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Schema-based learning of adaptable and flexible prey-catching in anurans I. The basic architecture

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Abstract A motor action often involves the coordination of several motor synergies and requires flexible adjustment of the ongoing execution based on feedback signals. To elucidate the neural mechanisms underlying the *construction* and *selection* of motor synergies, we study prey-capture in anurans. Experimental data demonstrate the intricate interaction between different motor synergies, including the interplay of their *afferent* feedback signals (Weerasuriya 1991; Anderson and Nishikawa 1996). Such data provide insights for the general issues concerning two-way information flow between sensory centers, motor circuits and periphery in motor coordination. We show how different afferent feedback signals about the status of the different components of the motor apparatus play a critical role in motor control as well as in learning. This paper, along with its companion paper, extend the model by Liaw et al. (1994) by integrating a number of different *motor pattern generators*, different types of afferent feedback, as well as the corresponding control structure within an adaptive framework we call Schema-Based Learning. We develop a model of the different *MPGs* involved in prey-catching as a vehicle to investigate the following questions: What are the characteristic features of the activity of a single muscle? How can these features be controlled by

the premotor circuit? What are the strategies employed to generate and synchronize motor synergies? What is the role of afferent feedback in shaping the activity of a MPG? How can several MPGs share the same underlying circuitry and yet give rise to different motor patterns under different input conditions? In the companion paper we also extend the model by incorporating learning components that give rise to more flexible, adaptable and robust behaviors. To show these aspects we incorporate studies on experiments on lesions and the learning processes that allow the animal to recover its proper functioning.

1 Introduction

We present a model that can account for a variety of data on motor pattern selection and coordination. In the companion paper we extend the model to also account for motor learning during the animals developmental stages and after bilateral hypoglossal (HG) transection. This study is an ongoing development of Rana Computatrix, the computational frog, an evolving account of a single animal integrating aspects of perception with mechanisms for the control of an expanding repertoire of behavior (Arbib 1987). Ewert and colleagues (Ewert 1997, 1987; Ewert and Arbib 1989, 1991; Ewert et al. 1992) have studied the anatomy, and physiology of anurans and have provided many insights for a functional perspective which have been the basis for the development of Rana Computatrix. Complementarily, Roth (1987) and colleagues have studied the anatomy and physiology of salamanders and have also provided insights that have helped to enrich the computational perspective. A motor action often involves the coordination of several motor synergies and requires flexible adjustment of the ongoing execution based on feedback signals. This overall project also includes elements of adaptation. Anurans learn effective ways of feeding that are both flexible as well as robust under noise and missing information.

Although we agree that in order to be able to understand how the nervous system generates behavior with the nerve

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cells as the building blocks, one needs to work on all neural levels of organization from molecules, cell, and synapse to network and behavior (Grillner 1997; Schöner 1995) we shall restrict the model to only contain the essential ingredients for the task at hand. A wide variety of motor tasks reveals correlations between features of the electromyography (EMG) record and task parameters (e.g. Schmidt et al. 1988; Sherwood et al. 1988; Gottlieb et al. 1992). However, the neural mechanisms responsible for the control of muscle activity are poorly understood due to the complexity of the premotor and motor circuits involved. Most of the modeling work on *goal-directed* movements concentrates on the optimization criteria used in the computation of inverse kinematics (e.g. Bizzi et al. 1992; Hoff and Arbib 1993). Also abstract models of coordinating serial motor synergies have been proposed (e.g. Rumelhart and Norman 1982 for typing; Schomaker 1992, for handwriting; Sanguineti et al. 1998, for speech production). Research on *motor pattern generators* (MPGs), on the other hand, has thrived in studying rhythmic behavior such as gastric mill rhythms in lobsters (Selverston and Moulins 1987) and locomotion (Cruse et al. 1995a,b; Grillner et al. 1995; Kozlov et al. 2002).

Recent research projects bridge the gap by extending the simulation models to include also the muscular generation of the movements, thereby verifying that the motor patterns produced actually correspond to the expected real movements (Cruse et al. 1995a,b; Ekeberg 1993; Ekeberg et al. 1995; Hatsopoulos 1996; Huerta et al. 2000; Ogiwara and Yamazaki 2001). In this regard the model described in this paper can be linked to the biomechanical model for the simulation of prey capture in toads described by Nishikawa et al. (1997).

However, several aspects regarding the neural mechanisms of the MPG involved in coordinating goal-directed episodic motor synergies are still poorly understood. The accessibility of the premotor circuitry in anurans presents an excellent opportunity to study the neural mechanisms underlying the coordination of multiple motor synergies. This behavior carries all the essential aspects of motor control, including the interaction of an agonist and an antagonist in generating a single motor synergy (e.g., the protraction and retraction of the tongue), and the synchronization of multiple motor synergies. Also in anurans, visual information about the target and proprioceptive information about the animal's starting position interact in feedforward control of prey capture. However, it is unclear where and how these sensory modalities interact in the brain. The model we propose attempts to shed a light on this matter by proposing a specific integration of sensory modalities, e.g., depth perception, proprioceptive feedback, etc. Related work includes the analysis of reflexive feedback control loops (Steinkühler and Cruse 1998; de Vlugt et al. 2001), motor modular organization (Bizzi et al. 1998; Eilam and Smotherman 1998; Loeb et al. 1999), the interactions between different motor components (e.g. between eye and head control signals, Edward and Freedman 2001), construction of movement (Tresch et al. 1999; Sumbre et al. 2001), action selection (e.g. Gurney et al. 2001a,b), sensory integration (e.g. van der Kooij et al.

