

## **The relation between morphology and behaviour during ontogenetic and evolutionary changes**

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During development, form and function (behaviour) change while the match between them must be maintained. The quality of this match determines the importance of morphological parameters in constraining behaviour. If the match is close, the morphology of organisms will be more constraining to the behaviour than when there is a large reserve capacity that creates a certain flexibility. This leads to two questions: (1) How good is the match between form and function during development? The quality of the match necessarily changes during development because changes in structural capacity often cannot proceed at the same speed as changes in functional demand. The evidence for these changes is discussed. (2) What are the mechanisms that maintain the match between form and function during developmental and evolutionary changes? Two mechanisms for maintaining the match are discussed: (a) reserve capacity and (b) flexible muscle activity patterns. Special emphasis is given to fish examples throughout this review.

Key words: development; muscle modulation; cichlids; electromyography; critical periods; reserve capacity.

### **INTRODUCTION**

At all stages of development, an organism must function effectively. It is generally accepted that form and function are adjusted to each other in a qualitative sense, but it is highly controversial whether this is true in a quantitative sense (e.g. Taylor & Weibel, 1981; Garland & Huey, 1987; Lindstedt & Jones, 1987; Weibel *et al.*, 1991; Diamond, 1992). It is important to know how good the quantitative match is, because if the match is close, the morphology (and physiology) of organisms will be more constraining to their behaviour than when there is a large reserve capacity (Fig. 1) that creates a certain flexibility. This has relevance to questions such as how important is the role of morphology in inducing ontogenetic niche shifts and how much plasticity is available in organisms for ontogenetic and evolutionary changes.

### **THE MATCH BETWEEN FORM AND FUNCTION**

Taylor & Weibel (1981) used the term symmorphosis for the hypothesis of a quantitative match between the capacity of organisms and the demand. This idea of symmorphosis goes back to old ideas of functional morphologists regarding optimal matching of structure and function (e.g. D'Arcy Thompson, 1917; Hertel, 1963; Dullemeijer, 1974) and optimal safety factors (Alexander, 1981; Lowell, 1985). Several authors have suggested that a precise quantitative

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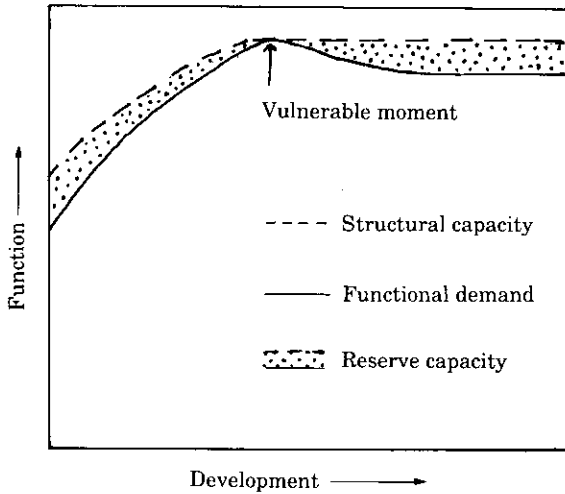


FIG. 1. Schematic diagram illustrating how structural capacity (---) and functional demand (—) of a function may vary during developmental time. When structural capacity exceeds functional demand there is a reserve capacity (stippled area). When there is little or no reserve capacity the animal is vulnerable.

match is impossible given constraints imposed by other functional systems and because of ontogenetic and phylogenetic constraints (Garland & Huey, 1987; Dudley & Gans, 1991).

Following an impressive research programme investigating the oxygen demand and uptake capacity of a large number of mammals, Weibel *et al.* (1991) have concluded that at each step, from the uptake of oxygen in the lungs to the supply of oxygen to the mitochondria, maximum demand is matched to maximum aerobic capacity, with the exception of a large reserve capacity in the oxygen diffusion capacity of the lungs and a smaller reserve capacity in the ability of the heart to deliver oxygen. The evidence for this conclusion comes from comparisons of different mammals and does not test directly whether structural capacity is matched to functional demand because of the difficulty in determining the size of the latter. Determination of the maximum capacity of structures presents less problems and is also in general more straightforward than determination of the functional demand. In other functional systems, too, it will be difficult to determine the exact size of functional demands because of variability and limited predictability of circumstances during development (Alexander, 1988) and because the relation between functional demands and fitness is usually indirect and therefore difficult to measure. However, despite practical problems it is a useful approach. To cope with objections regarding ontogenetic and phylogenetic constraints, the symmorphosis hypothesis should be studied in an ontogenetic and evolutionary context, and the following questions need attention: (1) how good is the match between form and function during ontogenetic and phylogenetic transformations (and how general is the outcome across different functional systems? Are there examples of apparent conflicts between different functional demands?)? (2) what are the mechanisms that allow the preservation of the

match throughout these transformations (and why are these mechanisms sometimes insufficient?)?

