cycle typically takes only 110 msec (Van Damme and Aerts, 1997), the boundary layer can grow to a maximum of 1 mm in thickness, and for that reason friction can be neglected (*cf.*, Muller *et al.*, 1982). Moreover, in turtles, water can only enter the expanding oropharyngeal cavity through the mouth (contrary to fishes). Therefore, the mathematical model is completely determined for the entire strike.

In other words, we can calculate, with great precision, the flow velocities at any location within the oropharyngeal cavity (*relative to this cavity*:  $V_{rel}(x,t)$  in Fig. 2) at any time during the strike by means of the model of the 14 serially arranged expanding frusta (see Fig. 2). This spatio-temporal flow pattern is shown in Figure 6A for a typical strike by *Chelodina*. The velocity in the earth bound frame of reference (see Fig. 6B;  $V_{abs}(x,t)$  in Fig. 2), which is relevant for momentum calculations, is the relative flow minus the forward speed of the head/neck ( $V_{trans}(t)$  in Fig. 2). Also, in front of the mouth, water can have backwards momentum. Muller *et al.* (1982) showed that the external flow velocity along the striking axis can be estimated, based on the strength of a circular vortex

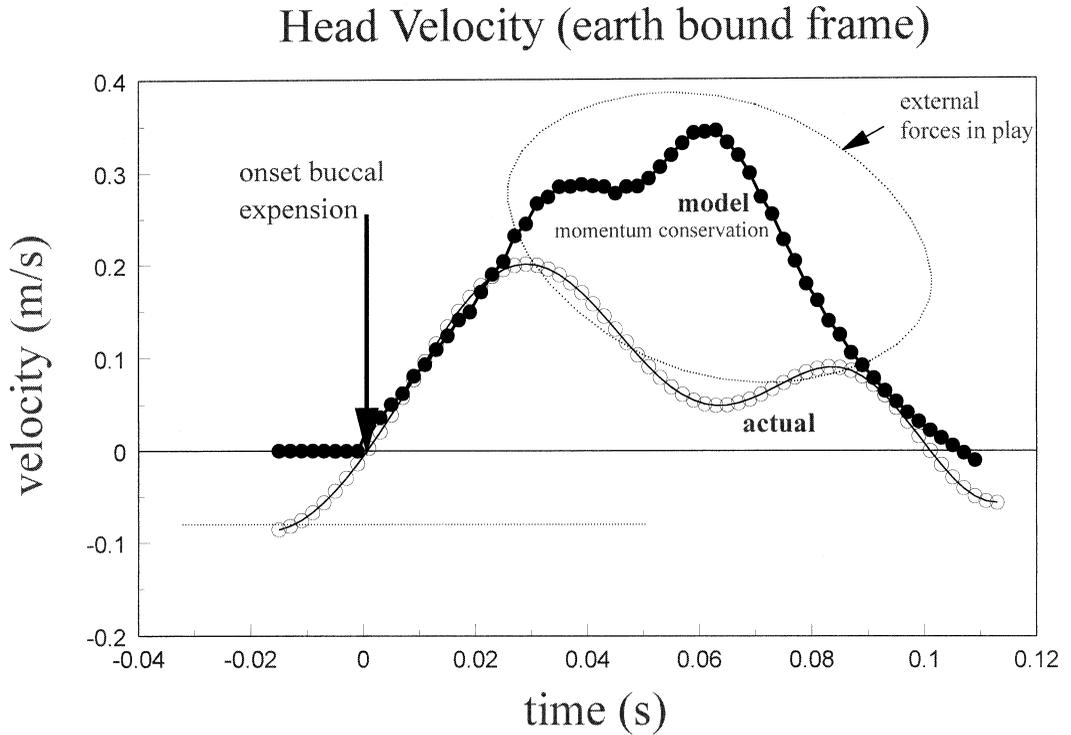


FIG. 3. Forward velocity profiles for the head for typical strike in *Chelodina*, obtained from the high speed video sequence (actual) and the multi-frustum-model (momentum conservation). In the model the head starts from rest. Actually, the turtle head is already moving slowly towards the prey (neck and body movements) at the onset of the strike. (For further information: see text.)

filament situated at the level of the opening mouth (the strength itself depends upon the rate of gaping). We calculated for *Chelodina* that the flow velocity drops, along this axis, virtually to zero within two centimetres in front of the mouth ( $X_f$  in Fig. 2; see above).