2001) and neural modulation of visuomotor functions (e.g. Ewert 1997; Ewert et al. 2001). We provide insights for the general issues concerning two-way information flow between sensory centers, motor circuits and periphery in motor coordination. We also show how *afferent feedback* carrying the signal about the status of the motor apparatus plays a critical role in motor control (Cruse 1999; Schöner et al. 1998). The transformation of sensory signals into appropriate *spatio-temporal* patterns of activity in the motoneurons is postulated to be carried out in part by MPG. In this paper we extend the model described in Liaw et al. (1994) by incorporating a larger number of components along with their corresponding control structure, in turn giving rise to the emergence of several MPGs.

In (Corbacho et al. 1996a,b) we focused on the dynamics of jaw opening. In this paper we also model tongue protraction and retraction, head flexion and lunging. The model proposed in this paper simulates jaw muscles Depressor Mandibulae, and Levator Mandibulae, and tongue muscles, Genioglossus and Hyoglossus which protract and retract the tongue respectively. It also includes MPGs for Lunge and head ventro flexion as well as the corresponding *premotor* control circuits in the reticular formation (RF). The model also includes a variety of *sensory feedback* components. For instance, we introduced *sensory feedback* about the state of the jaw by muscle spindles in jaw muscles through the trigeminal nerve. It has already been shown that muscle spindles from the jaw muscles project to the cerebellum (Lund and Enomoto 1988). We now hypothesize that they also project to the reticular formation. This is also analogous to the Hypoglossus nerve which projects to the granular layer of the cerebellum as well as to the reticular formation.

The model explains data on *motor program selection* based on parameters of the visual input. The same structure can give rise to different motor patterns by changing the input stimuli. Jaw Prehension (JP) and Tongue Prehension (TP) correspond to whole *coordinated control programs* (CCPs) involving a complex set of control decisions through different *spatio-temporal patterns*. For instance in JP there is a bigger lunge and the head is flexed ventrally. Nishikawa and Gans (1992) have shown that mandibular levators (LM) activity is delayed with respect to mandibular depressors (DM) activity if the mouth is to open. In the model HG modulates premotor LM so that before the hypoglossal nerve (HG) transection LM is delayed with respect to DM. For large prey interneuron (INT1) is active in turn inhibiting premotor LM giving raise to the jaw prehension. On the other hand, for small prey INT1 is not active enough so that premotor LM is inhibited through HG giving raise to the tongue prehension.

In the companion paper we will also show that the ability to form, store and retrieve spatiotemporal patterns is essential to go from basic motor programs to coordinated motor programs (CMP). Some CMPs are innate others must be constructed as the animal faces situations that it cannot handle with pre-existing programs. A special case occurs when the animal undergoes a lesion so that some previous program is no longer available but components of it may be. We will

later show how schema-based learning (SBL) is capable of “taking” motor components to construct a new motor program to “restore” the lost functionality.

2 Anuran snapping: behavioral observations

In this section we summarize the most relevant behavioral observations concerning anuran prey catching. The key stimulus that elicits prey capture is either visual, tactile or olfactory, and the outputs of their respective sensory analyzers share common access to motor pattern generators responsible for the elaboration of the appropriate motor outputs. A toad when confronted with a prey in its visual field will first orient towards the prey and then approach to the snapping distance from the prey (Ingle 1983; Ewert 1997). Once the prey is within the snapping distance the toad will perform one of the following catching strategies defined below.

Anuran prey capture consists of a sequence of motor synergies released by a specific stimulus. This series of steps includes an approach or orientation towards the prey stimulus, a fixation of the prey in the frontal visual field and the consummatory event of snapping at the prey and swallowing it (Ewert 1987). Snapping starts with a lunge of the head towards the prey, followed by mouth opening, protrusion of the tongue, retraction of the tongue with the prey, closure of the mouth, return of the head and body to resting position, and swallowing of prey. Gans and Gorniak (1982) divided the feeding sequence of toads into four phases, (1) preparatory, (2) tongue protrusion, (3) tongue retraction, and (4) mouth closing. Since the observation that the sequence proceeds to completion once initiated, despite removal of the target (Hinsche 1935), snapping has been regarded as highly *ballistic* with little or no variability based on sensory feedback (Ingle 1983; Ewert 1984). Nevertheless, recent behavioral observations by some of the authors have revealed a feedback component in snapping (Liaw et al. 1998).

2.1 Prey catching motor patterns

Anurans have evolved at least two different motor patterns for prey-catching. Motor selection is based on the visual signal (e.g., prey size) (Anderson and Nishikawa 1993). *Rana pipiens* exhibits differing behavior patterns depending upon prey type (Anderson and Nishikawa 1993). When feeding on small prey such as waxworms *Rana pipiens* uses TP to catch the prey, minimizing head and body movements (Fig. 1 Left). On the other hand, when feeding on the larger earthworm, it arches its body, flexes the head downwards and uses JP to capture the prey - the animal lunges further and ventroflexes its head to grab the prey with its jaws (Fig. 1 Right).

The onset of mouth opening is different for the jaw and the tongue pattern (Anderson and Nishikawa, 1993). The total time that the mouth is open and maximum tongue reach were significantly longer during waxworm feedings than during earthworm feedings. The tongue angle and degree of head