#### VARIATIONS IN THE SIZE OF THE RESERVE CAPACITY

Functional demands are not constant and at times vary quite rapidly. Instantaneous changes in structures to meet changed demands are impossible and, therefore, one expects fluctuations in the size of the reserve capacity (Fig. 1). Examples of a temporarily lowered reserve capacity are the increased vulnerability of animals during drastic structural and behavioural transitions (Galis, 1993a), e.g. the metamorphosis of anurans (de Jongh, 1968; Wassersug & Sperry, 1977; Arnold & Wassersug, 1978) and marine fishes (Sette, 1943; Thorisson, 1994); the period of first feeding in fish larvae (Hjort, 1914; Blaxter, 1988); the transition from cutaneous to gill respiration in fish larvae (De Silva & Tytler, 1973; see also Osse, 1989); the bottleneck period before the functional development of the auditory system and the cephalic lateral line system in herring larvae (Fuiman, 1989; Blaxter & Fuiman, 1990; see also Fuiman, 1994); and the myelination of neurons in mammals (Davison & Dobbing, 1966; Oppenheim, 1981). These examples show that the match between form and function changes and is at times constrained due to developmental changes (developmental constraints) leading to a capacity that may even be insufficient to cope with functional demands, i.e. the reserve capacity is negative for certain individuals and they die. On the other hand, there are examples of large reserve capacities that even seem to exceed the necessary safety factors (Alexander & Pond, 1992; Galis, 1992; compare Fig. 6 and Table 6 in Galis, 1993a). There are no examples in the literature of strongly diminished performance during more gradual transitions. Possibly such questions have not been addressed in enough detail, but a plausible explanation could be that mechanisms that are responsible for preserving the match between form and function are more successful during gradual transitions than during drastic ones.

#### MECHANISMS TO COPE WITH DEVELOPMENTAL CHANGES

Organisms have the following mechanisms to cope with challenges posed by developmental changes that may reduce the quality of performance: (1) the complete use of structurally present (reserve) capacity and (2) the enlargement of structurally present capacity *in response to* changes in demand (phenotypic plasticity). This phenotypic plasticity can be divided into (a) plasticity because of changes in form (e.g. the increase in cross-sectional area of bones when exposed to increasing loads) and (b) plasticity because of changes in processes, for example flexible muscle activity patterns in response to sensory perception (muscle modulation, e.g. Ballintijn *et al.*, 1972; Elshoud-Oldenhave & Osse, 1976; Liem, 1978, 1979; Lauder, 1983; Sibbing *et al.*, 1986; Wainwright, 1986, 1989; Sanderson, 1988; Aerts, 1990; Galis, 1992). Possibilities that are not discussed here are the mitigation of vulnerability because of cryptic coloration and behaviour, synchronization, and aggregation during and rapid passage through the vulnerable stage (Wassersug & Sperry, 1977; Arnold & Wassersug, 1978; Stearns, 1982). In the following section I will use examples of flexible

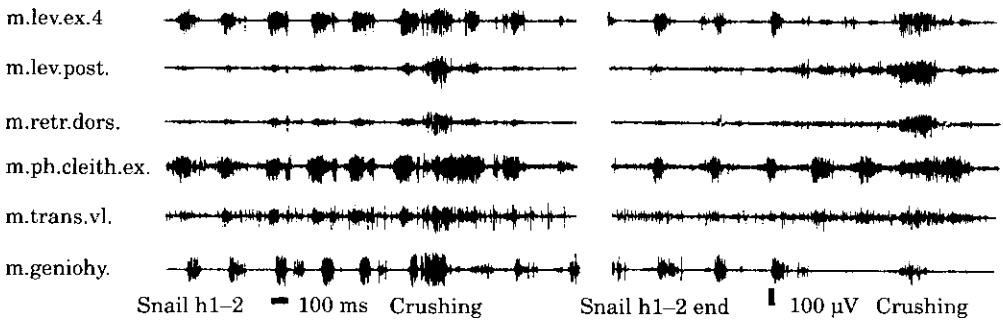


FIG. 2. Electromyogram to show the activity of six muscles during crushing of a snail in the pharyngeal jaw apparatus of a *Labrochromis ishmaeli* (experiment H1-2). All six muscles are active during crushing. The activity of the m. geniohyoideus during crushing is larger in crushing phases at the beginning (left) than at the end (same snail). A possible explanation is given in Fig. 4. For abbreviations, see Fig. 3.

muscle activity patterns from the cichlid fishes *Astatotilapia piceatus* Greenwood and *Labrochromis ishmaeli* Boulenger.