To obtain the backwards momentum given to the water as a result of oropharyngeal expansion, the flow rate (absolute flow velocity times the surface area for which this velocity applies) must be integrated over the entire length of the 14 frustum segments and the flow region in front of the mouth (from  $X_o$  to  $X_f$ ; see Fig. 2). For the internal flow, cross-sectional surfaces are known at any location ( $S(x,t)$  in Fig. 2; model input); for the external flow (in front of the mouth) the instantaneous surface area of the gape is used (*cf.*, Van Leeuwen, 1984).

The momentum output of the model allows us to calculate the displacement of the

head/neck system during a fast strike, exclusively as the results of its own inertial suction. Starting from zero speed, the instantaneous forwards velocity of the head/neck can be obtained by dividing the initial backwards momentum by the mass of the head/neck ( $H-N_{mass}$  in Fig. 2). This speed can be used in the next iteration of the numerical procedure to calculate the flow velocity in the earth bound frame, which is used again to get the head speed; and so on (see Fig. 2). A linear velocity profile of the head/neck will be the final result. This can be compared with the actual profile measured from high speed recordings.

The results for a typical strike in *Chelodina longicollis* are shown in Figure 3 (application of the flow pattern presented in Fig. 6B). The required head/neck mass was estimated from a preserved specimen. The added mass is assumed to be very small compared to anatomical mass, because of

the short duration of the strike (the wake needs time to develop) and the tangential direction of displacement. Apparently, the velocity increase of the head observed during the fast strike (*i.e.*, acceleration after mouth opening) can be entirely due to suction (both curves on top of each other). This conclusion is reinforced by the fact that, in the model (which can be considered as an isolated head/neck system), the head should even keep on accelerating when in reality it decelerated already. Since the real head/neck is not isolated from the rest of the body, this deceleration is due to external forces such as muscle activity and passive elastic forces. It is remarkable that at the end of the strike both velocity profiles coincide once again.

It seems that the pulling force that simplified the ruler paradigm applies also to neck extension in *Chelodina*. There is, in theory, no need for control of the fast neck extension during the strike. Once the longitudinal axis of the head is aligned with the prey during the slow approach, the symmetrical expansion of the oropharyngeal cavity ensures a (quasi) rectilinear displacement of the head whenever other forces (*e.g.*, from neck muscles) are small compared to the protrusive suction force. Oropharyngeal expansion will also push water sideways. However, given the symmetry of the movement, the momenta involved in this will largely cancel each other out and will have only minimal (if any) effects on the head/neck displacements. We conclude that the precise and highly directional displacement of the head during the strike is a consequence of the pre-strike behavior (aiming and alignment) rather than being the result of complex feedback modulation. Still, it must be considered that online feedback during the strike might be useful to adjust the strike direction, although perhaps the short duration of the strike does not leave enough time for this.

#### SUCTION FEEDING

Compensatory and inertial suction require precisely controlled and attuned expansion movements of the compartments of the oropharyngeal cavity. Based on the comparative functional analyses of primary

aquatic feeders, it is often argued that the functional demands (obtaining food and carrying it through the mouth cavity) combined to the physical properties of the water limits the theoretically available solutions for this ecological task (*cf.*, for instance Lauder, 1985; Lauder and Prendergast, 1992; Lauder and Shaffer, 1991; Shaffer and Lauder, 1985). In aquatic turtles, the functional morphology of the expansion apparatus (structural and neuromotoric) had to evolve *de novo*, starting from a design adaptively tuned to terrestrial feeding (see for instance Gaffney *et al.*, 1987; Lauder and Prendergast, 1992; Lee, 1997; Pough *et al.*, 2001; Van Damme and Aerts, 1997). It can thus be questioned to what extent phylogeny (through the basic terrestrial design) constrains aquatic feeding performance in these turtles?