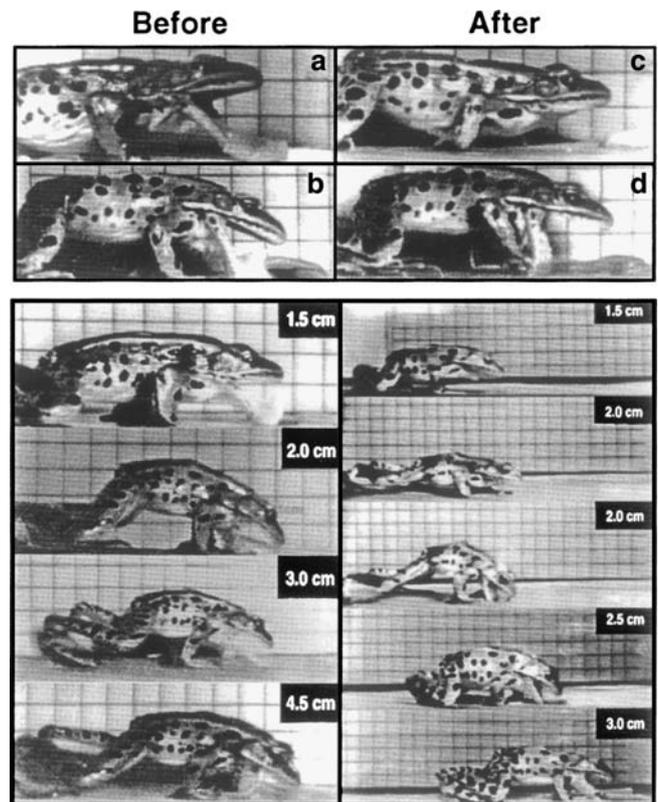


Fig. 1 Prey capture in *Rana pipiens*. The upper photograph (a) is taken from a waxworm capture and corresponds to *Tongue Prehension*, and the lower photograph (b) is taken from an earthworm capture and corresponds to *Jaw Prehension*. [From Anderson and Nishikawa 1993; reprinted with permission.]

flexion were significantly greater during earthworm feedings. For the JP the tongue is protracted through an angle of less than 90° whereas for the TP tongues are protracted more than 180° , and the prey is captured with the tongue only. So the parameters which define the stimulus must also determine the motor parameters. Differences in prey size, shape and mobility may produce differences in the kinematics and motor patterns of feeding.

2.2 Bilateral hypoglossal nerve (XII) transection

Following bilateral transections of the hypoglossal nerve, toads and frogs lunge toward mealworms with no accompanying tongue or jaw movement (Weerasuriya 1989, 1991; Anderson and Nishikawa 1993). The lack of tongue projection and retraction is a direct consequence of the transection of axons that innervate tongue muscles. Nevertheless, the nerves that innervate the jaw muscles are intact, thus leaving the lack of jaw movement as a paradox to be resolved. Two main effects are inactivation of tongue protractor muscles and an alteration of the sensory information traveling from the tongue to the brain (Nishikawa and Gans 1992). When feeding on small prey, sensory feedback from the tongue through the hypoglossal nerve is necessary to trigger mouth

opening. Without the sensory feedback, the mouth fails to open although the feeding behavior appears otherwise normal. However, when feeding on large prey, the mouth opens normally even after the hypoglossal nerve has been transected. Thus, hypoglossal sensory feedback is not necessary to trigger mouth opening when feeding on large prey. This result is also found in primitive frog species (Nishikawa and Roth 1991). Figure 2 displays both normal feeding behavior (left) as well as feeding behavior after the hypoglossal nerve transection (right).

When comparing before versus after hypoglossal transection for earthworm (large prey) feedings, the duration of tongue protraction, the tongue angle, and the maximum tongue reach are all significantly less following surgery (Anderson and Nishikawa 1993).

3 Anatomy and physiology

This section reviews the principal structures involved in the behaviors described in this paper. In doing so we try to provide as many biological constraints as possible to the computer model. We will introduce structures all the way from perceptual to motor with different emphasis as they pertain to the behaviors studied in this paper.

3.1 Perceptual structures involved

The key stimulus that elicits prey capture is either visual, tactile or olfactory, and the outputs of their respective sensory analyzers share common access to motor pattern generators responsible for the elaboration of the appropriate motor outputs. In this paper we will emphasize visual input. Visual input is first processed by the retina. The output of the retina consists of R2, R3, and R4 ganglion cell axons projecting to the tectum and pretectum (Ewert 1984). For more details on the *retina* we refer the reader to Ewert (1984), Teeters et al. (1993) for a computer model and Gaillard et al. (1998) for an exhaustive analysis of physiological properties. Based on physiological criteria, ten classes of neurons (T1–T10) have been identified in *optic tectum* (for review see Grüsser and Grüsser-Cornehls 1976; Ewert 1984). The activity of these tectal cell types is correlated with a variety of behaviors such as prey-catching, predator-avoidance, and general arousal. Here we review the tectal cells involved in prey-catching behavior. Based on their sensitivity to different stimulus features, Ewert and Wietersheim (1974) divided the T5 cells into three subclasses. Among them the activity of worm-selective T5.2 cells is highly correlated to prey-catching behavior. T5.2 neurons respond to a worm-like stimulus with discharge of increasing frequencies for about 200 ms before snapping (Schürg-Pffieffer 1989). The firing rate is low for the first 150 ms and then increases dramatically to about 150–200 spikes/s 50 ms prior to snapping. These discharges precede snapping; T5.2 are silent during snapping. T4 neurons have a large receptive field and can be activated by either