#### FLEXIBLE MUSCLE ACTIVATION

Flexible muscle activity patterns in pharyngeal biting are a necessary requirement for the zooplanktivorous cichlid *Astatotilapia piceatus*, not only to cope with prey of different sizes and with agile prey, but also to cope with ontogenetic changes (Galis, 1993a, b). These results are based on a biomechanical analysis of pharyngeal biting (Galis, 1992). Simulations with a static biomechanical model show that depending on prey size, prey position and biting direction, the motor activity pattern must change. In addition, there are differences in the motor pattern predicted for the adult and the juvenile fish. Therefore, the fish should be able to adjust its muscle activity pattern in response to sensory perception.

Experimental evidence for modulation of the muscle activity patterns during pharyngeal biting comes from electromyography experiments that were carried out to test the predictions of the model on the molluscivorous *Labrochromis ishmaeli* (Galis & Terlouw, in prep.). The muscle activity patterns of pharyngeal biting are not always the same. When a snail is being crushed, all recorded muscles are strongly active, high amplitude in the power phase Fig. 2 and see Fig. 3 for the position of the muscles; a quantitative analysis of the EMG patterns is described in Galis & Terlouw (in prep.). The antagonist m. pharyngocleithralis externus is also active, but usually starts somewhat later than the other muscles and continues longer. Possibly the m. pharyngocleithralis externus is active in the power phase to balance the large forces that are simultaneously generated. A similar overlap in the activity of antagonistic muscles is found in mollusc-crushing centrarchids (Lauder, 1983), during the food uptake of perches (Osse, 1969) and in piscivorous cichlids when they catch elusive prey (Liem, 1978). In the latter case there is far more overlap in the activity of antagonistic muscles than when less active prey are caught, which presumably requires much smaller forces (Liem, 1978). The power phases towards the end of the handling of a snail often show a significantly decreased activity of the m. geniohyoideus. Since it seems likely that the snail becomes smaller toward the end of crushing,

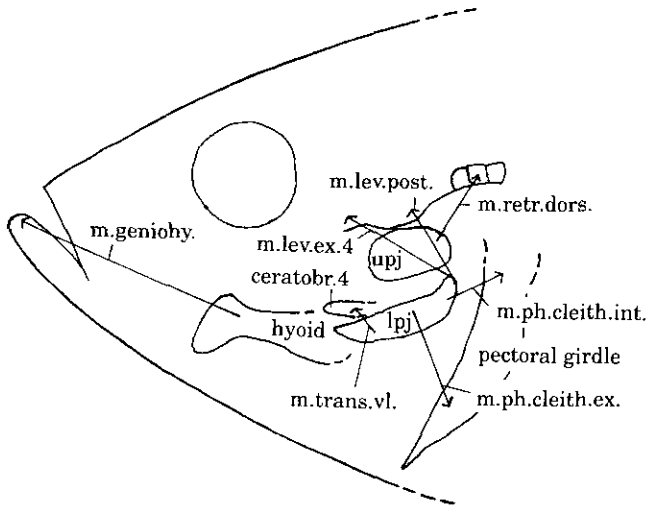


FIG. 3. Schematic diagram of muscles and bony elements in the head of *Labrochromis ishmaeli* to show the position of the muscles from which recordings were made in this study. m. geniohy., m. geniohyoideus; m. lev. post., m. levator posterior; m. retr. dors., m. retractor dorsalis; m. lev. ex. 4, m. levator externus 4; ceratobr. 4, ceratobranchiale 4; m. ph. cleith int., m. pharyngocleithralis internus; m. ph. cleith. ex., m. pharyngocleithralis externus; m. trans vl, m. transversus ventralis; upj, upper pharyngeal jaw; lpj, lower pharyngeal jaw.