In order to feed under water, turtles have to generate a backwards flow relative to the mouth cavity, not only to capture food but also to transport it towards the oesophagus. This can be done by moving the expanding head through the water, engulfing the prey without inducing any flow in the earth bound frame. We call this "compensatory suction" (Van Damme and Aerts, 1997) and according to Lauder and Prendergast (1992) and Summers *et al.* (1998) this is what happens in the snapper and the terrapin, respectively. Alternatively, oropharyngeal expansion sucks water into the 'immobile' mouth cavity by "inertial suction" (Van Damme and Aerts, 1997). Most often, a combination of compensatory and inertial suction will be applied.

Whatever type of suction is used, the oropharyngeal cavity must expand. In turtles expansion largely relies upon the movements of the hyobranchial apparatus which is in *Chelodina* strongly elongated and ossified (see Fig. 4). The mid-sagittal hyoid body is depressed and retracted by the activity of the *coracohyoideus* muscle connecting the pectoral girdle with the hyoid body (Van Damme and Aerts, 1997; Figs. 4, 5). Lateral expansion occurs through rotation of the curved ceratobranchials 1 and 2 (CB1,2) about their articulations with the hyoid body (see Fig. 4). Muscles involved in this are the *branchiohyoideus* muscle

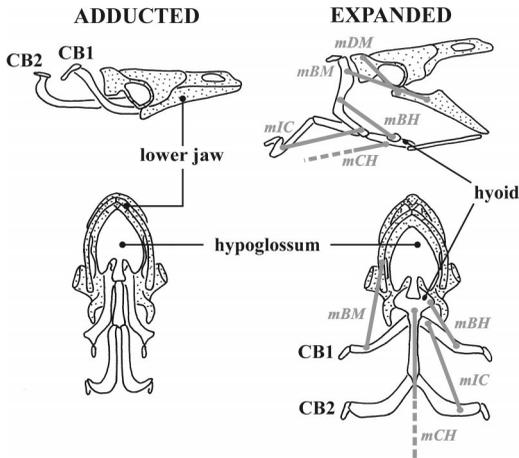


FIG. 4. Schematic representation of the head skeleton of *Chelodina* in the adducted and expanded configuration. Arrows indicate position and orientation of the major expansion muscles. Abbreviations: CB1 = *ceratobranchial 1*; CB2 = *ceratobranchial 2*; mBH = *m. branchiohyoideus*; mBM = *m. branchiomandibularis*; mCH = *m. coracohyoideus*; mDM = *m. depressor mandibulae*; mIC = *m. intercornuatus*.

(connecting CB1 with the rostral part of the hyoid body; Figs. 4, 5) and the *intercornuatus* muscle (running between the distal half of CB2 and the base of CB1; Figs. 4, 5). The orientation of the hinge between CB2 and the posterior margin of the hyoid body also causes a ventral expansion of the posterior most part of the pharyngeal cavity (Van Damme and Aerts, 1997; Fig. 4). Moreover, this movement ensures active opening of the rostral part of the oesophagus, since the latter's orifice is strongly connected to the posterior margins of the left and right CB2's. Depression of the lower jaw occurs through contraction of the *depressor mandibulae* (between neurocranium and jaw) and the *branchiomandibularis* (between CB1 and jaw) muscles (see Figs. 4, 5). The activity of the latter presumably also adds to the lateral expansion of CB1. The buccal floor, in-between the jaw ramus and the hyobranchial apparatus, is reinforced by the stiff hypoglossum. This ensures functional ventral expansion of the buccal cavity (see Fig. 4). During jaw depression, the mouth corners are sealed by skin-folds.

Despite the large structural differences, however, suction feeding proceeds func-