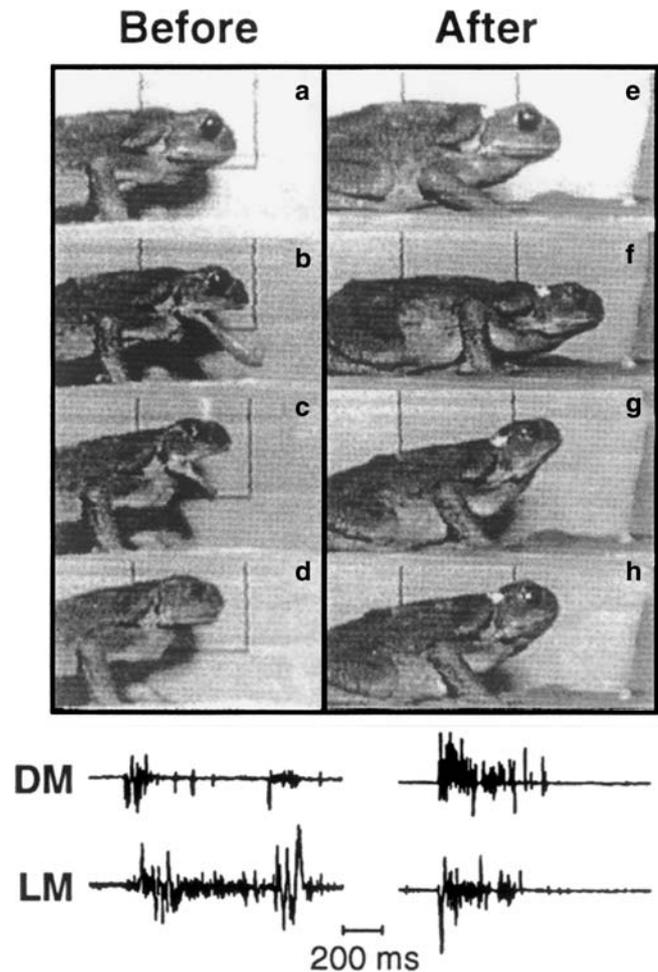


Fig. 2 *Top* The left-hand set of photographs correspond to normal feeding behavior in *Bufo marinus*. The right-hand set corresponds to feeding behavior in *Bufo marinus* after bilateral transection of the hypoglossal nerve. These toads search actively for prey, orient toward it, and fixate it in their gaze in a normal fashion. Whenever they initiate prey capture, (a) they rotate forward on the forelimbs, (b) raise the cranium and retract the eyes normally, (c, d) but the mouth fails to open. *Bottom*. Electromyographic activity of the mandibular depressors (DM) and levators (LM) during feeding before (*Left*) and after (*Right*) bilateral transection of the ramus hypoglossus. The onset of activity is nearly simultaneous both before and after surgery. Before transection, the depressors reach their peak of activity on average 86.7 ms earlier than the levators. After transection, the peak of activity of the levators occurs nearly simultaneously with the peak of activity of the depressors. [From Nishikawa and Roth 1991; reprinted with permission.]

visual or tactile stimuli. Some of the T4 neurons show the property of general arousal (“newness”).

3.2 Medulla and reticular formation

The transformation of sensory signals into appropriate spatio-temporal patterns of activity in the motoneurons is considered to be carried out by an MPG network in the medial reticular formation of the medulla (Weerasuriya 1983, 1989; Schwippert et al. 1989). The reticular formation in the

medulla has been considered a major premotor area in many species including anurans. Schwippert et al. (1989, 1990) and Ewert et al. (1990) recorded in toads from this premotor area and categorized ten functional units (M1–M10) pertinent to sensorimotor integration. Weerasuriya (1989) and Matsushima et al. (1989) found that the premotor neurons in the medulla send axon collaterals into motoneuron pools.

T5.2 cells send projections to the medulla M5.2 cells. M5.2 neurons, whose receptive field is relatively small and located mostly in the frontal regions, show strong preference to worm-like stimuli. Hence, further enhancement of discrimination may occur in the M5.2 cells by performing perceptual sharpening of the input from T5.2. In turn M5.2 cells project to several MPGs as indicated below (Weerasuriya 1989). M5.2 cells serve as the portal neurons of the excitatory pathway into the motor system. On the other hand, the M4 neurons, which have the property of general arousal are most suitable to serve as the portal neuron for the inhibitory pathway. It receives signals from its tectal counterpart, the T4 neuron, and elicits in the motor neurons an initial inhibitory post-synaptic potential (IPSP) which may serve two purposes: (1) resetting the system before initiating a new movement, and (2) preventing the toad from snapping at undesirable objects which are capable of eliciting low activity in T5.2 neurons. The direct projection from M4 to motoneurons (without going through the rest of the premotor neurons) results in a shorter latency for the inhibitory pathway.

Among the physiologically identified premotor neurons, two classes of neurons exhibit opposite firing characteristics. Shortly before a movement, M8.1 firing rate increases from a baseline of less than 5 Hz to about 40 Hz, while that of M8.2 decreases from 40 Hz to less than 3 Hz. Such duality between M8.1 and M8.2 is observed in a wide variety of movements including eye closure, walking, stalking, orienting, and snapping (Schürg-Pffieffer 1989). M10 neurons discharge a sequence of bursting spikes at an average frequency between 15 to 20 Hz. The bursting activity of M10 is closely correlated to muscle movement (e.g., neck movement). Premotor bursting cells in mammals have been found to contact motoneurons (MNs) directly in controlling eye, neck and limb movements (Robinson 1981; Ito 1986; Grantyn and Berthoz 1988). Therefore, it is postulated that M10 bursting cells are the output neurons of the snapping MPG and provide signals to drive the motoneurons in the facial and hypoglossal nuclei. Several other medullary premotor neurons are relevant to the control of snapping behavior. For instance M4 neurons with large receptive fields are more sensitive to a novel stimulus.

Control of jaw

In the toad *Bufo*, sensory feedback from the tongue is necessary for normal mouth opening during feeding behavior (Weerasuriya 1989, 1991; Nishikawa and Gans 1992). Sensory receptors in the tongue send a signal to the brain via the hypoglossal nerve. The signal inhibits the jaw levators and thus enables mouth opening (Nishikawa et al. 1992) since *tonic activity* of the mandibular levators prevents mouth opening even when the mandibular depressors are stimulated.