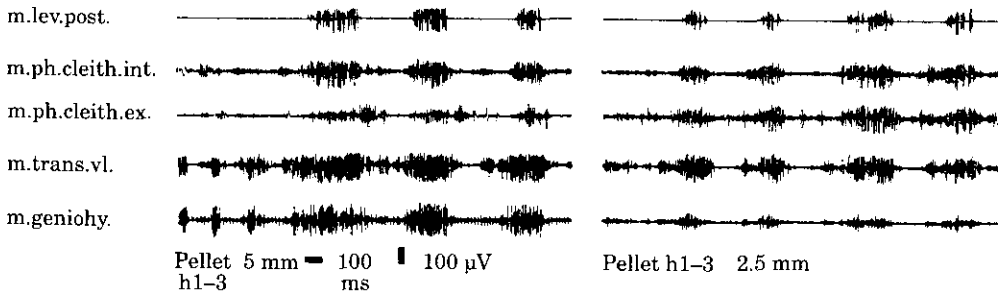


FIG. 4. Electromyogram to show the activity of five muscles during crushing of artificial food pellets in the pharyngeal jaw apparatus of a *Labrochromis ishmaeli* (experiment H1-3). The m. geniohyoideus is less active when crushing a thin pellet than when crushing a thick pellet that is otherwise similar (same experiment). This result is predicted by the biomechanical model of Galis (1992) because the position of the m. geniohyoideus is more favourable for biting when the lower pharyngeal jaw is rotated downward to accommodate a large prey item.

the reduced distance between the jaws implies a less depressed lower pharyngeal jaw and therefore a less effective position of the m. geniohyoideus for crushing (Galis, 1992). Evidence for the importance of the position of the m. geniohyoideus comes from the comparison of results of feeding on artificial food pellets of varying sizes. When pellets with a thickness of 0.5 mm are crushed, the activity of the m. geniohyoideus was markedly larger than when similar pellets of 0.25 mm are crushed (Fig. 4). Another possible explanation for the decreased activity of the m. geniohyoideus may be that less force is necessary at the end of a crushing cycle when the food bolus is smaller.

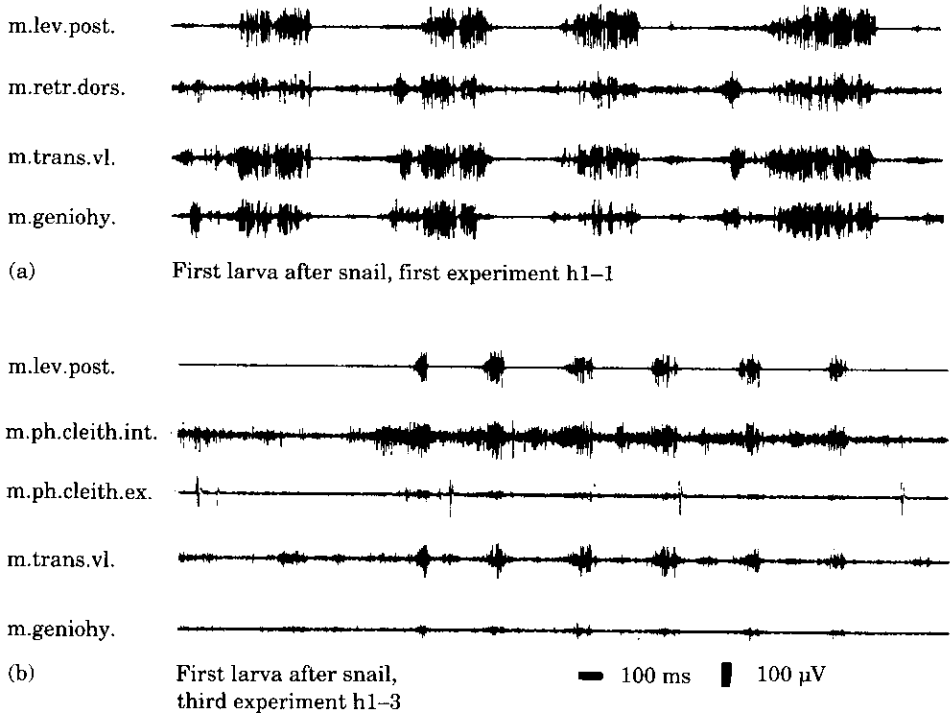


FIG. 5. (a) Electromyogram to show the activity of four muscles during crushing of a *Chaoborus* larva in the pharyngeal jaw apparatus of a *Labrochromis ishmaeli* that had no prior experience with this prey type (experiment H1-1). The pattern strongly resembles the pattern of snail and pellet crushing. (b) Electromyogram of the same fish after 4 weeks experience crushing *Chaoborus* larvae. It shows the activity of five muscles and the typical pattern that emerged after experience with this food type (experiment H1-3). The activity of the muscles has a shorter duration and the m. pharyngocleithralis externus and m. geniohyoideus are hardly active.