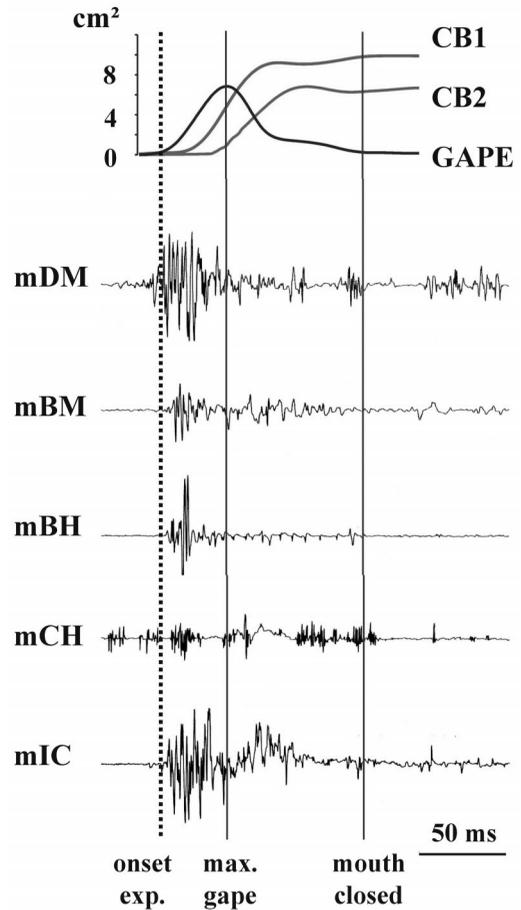


FIG. 5. Electromyographical signals of the major expansion muscles during a typical strike in *Chelodina*. The top panel represents the change of the cross sectional surface of the oropharyngeal cavity at the level of the gape, CB1 and CB2 (see text). Abbreviations as in Figure 4.

tionally the way it does in primary aquatic feeders. In *Chelodina* the feeding process even fulfils the optimal conditions as deduced for fishes (Van Leeuwen and Muller, 1984). Oropharyngeal expansion proceeds in a rostro-caudal wave (Fig. 5, top panel). Nevertheless, as in fishes, the onset of the abductor muscles occurs nearly simultaneously (references in for instance Aerts, 1990; see Fig. 5). The activity of the *intercornuatus* muscle, for instance, starts well before any expansion of the CB2 is observed (see Fig. 5). This contrasts to the temporal spacing of the muscle activity usually observed in terrestrially feeding tet-

rapods (for examples see Schwenk, 2000; Herrel *et al.*, 2001). Obviously, the dynamics intrinsic to a musculo-skeletal system acting in an aquatic medium, together with the requirement for explosive expansion, dictate such synchronisation.

The importance of these hydro-dynamic constraints on the feeding process is further illustrated by its optimization (see above). Van Leeuwen and Muller (1984) inferred from their modelling that (next to the rostral-caudal expansion wave) fishes should expand their oropharyngeal cavity at the maximal rate when the prey enters the mouth (mostly coinciding with maximal gape) and that at that instant the velocity of the prey (*i.e.*, ultimate prey velocity; see above) should be maximized (rather than optimizing the initial prey distance). In all trials analysed thus far, the maximal rate of caudal oropharyngeal expansion by rotation of CB2 coincides with the prey entering the mouth. Moreover, at that instant, prey velocity is maximal (see Figs. 6, 7; *cf.*, Van Damme and Aerts, 1997). Compared to fishes, it thus seems that the CB2 plays the role of the expanding opercula and branchiostegal membrane (*i.e.*, lateral and ventral expansion of the caudal region of the head), whereas rotation of CB1 is equivalent to suspensorial and hyoid abduction. Drawing this parallel, oesophageal bulging is comparable to the flow of water through the opercular slits in fish. As mentioned, the rostral part of the oesophagus can act as a suction pump through its connection with the caudal margins of the CB2's. Obviously, the size of these skeletal elements is related to this function. However, the majority of the bulging to accommodate the engulfed water undoubtedly occurs passively as a result of the inertia of the water (and the rostral compression of the buccal cavity at mouth closure). Figure 6A shows the spatio-temporal velocity profile with respect to the turtle's head. Clearly a continuous backwards flow is present. Even in the earth bound frame, flow reversals are minimal (Fig. 6B).

From the comparison of the relative and absolute spatio-temporal flow patterns shown in Figure 6A and 6B there is little doubt that *Chelodina* applies primarily in-

ertial suction. Otherwise all flow speeds in Figure 6B would be zero (*i.e.*, pure compensatory suction). Support for the reliability of these calculated flow patterns comes from the fact that the computed flow speed at the level of the gape at the instant the food item enters the mouth coincides precisely with the speed of this food item as measured from the high speed video (see Fig. 6A, B). We have already shown that this flow serves the fast strike in that the head is drawn towards the prey. Moreover, from the video scenes we know that the food items are carried by the flow, at least at the level of the gaping mouth. But, how efficient is suction feeding in *Chelodina* in terms of food transport towards the oesophagus? Due to the reduction of the hyoid and branchial arches, no other means than the suction flow seems to be available for this function.