Nishikawa and Gans (1992) suggest that hypoglossal inhibition of jaw elevators occurs not only during feeding but also in a non-feeding preparation in which none of the premotor circuits normally associated with feeding are active. Figure 2 bottom displays the electromyographic activity of the mandibular depressors (DM) and levators (LM) during feeding before (Left) and after bilateral transection (Right) of the ramus hypoglossus. In *Bufo marinus* before transection, the depressors reach their peak activity about 90 ms earlier than the levators (Nishikawa et al. 1992, see Fig. 2 bottom) –120 ms for jaw pattern-. This corresponds to the time normally required for the mandibular depressor to open the mouth (Nishikawa and Gans 1992). After transection, the peak activity of the levators and depressors occurs simultaneously.

Control of tongue

Anatomical studies in the frog *Rana pipiens* have demonstrated that the hypoglossal nerve is composed of both sensory and motor fibers carrying sensory signals coming toward the brain and motor signals going out to the tongue. However, Nishikawa et al. (1992) pointed out that the central projections and the *sensory receptors* associated with the hypoglossal sensory feedback system remain to be described.

3.3 Motor neurons and muscles

Each single *motor synergy* is the result of the interaction of (at least) an *agonist* and an *antagonist* muscle, the overall motor behavior being the result of the synchronization/interaction of multiple motor synergies. The motoneurons controlling the tongue muscles are located in the *hypoglossal nucleus* of the medulla oblongata. Intracellular recording from the tongue-muscle-controlling motoneurons during electrical stimulation of the ventrolateral optic tectum (called the “snapping zone”, based on the observation of tongue snapping after stimulating this area) provides important insight into the structure of the motor system. A weak stimulation elicits IPSPs in the motoneurons while a train of stronger pulses elicits bursting EPSPs excitatory post-synaptic potentials (EPSP). The latency of IPSPs is shorter than that of EPSPs. They concluded that there are two separate pathways from the optic tectum to the motoneurons and that the inhibitory pathway has a lower threshold, possibly to reset the different motor components (Liaw et al. 1994).

The different motor nuclei connect with the muscles through several different nerves. For instance in our current model we have included: *facialis* (VII) which carries the axons from the DM motoneurons to the DM muscle; *trigeminal* (V) which carries the motor command from LM motoneurons to the muscle and also carries the sensory feedback from muscle spindle receptors in the jaw muscles; and *hypoglossal* (XII) which carries the motor commands for the tongue muscles Genioglossus (GG) and Hyoglossus (HO) as well as sensory feedback from mechanoreceptors in the tongue.

We begin our investigation of issues concerning motor control by examining what characterizes muscle activity as

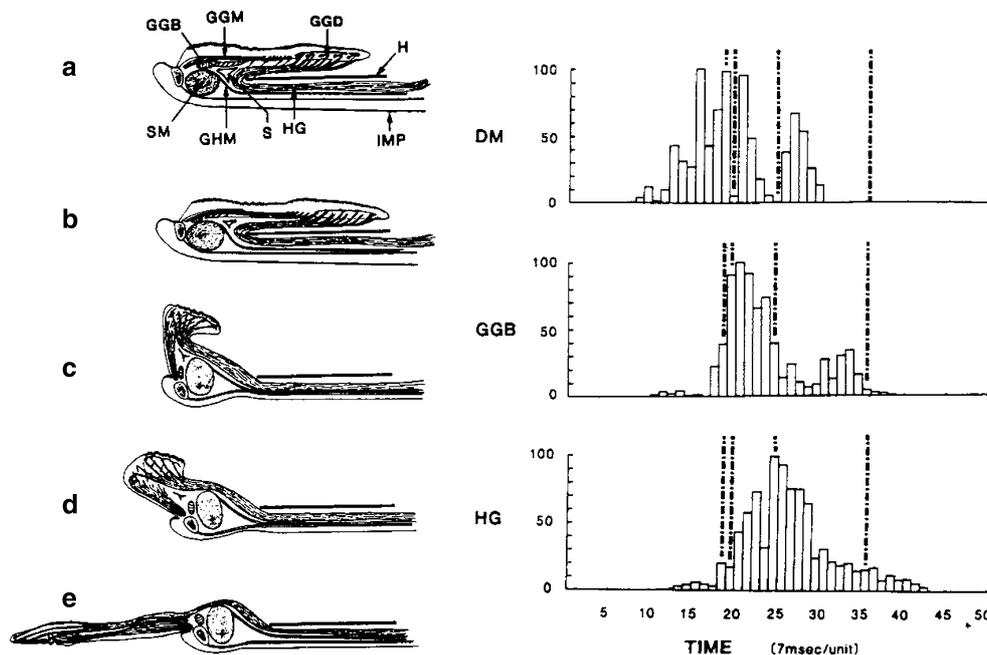


Fig. 3 Myology of Snapping in anurans. A sequence of drawings of tongue flip is shown on the left and the EMG recording of three major muscles involved in snapping is given on the right. Median (a) and sagittal (b) sections of the tongue at rest. (c) The tongue is lifted. Note that the musculus submentalis (SM) rotates from a horizontal position (in b) to a vertical one (in c and d). A vertically oriented, rod shaped mass (the lingual rod) is formed by the contraction of musculus genioglossus (GGB, GGM, and GGD). (d) The lingual rod and lingual pad pass beyond SM. SM is pulled caudally by musculus geniohyoideus medialis (GHM) and musculus intermandibularis posterior (IMP). (e) The tongue is fully protruded. right. Each bar of the graph represents the product of the mean spike number times the mean amplitude as a percentage of the maximum value. [From Gans and Gorniak 1982; reprinted with permission.]

reflected by its EMG recording and how these characteristic features can be controlled. The action potential transmitted from the axons of motoneurons to the muscle fibers is called the muscle action potential. Electrodes placed on the surface of a muscle (or inserted in the muscle) will record the algebraic sum of all muscle action potentials being generated in the muscle fibers near the electrode (Winter 1979; Loeb and Gans 1986; Gans 1992). That is, an EMG record is a measure of the output of a population of motoneurons which send action potentials to muscle fibers that are near the tip of the recording electrode. Therefore, the average of EMG recorded from repeated performance of a motor task is a good indicator of the output of the motoneuron population. In general, an EMG record can be characterized by its time of onset, rising rate, peak amplitude, duration, total activation (the area of the EMG) and decay rate.