### Indications of learning

Additional evidence for flexibility in the motor pattern comes from an analysis of the motor patterns of a fish that had no experience with eating *Chaoborus* larvae at the start of our experiments (Fig. 5). When first feeding on these insect larvae, the pattern was similar to that when handling snails with which the fish had been fed mainly i.e. long and strong activity during the power phases of all the muscles recorded. After some larvae were eaten, the pattern became variable in that the activity of the m. geniohyoideus was negligible, intermediate, or strong. With increasing experience the variation disappeared and a typical *Chaoborus* pattern emerged which showed little activity of the m. geniohyoideus and m. pharyngocleithralis externus. The snail pattern stayed the same and continued to show pronounced activity of the m. geniohyoideus. The reduced activity of the m. geniohyoideus when eating *Chaoborus* larvae is again in agreement with the hypothesis that this can be explained by the changed distance between the jaws when biting. After 7 months of not being exposed to *Chaoborus* larvae, or other food items with a thin diameter, renewed experience with *Chaoborus* larvae led to a return in the variability of the activity of the m. geniohyoideus suggesting that the earlier experience was forgotten.

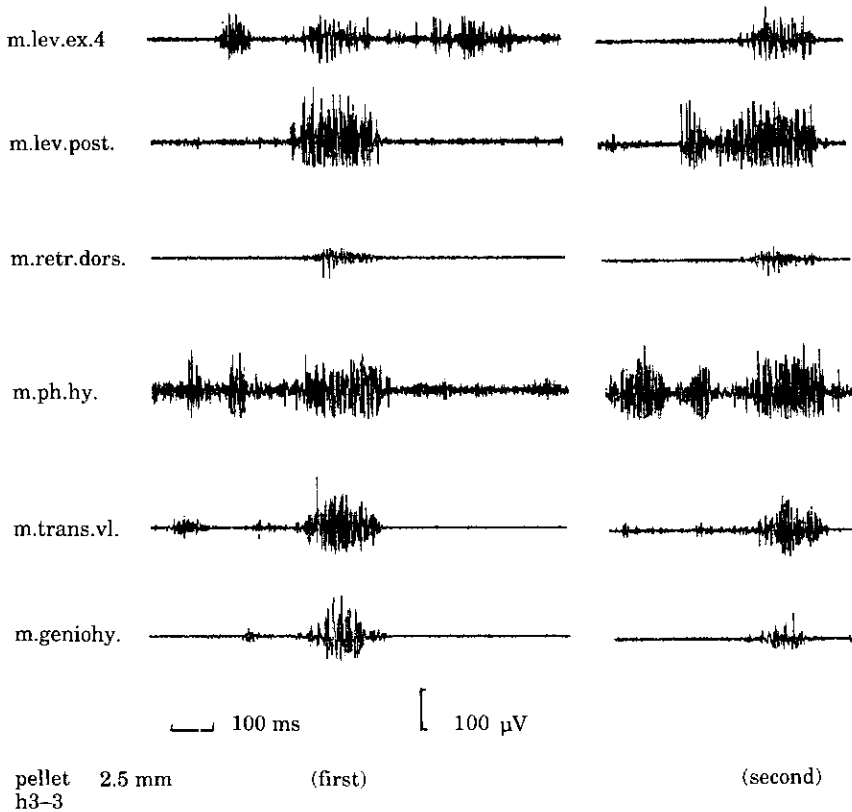


FIG. 6. Electromyogram to show the activity of five muscles during crushing of thin artificial food pellets in the pharyngeal jaw apparatus of a *Labrochromis ishmaeli* (experiment H3-3). The fish only had experience with snails and thick pellets. The first pellet eaten (left) induces considerably larger activity (higher amplitude) of the m. geniohyoideus than the second and later pellets.

Further indications for learning come from the results of two other *L. ishmaeli* individuals. They were presented with thin pellets, after ample experience with snails and thick pellets but no experience with thin pellets or other thin food items. The first time all muscles were strongly active (see Fig. 6 for individual H3; the lower activity of the m. retractor dorsalis is due to the bad quality of the signal). By only the second time, the response of the m. geniohyoideus was markedly less strong, as turned out to be the typical pattern for thin pellets (see also Fig. 4). This time the behavioural change occurred rapidly.

One more example of this type of change in muscle activity patterns in response to experience is presented in Fig. 7. An individual of *L. ishmaeli* that had experience with snails, thick and thin pellets, and *Chaoborus* larvae and pupae was presented for the first time with a mixture of *Daphnia* and *Cyclops*. Initially the electromyographical pattern strongly resembled the pattern of the power phases of processing *Chaoborus* larvae and pupae. *Chaoborus* larvae and pupae were the smallest and thinnest prey items that had been experienced before and, in addition, were the food items most recently processed. The pattern gradually changed and within 4 min of eating the zooplankton mixture a typical