Internal food transport cannot be observed from the conventional video sequences as it becomes invisible for the camera. However, the flow patterns presented in Figure 6 allow us to calculate the displacement of the food item inside the oropharyngeal cavity as long as it can be assumed that the particle behaves more or less like an element of the water. For the pieces of meat (liver) we offered, or for free floating or slowly sinking food items, this condition is certainly fulfilled. For heavy prey such as snails this assumption is violated. Knowing the flow (and prey) velocity at the instant the prey passes the mouth border, the displacement of the prey over a small time increment can be calculated by multiplying this velocity by the time increment. From the flow patterns the speed at this new position can be deduced and the procedure can be repeated (Fig. 7). Applying the spatio-temporal flow patterns relative to the turtle's head, food transport with respect to the oropharyngeal cavity is calculated. For the strike analysed in Figure 6 the particle is carried 3.5 cm backwards, which means that the prey is brought directly behind the CB2's inside the rostral part of the oesophagus. X-ray films taken during feeding showed such a food transport through the oropharynx during the strike (own unpublished observations). When the absolute

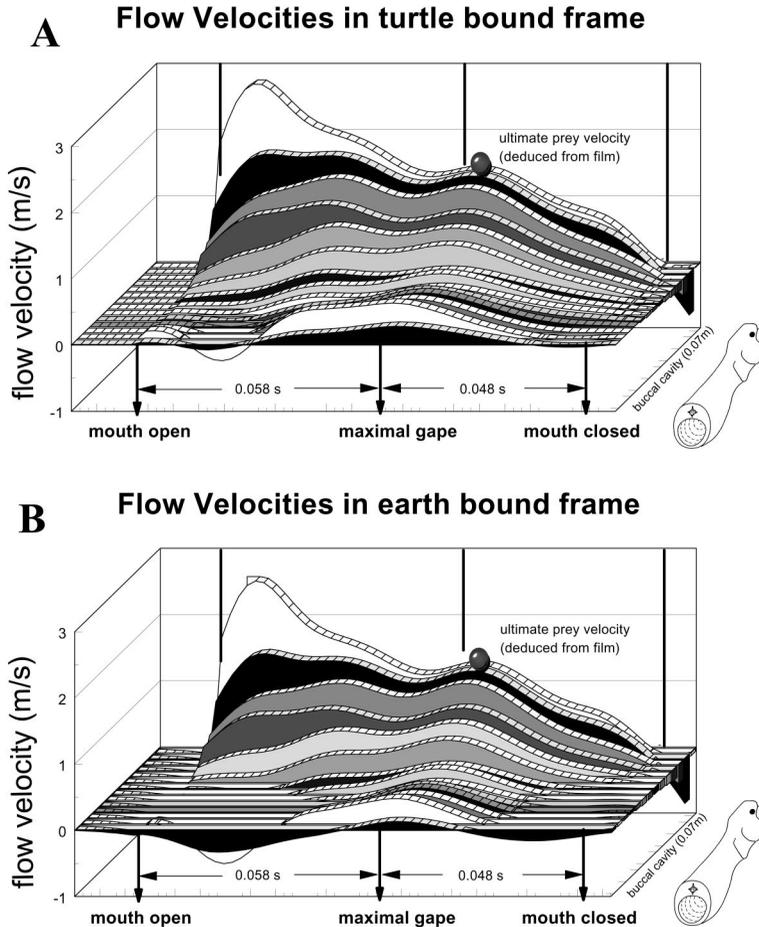


FIG. 6. Spatio-temporal flow velocity patterns inside the oropharyngeal cavity in the turtle bound frame of reference (A) and the earth bound frame of reference (B) for a typical strike in *Chelodina*. Frontal profiles represent flows at the level of the bulging oesophagus; deepest profiles are those at the level of the gape (see cartoons next to graphs). (For more information see text.)

flow pattern is applied, prey displacement in the earth bound frame can be calculated. Once the prey has passed the mouth, “inertial transport” rapidly drops. Anyway, it seems that suction feeding in *Chelodina* is efficient in terms of food transport, too.