3.4 Myology of prey capture

Gans and Gorniak (1982) divided the feeding sequence of toads into four phases, (1) preparatory, (2) tongue protrusion, (3) tongue retraction, and (4) mouth closing. Figure 3 illustrates the protrusion of the tongue (left) and the EMG recording of the major muscles involved in snapping (right). In the preparatory phase prior to mouth opening, M. DM lowers the jaw—activation of DM reaches its first peak before

the mouth starts to open. Shortly after the activity in DM reach its peak, M. GG starts to contract to project the tongue. During its contraction, GG forms a transverse, rod-shaped mass (the lingual rod in Fig. 3), shortens the lingual tissue and provides a forward momentum. In the retraction phase, M. HO provides the major force to bring the tongue back into the mouth. The activation of HG begins before, and peaks at, the start of retraction. The second burst of activity in DM opens the mouth even wider to allow the prey to be brought in, followed by the “melting” of the lingual rod (small increase of GG near the ending of the retraction phase).

4 Schema-based model for prey-catching

In this section we introduce the main functional components of the model. Some components are implemented all the way down to neurons and others for which the detailed neural circuitry is not known or involves unnecessary computation for the range of phenomena under study are modeled as functional units, here called *schemas* (Arbib 1992; for a comprehensive review). We might then analyze interactions between schemas subserving a particular emergent behavior or the learning of new schemas from the current stock of schemas (see the companion paper). Notice that once a schema model is proven to give rise to a set of desired phenomena then the appropriate neural networks may be sought that implement

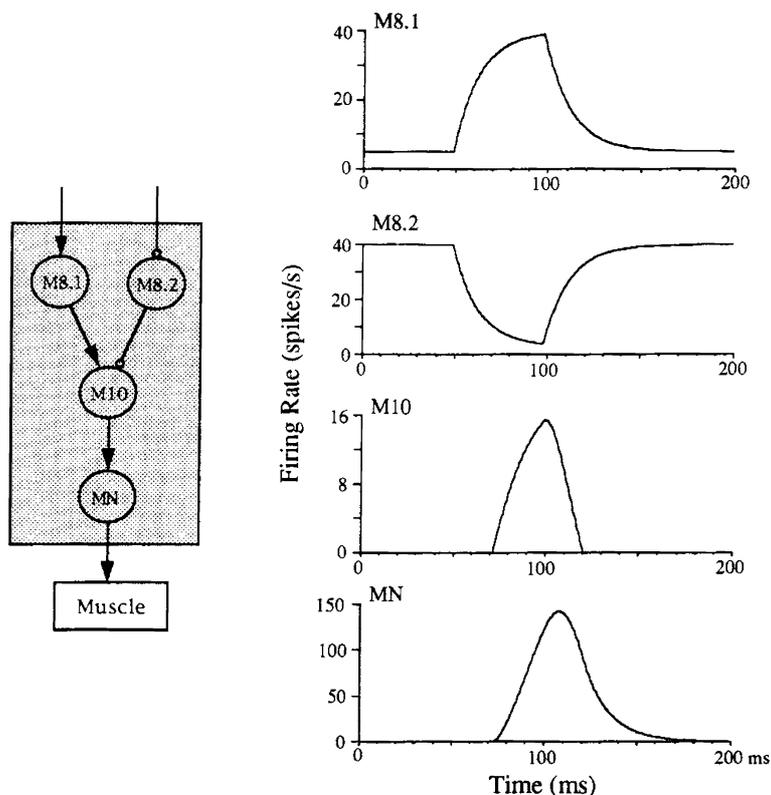


Fig. 4 Basic MPG module. *Left* The push-pull between M8.1 and M8.2 forms the core of the basic MPG module. They receive independent inputs and send excitatory and inhibitory signals, respectively, to M10. In the model, each module is postulated to control one muscle synergy. *Right* The temporal profile of M8.1, M8.2, M10, and motoneuron (MN) in response to an input signal that excites M8.1 and inhibits M8.2 at the same time. [Adapted from Liaw et al. 1994.]

that functionality. Arbib (1992) stress that schema-level models can be invalidated, and provide the basis for yet better models, without descending to lower levels, on the basis of lesion and behavioral data.

To afford including all the major components involved in prey-catching we moved into *schema-based* modeling as it allows for some components to be specified as neural networks whereas others can be left as functional units for which only the input/output mapping needs to be specified without having to specify the inner mechanisms that give rise to such a mapping. For instance little is known about the neural circuitry that “implements” lunging and head-ventroflexion. So we have modeled them by schemas LUNGE and HEAD_DOWN respectively meeting certain functional specifications as we shall explain in later sections.