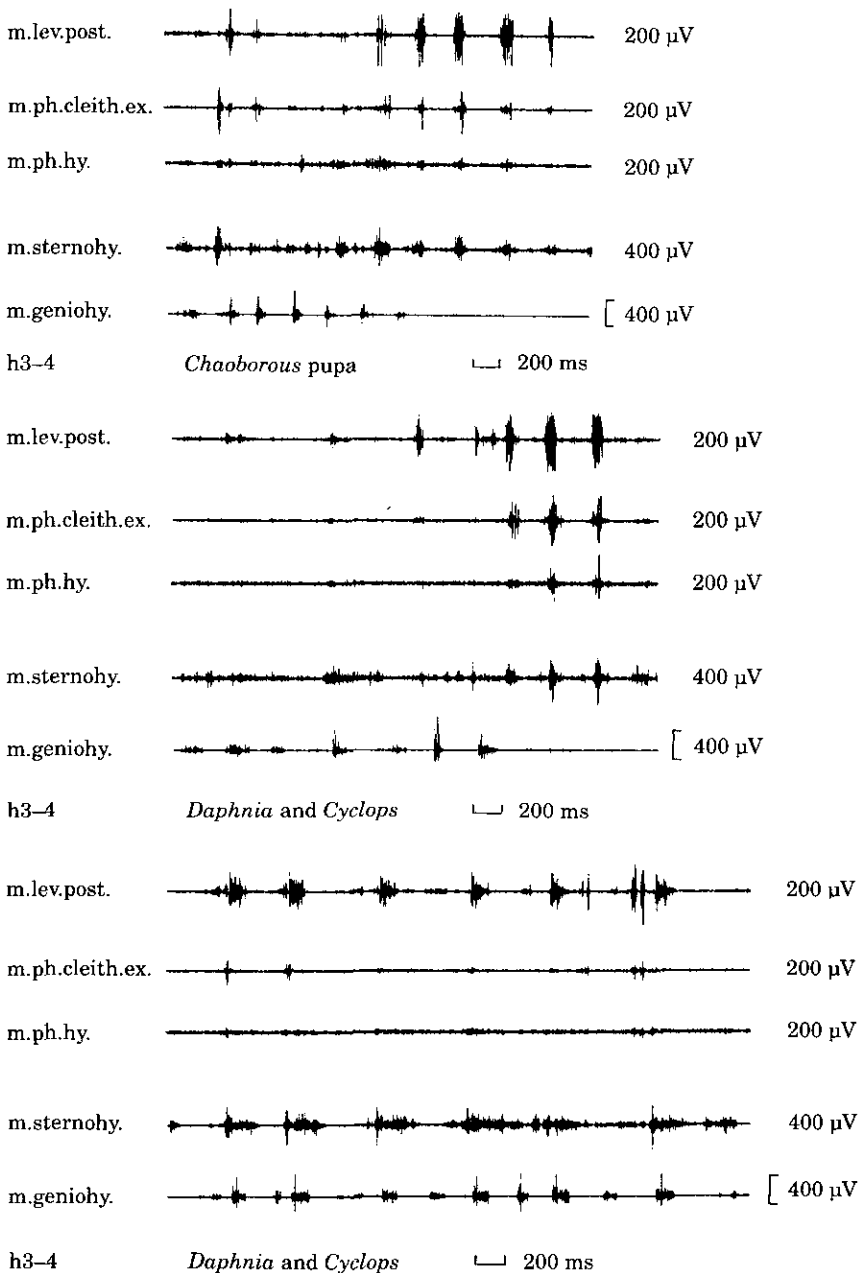


FIG. 7. Electromyogram to show the activity of five muscles during processing of *Chaoborus* pupae and *Daphnia* and *Cyclops* spp. by a *Labrochromis ishmaeli* (experiment H3-4). Before the experiment the fish had experience with snails, thick and thin pellets, *Chaoborus* larvae and pupae, but not with *Daphnia* and *Cyclops* or other very small food items. Initially the pattern resembled the power phases of *Chaoborus* larvae and pupae processing with little activity of the *m. geniohyoideus*. The *m. geniohyoideus* is active in the preparatory phase (upper and middle electromyogram). Gradually the pattern changed into one where there is activity of the *m. geniohyoideus* and virtually none of the *m. pharyngocleithralis externus* and the *m. pharyngochoyoideus* (lower electromyogram). The activity of the *m. sternohyoideus* is prolonged.