One problem remains. During adduction of the expanded head/neck cavities, water has to leave through a very narrow mouth slit and through the nares. Consequently, flow reversal has to occur. The muscles involved in this are primarily the *sphincter colli* and the *intermandibularis* muscles. However, this pharyngeal constriction occurs extremely slowly compared to the suction act itself; it lasts several seconds. As a

result induced forward flows are equally slow. Since transport relies upon friction between medium and food particle (being velocity dependent), the effect on the particle must be small. Moreover, it seems probable that local constrictions of the oesophagus retain the particle when the water is expelled.

#### HEAD RETRACTION

In retracting the head, the open kinematic chain of 10 links suffers theoretically from the same redundancy and complexity problems as mentioned for the strike, although in case of an escape response, when the head is completely retracted in the outer

## Prey Displacement

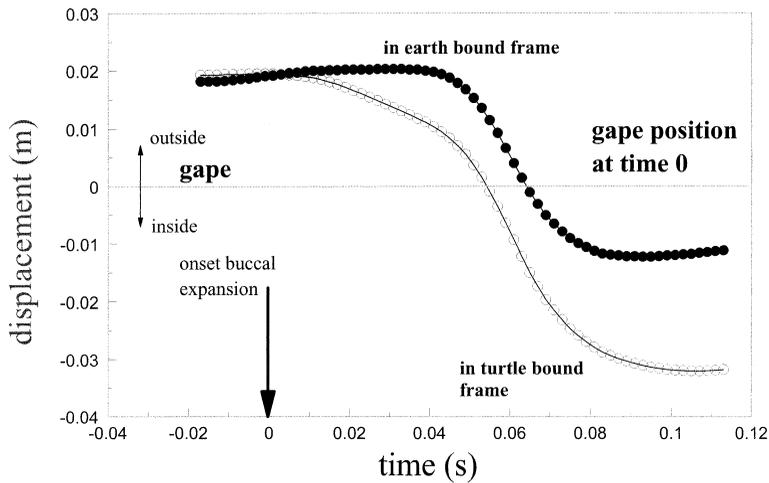


FIG. 7. Displacement of the prey in the earth bound frame of reference and relative to the turtle's head (relative to gape). Zero position coincides with the position of the gape at the onset of suction. Displacements outside the gape are obtained from the video recordings; inside the mouth cavity from the model calculations (see text).

carapacial chamber, the final neck configuration appears to be highly persistent (Van Damme *et al.*, 1995). Apart from the intrinsic neck muscles also useful in the flexion of the individual joints (see above), retraction is likely primarily driven by large extrinsic neck muscles connecting the inner side of the carapace and the dorsal vertebra with the neck vertebra and the skull base (see Van Damme *et al.*, 1995). Questions on the control (fixed program and/or instantaneous feedback modulation?) of the high number of degrees of freedom remain.

Remarkable are the long bundles (left, right) of the *retrahens capitis collique* muscle, originating on the carapace and the vertebral column immediately anterior to the pelvic girdle and inserting by means of a long tendon at the base of the skull (basioccipital; Van Damme *et al.*, 1995). This length (*i.e.*, many sarcomeres in series; *cf.*, *e.g.*, Enoka, 1994) is required to provide the necessary working range and contraction speed for a fast and complete retraction of the head into the outer carapacial chamber. Electromyographical recordings of this muscle always show a bilateral synchronous activity, irrespective of whether the head retracts to the left or right side of the body (Van Damme *et al.*, submitted). The

scheme of Figure 8A shows how bilateral activity can be effective in the unilateral bending of the head. Head retraction usually starts from an incompletely extended neck configuration. Since the *retrahens capitis collique* muscle does not follow the mid-sagittal axis of the vertebral column (see Fig. 8A), instantaneous moment arms are already present at the onset of the retraction. These moment arms dictate the direction of the retraction movement.

However, occasionally the neck extends completely during a feeding strike (*i.e.*, no bends remain). This might constitute a serious problem in terms of control and stability of the subsequent head retraction as a result of the bilateral contraction of the *retrahens capitis collique* muscle. From Figure 8B it is obvious that the extended neck configuration coupled to such bilateral contraction brings the system in an unstable equilibrium. The retraction force is aligned with the extended mid-sagittal axis and in theory no movement will occur. But it is obvious that any minimal disturbance of this equilibrium (small transversal force, shift in one of the joint centres, . . .) will cause an immediate and unpredictable folding of the system.