4.1 Basic MPG modules: neural networks involved

Based on the experimental data Liaw et al. (1994) constructed a *basic MPG module* consisting of a triplet of M8.1-M8.2-M10, as shown in Fig. 4. They claimed that the *premotor* circuit consists of several such basic modules with each one controlling a particular muscle. The opposing characteristic of M8.1 and M8.2 provides a *push-pull* mechanism for

coordinating the activity of various motoneuron pools: a trigger command which is postulated to activate M8.1 is insufficient to evoke a motor action. The inhibition from M8.2 must also be removed to allow an action to occur, thus allowing an extra degree of flexibility in controlling motor patterns. For example, one brain region which recognizes a barrier in front of a prey may inhibit (via M8.2) the snapping response usually activated by prey-related neurons in another brain regions (via M8.1). Therefore, in the model M8.1 and M8.2 neurons receive signals through independent input lines and project to M10 with excitatory and inhibitory signals, respectively. M10 neurons integrate signals from M8 neurons and discharge with bursting spikes to drive the motoneurons (Fig. 4). That is, the *tonic inhibition* from M8.2 to M10 is released when an input arrives at M8.2. At this time, the excitatory input from M8.1 is sufficient to drive M10.

In (Liaw et al. 1994) the motoneuron plays a passive role, i.e., it simply scales the activity of M10. The motor pattern is generated by the premotor neurons. However, as we will see later, the motoneuron may receive other inputs such as feed-forward inhibition and afferent feedback which will *modulate* the basic motor pattern generated by the premotor neurons. We have extended Liaw et al. (1994) by introducing more inputs to the motoneurons. For instance, some motoneurons receive sensory feedback about distance to prey and about position of the jaw.

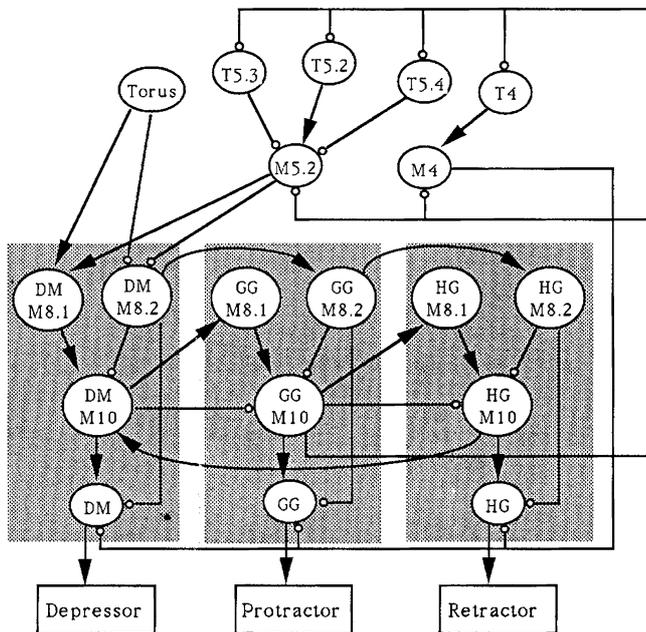


Fig. 5 A network of MPGs for coordinating motor synergies can be constructed using the triplet in Fig. 4 as a building block. Notice the M4 neuron resetting the different motor neurons. [Adapted from Liaw et al. 1994.]

4.2 MPGs: coordinating motor synergies

A network of MPGs for coordinating motor synergies can be constructed using the triplet defined in the previous section as a building block. Figure 5 depicts a network of basic MPG modules coordinating motor synergies.

Two types of input signal of an MPG have been distinguished. The first type of input is the *trigger command* that activates an MPG and the other type is the *control signal* that sculpts its temporal pattern. The control signal conveys such information as the direction and amplitude of a movement. Separate pathways have been reported to carry these two types of signal from optic tectum to medulla (Ingle 1983; Grobstein 1989). Similar functional separation of the sensorimotor signal has been observed in other episodic goal-directed MPGs, such as those seen in controlling saccadic eye movements (Robinson 1981; Scudder 1988). Based on such observations, Liaw et al. (1994) put forth a general principle for constructing the snapping MPG: The intrinsic connectivity between the modules is responsible for generating a “default” snap upon the arrival of a trigger command which is modified by the control signal coming into each module. In this paper we maintain such a principle. The *intrinsic connectivity* between the basic modules in an MPG provides the primary *coordination* of the muscle synergies involved which is fine tuned by control signals. Liaw et al. (1994) introduced an example involving three major muscles (DM, GG, and HG) for snapping and show how the push-and-pull mechanism between M8.1 and M8.2 can be utilized to achieve motor coordination in synchronizing the jaw opening and

the protraction and retraction of the tongue. They also explored two plausible intrinsic connectivity schemes between the jaw and tongue modules which produce the temporally ordered sequence of the mouth opening, tongue protraction and retraction. These two connectivity schemes correspond to the sequential and parallel activation modes elaborated below.

Sequential versus parallel activation

Liaw et al. (1994) tested two schemes for connecting modules in the MPG model. In the first, the temporal order of snapping behavior is generated by a sequential connectivity pattern between the modules. In this scheme, the DM module is the first of the three to be triggered by M5.2 neurons. Activation is propagated from the DM to the GG and then from GG to HG, thus creating temporal delays between the activation of DM, GG and HG. Inhibition from the premotor system terminates the activation from tectal neurons. With this modular architecture, each module is allowed to communicate with others only via its “output” neurons, i.e., there is no connection between the M8.1s and M8.2s across modules. However, either the M10 or the motoneuron can be the output port of the module. Anatomical studies have shown that the motoneurons controlling tongue protraction are not connected to those controlling retraction (Weerasuriya 1983). Therefore, the coordination between modules is postulated to be carried out via M10 neurons. With this sequential scheme Liaw et al. (1994) obtained a temporal pattern for each motor synergy that is a good match with the EMG data. However, there is a discrepancy in the temporal delay between the onset of GG and HG activation (~ 35 ms in the simulation vs. ~ 7 ms in the EMG data). Instead, the data shows that the difference in the time of peaking in GG and HG is more significant (a 35 ms delay between them, which corresponds roughly to the delay between tongue protraction and retraction). Such a discrepancy suggests a different connectivity pattern for the MPG.