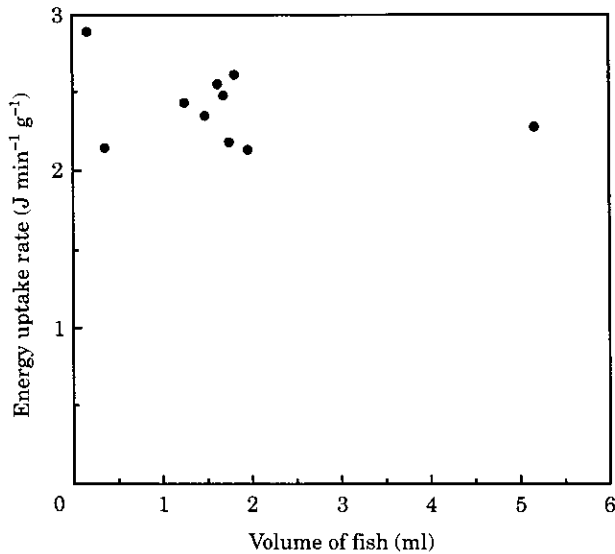


FIG. 8. Diagram showing that the energy uptake rate ( $\text{J min}^{-1} \text{g}^{-1}$ ) of *Astatotilapia piceatus* when eating *Chaoborus* larvae does not vary with the volume of the fish (data from Galis, 1990). A volume of 0.17 ml coincides with s.l. 1.9 cm, 1.6 ml with 4 cm and 5.2 ml with 6 cm.

pattern emerged that was considerably different from the patterns of processing snails, pellets, and insects.

These results indicate strongly that learning is involved in response to sensory perception of different kinds of food. Wainwright (1986) found similar indications of learning during the food uptake of the centrarchid *Lepomis gibbosus* (L.).

Claes & De Vree (1991) found ample variability in the kinematic patterns of pharyngeal jaw movements of the zooplanktivorous cichlid *Oreochromis niloticus* L. Thus, modulation of the muscle activity patterns during the powerphases of pharyngeal biting seems to be a general phenomenon in cichlids. These results on cichlids are in contrast with earlier reports of stereotypy in pharyngeal prey processing in centrarchids (Lauder, 1983, 1990). Centrarchids are basal percoids whereas cichlids are derived percoids (labroids) (Kaufman & Liem, 1982; Stiassny & Jensen, 1987), suggesting that the flexibility could be limited to cichlids and possibly labroids in general, which are characterized by a specialized pharyngeal bite (Liem, 1973; Liem & Greenwood, 1981). However, Vandewalle *et al.* (1992) found variability in the kinematic patterns of pharyngeal processing in serranids, which like centrarchids are basal percoids, suggesting that the phenomenon might be more general.

#### *Gradual transition*

The food uptake behaviour of *A. piceatus* during ontogeny provides a good example of a gradual transition. The capability of the pharyngeal jaw apparatus to handle prey increases linearly with weight (Galis & de Jong, 1988). When eating *Chaoborus* larvae, the energetic reward per unit time and unit body weight is similar for fish differing substantially in body weight (Fig. 8). Most parameters of the pharyngeal jaw apparatus change isometrically or slightly allometrically (Galis, 1990). When biting a similar prey item, the torques and positions of