Still, as mentioned above, the final neck

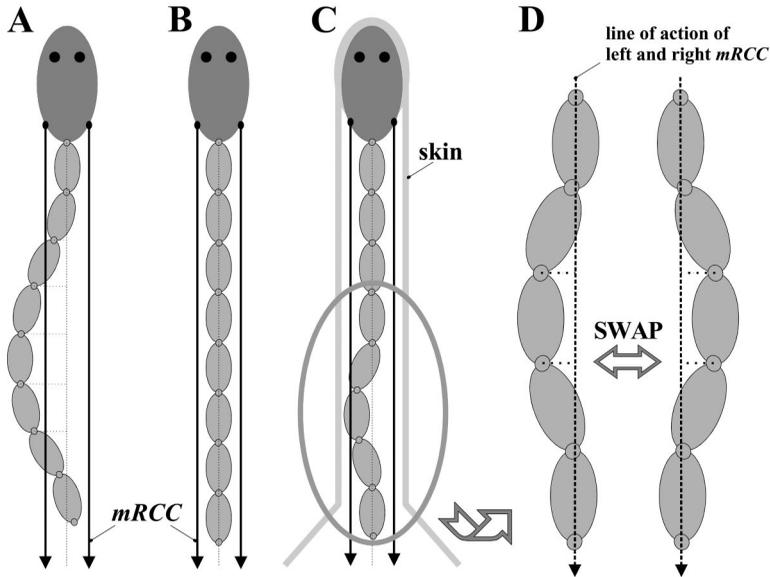


FIG. 8. Schematic representation of the head/neck system and the lines of action (A,B,C) or the common force vector (D) of the bilateral *retrahens capitis et collique* muscle (mRCC). Dotted lines represent moment arms of the co-contracting bundles with respect to the inter-vertebral joints. (For more information see text.)

configuration is highly persistent and erroneous neck folding diverging from this configuration is never observed. X-rays showed, however, that appraisal of neck extension from “external” video recordings might be misleading. It appears that necks which are externally completely extended, always show small initial angles in the joints between cervical vertebrae 8 and 7 and cervical vertebrae 6 and 5 (see Fig. 8C). In this way, small initial moment arms are always present in these joints (see Fig. 8D) and the risk for unpredictable neck folding upon bilateral contraction of the neck retractors does not exist: the direction of the subsequent retraction movement is entirely determined.

On the other hand, retractions from a completely extended neck configuration are the only occasions in which the head moves to the contralateral side of the body (*i.e.*, opposite to the side from which preceding neck extension was initiated). Observations on anaesthetized animals (X-ray films) showed that the just mentioned small initial angles disappear when considerable manual pulling forces are exerted on the head (*cf.*, Van Damme *et al.*, 1995). Strikingly, when the pulling force was released, these angles

often swapped to their mirror configuration (compare the two schemes of Fig. 8D), most likely as the result of the minimization of elastic strain in the joint capsules. Such swaps imply that subsequent bilateral contraction would lead to retraction of the head towards the other body side, just as it is occasionally observed.

Is it conceivable that the pulling forces resulting from inertial suction are sufficient to cause the swapping of the vertebra *in vivo*? In Figure 3 we showed that in the absence of external forces, the head would have moved even further as the result of its own expansion than was actually observed on the video recordings. When maximal extension is reached, this surplus is assumed to be sufficient to explain the vertebral mirroring described above. Moreover, due to the high accelerations involved in striking, also inertial effects must be considered.

#### CONCLUSION

Despite the redundancy and the complexity of the head/neck system in long necked aquatic turtles, the present results suggest that its control is far less intricate than expected on the basis of structure and behavior alone. We argue that the intrinsic me-

chanics (dynamics) of complex musculo-skeletal system play, next to essential neuronal control, an important role in dealing with large numbers of degrees of freedom. It is obvious that the structural complexity needed to fulfill essential ecological functions, does not necessarily require the evolutionary development of complex control systems. Perhaps, this point of view deserves more attention in future functional morphological analyses.

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