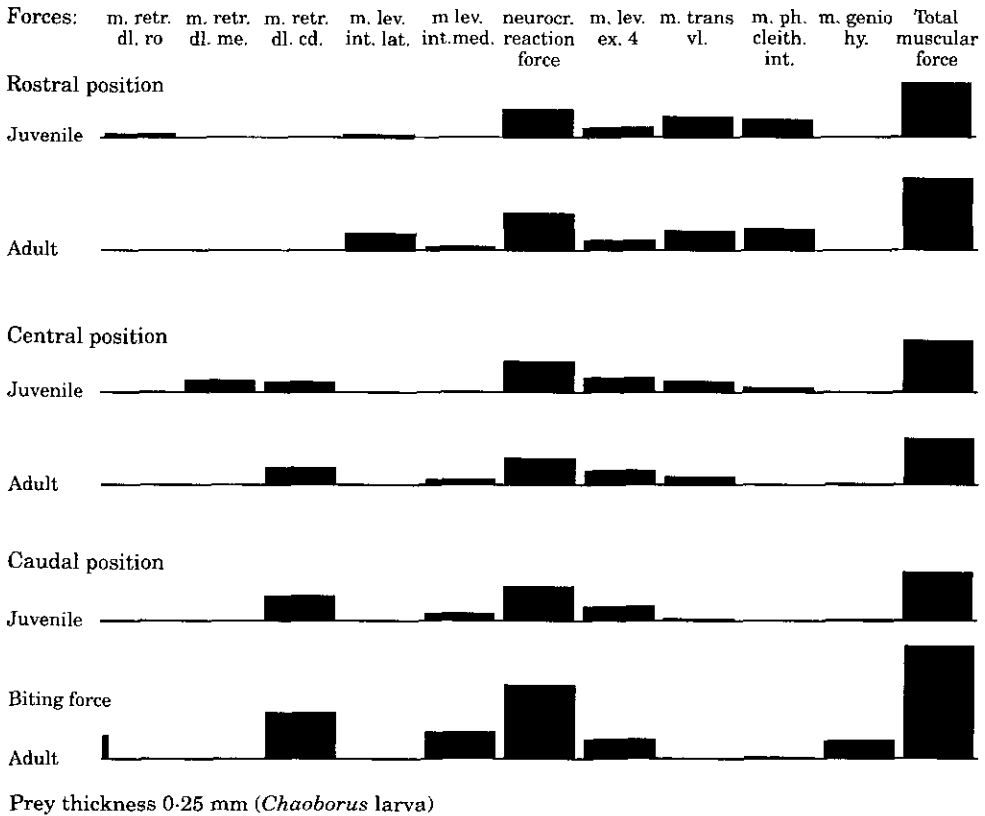


FIG. 9. Comparison of predicted juvenile (2.5 cm, s.l.) and adult (5.0 cm, s.l.) muscle recruitment for piercing of a *Chaoborus* larva at a rostral, central and caudal prey position in *Astatotilapia piceatus*. Contributions of individual muscles and of the neurocranial reaction force are indicated. Note that total muscular force does not include the neurocranial reaction force. The net biting force that is exerted on the prey is indicated in the left lower corner (from Galis, 1993b). m. retr. dl. r. o., m. retractor dorsalis, rostral; m. retr. dl. me., m. retractor dorsalis, mesial; m. retr. dl. cd., m. retractor dorsalis, caudal; m. lev. int. lat., m. levator internus, lateral; m. lev. int. med., m. levator internus, medial; m. lev. ex. 4, m. levator externus 4., m. trans. vers., m. transversus versalis; m. ph. cleith. int., m. pharyngocleithralis internus; m. genio. hy., m. geniohyodeus.

muscles during biting change with increasing size of the predator. This means that the motor patterns must adapt to these changes during ontogeny (Galis, 1993b and see Fig. 9). The biomechanical model shows that provided that motor patterns are flexible, maximum possible biting force increases linearly with cross-sectional area of the muscles (Galis, 1992, 1993b). Thus, flexible muscle activity patterns can explain the absence of developmental constraints that otherwise would limit the level of performance because they buffer the effects of morphological changes.

Heidweiller *et al.* (1992) found that flexible muscle activity patterns are necessary for chickens to maintain the ability to drink during ontogeny, adding evidence for the general importance of such mechanisms in avoiding developmental constraints. Furthermore, in mammals there are important shifts in muscle activity patterns during the transition from suckling to mastication (Herring, 1985; Langenbach, 1992; in press).

It is reasonable to expect that flexibility in motor patterns not only reduces developmental constraints by buffering the effects of changes but in a similar way reduces phylogenetic constraints (for the facilitation of evolutionary changes by phenotypic plasticity, see amongst others Mayr, 1974 on behavioural plasticity; Stearns, 1983; Hanken, 1983; West-Eberhard, 1989).

Thus, evidence for the importance of flexible muscle activity patterns is accumulating. Deich & Balsam (1993) have argued that the strong emphasis on stereotypy of muscle activity patterns in earlier literature is biased and can be explained in large part by stereotypy in the experimental conditions employed. It seems that researchers of vertebrates are becoming more and more aware of the importance of flexible motor patterns (Adams, 1984; Aerts, 1990; Langenbach, 1992, in press; Galis, 1992, 1993*b*; Deich & Balsam, 1993).

### RESERVE CAPACITY

It was mentioned earlier that the reserve capacity (Fig. 1) is not constant during ontogeny. A considerable reserve capacity at the start of a critical period may in itself be a mechanism that prevents developmental constraints and as such facilitates ontogenetic changes. Similarly, during ontogenetic stages in which the reserve capacity is large, there must be freedom for evolutionary changes (see also Gans, 1979).

### CONCLUSION

Flexible muscle activity patterns and reserve capacity probably provide organisms with mechanisms that buffer the effects of form and behaviour changes and enable them to reduce or avoid developmental constraints that hamper their performance temporarily. The same should hold for other types of phenotypic plasticity. Similarly, the freedom that is created by flexible muscle activity patterns and reserve capacity will facilitate evolutionary changes by accomodating morphological and behavioural novelties. Therefore, flexible muscle activation and reserve capacity most likely facilitate both ontogenetic and evolutionary changes.

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