Liaw et al. (1994) developed an alternative, parallel model for producing the temporal order seen in the snapping behavior. The basic organization is similar to the sequential model, except that in this model, DM activates both GG and HG, using the same push-pull mechanism of M8.1 and M8.2. Besides the change in their interconnection, there are some subtle differences in these two models. The parallel model produce temporal patterns that closely match the EMG data in terms of the delay between the onset of DM and GG, DM and HG, and the time to peak in all these three modules.

Delay lines for relative timings

We have thus adopted the parallel activation model as well. In order to achieve temporal patterns across units which receive parallel (synchronous) input, we have introduced different delay lines in the pathways (cf. the mouth must be open before the tongue can be protracted). Any neuron connects to any other neuron through several synapses. We assume that these different synapses will have different “delay constants”, thus introducing different delays on the presynap-

tic signal. Delays are induced by different synaptic properties across the population of synapses. We introduce different delay channels corresponding to different thickness and degrees of myelination to give a scatter of delay times. From the simulation point of view this is implemented by simply storing the signal for several simulated time steps.

$$DELAY_{\alpha}(x(t)) = x(t - \tau_{\alpha}) \quad (1)$$

We would claim that during learning, the synapse configuration that corresponds to the timing that induces the right pattern of interaction gets selected (refer to the companion paper on learning mechanisms). For instance, during development the synapse that produces the “best” timing between Lunging and Jaw opening gets selected as it gives rise to the most reliable and efficient prey capture.

In this paper we have modeled a large number of muscles and corresponding control structures to account for much of the complexity of prey-catching. We have also introduced an extra mechanism to achieve motor coordination by the use of delay lines hypothetically derived from synaptic properties. Next, we have shown that the parallel activation mode coupled with the use of delay lines can achieve the performance observed in animals. We will also demonstrate how the same set of schemas can give rise to different “emergent” behaviors dependent upon the input to the system.

4.3 Defining the basic schemas

In the following sections we will define several perceptual, sensori-motor and motor functionalities by schemas. We have simplified/abstracted certain components of the neural network to include and emphasize others. Schema-based modeling allows us to simplify some of the underlying circuitry to introduce more structures/functions and their corresponding control. We show a case in which the circuitry is fairly known and there even is a neural network model for it. Yet we choose to model it as a schema preserving the main properties of the neural mapping yet simplifying details which are less relevant for the phenomena under analysis. In particular we have just reviewed a neural network model of the basic premotor circuitry proposed by Liaw et al. (1994) that matches the physiology while taking into consideration the known anatomy. Yet for computational reasons we decided to simplify the model and build a schema that retains the main functional properties that are relevant for the behaviors under analysis. A similar example is the PREY_REC schema for which some of the neural circuitry is known (Ewert 1984) and for which models of the retina (Teeters et al. 1993; Gaillard et al. 1998) and tectal-pretectal circuitry exist (e.g. Cervantes-Pérez 1985). We include PREY_REC as a simplification of a whole neural network including retina, T5.2 and TH3 cells. Schemas encapsulate the means to achieve a certain specification/objective/goal. For instance LUNGE encapsulates how to activate (by a specific spatio-temporal pattern) certain set of muscles to move the body forward. It should by now appear obvious to the reader that a model including all

the details would be currently computationally intractable. So we take the alternative of having a more simplified model that can still account for most of the data instead of having models with so many parameters (degrees of freedom) that anything can possibly be fit.

In this regard, although separate input lines to M8.1 and M8.2 provide an extra degree of flexibility in controlling the motor system, they are not needed for the purposes of this paper. A further simplification consists of a direct mapping to M10 from the prey recognition system. This is enough since the extra degree of freedom allowed by the M8.1, M8.2 push-pull mechanism is not used at the level of coordination proposed in this paper. Hence, we replace the more complex mapping introduced by Liaw et al. (1994) by a single equation that approximates the mapping while maintaining some of the qualitative properties relevant for this study, namely, the onset, the amplitude (discharge frequency), and the duration of activity. In case future modeling involves analysis of more “precise” phenomena requiring more “precise/detailed” implementations of the components, the schema may be refined without affecting the other schemas. For instance future models of prey catching may want to substitute the current implementation of PREY_REC by a more refined neural implementation (e.g. Cervantes-Pérez 1985). We now present a schema-based model (Fig. 6) implementing two different motor patterns observed during anuran prey catching.

Figure 6 displays the overall *schema-based* organization with the main components/connections for prey catching in anurans. Namely, control circuitry for Depressor mandibularis, Levator mandibularis, tongue protractor Genioglossus, tongue retractor Hyoglossus, Head ventro-flexion and Lunging. Input about prey type is projected from the tectum to the medulla. In the model the signals about prey type excite *premotor* LM, DM, LU, HE, GG and HO as well as inhibit INT1 (Fig. 6). The role of this circuitry will be described later in terms of motor pattern selection as well as adaptation. We have two types of “prey” schemas: PREY_REC which codes the size of the prey by their firing frequency (above a minimum prey size, smaller prey size corresponds to higher frequencies), and PREY_NORM which is equally active if there is a prey in view, irrespective of its size (“normalized” within the boundaries of “prey”). This is so, since, for instance LM or DM activity does not appear to change significantly for large prey versus for small prey. INT1, on the other hand, depends on prey size to bias the motor pattern generation. Notice that PREY_NORM can be considered more as a *trigger signal* whereas PREY_REC can be considered more of a *control signal*.

As mentioned before the overall motor behavior is the result of the synchronization/interaction of multiple motor synergies. For instance the mouth must be open before the tongue can be protracted. Also lunging starts before the mouth begins to open. The different motor synergies/schemas must be temporally coordinated. All premotor components get input in parallel from PREY_NORM but their activations have different timings due to the different “delay lines” in their cor-

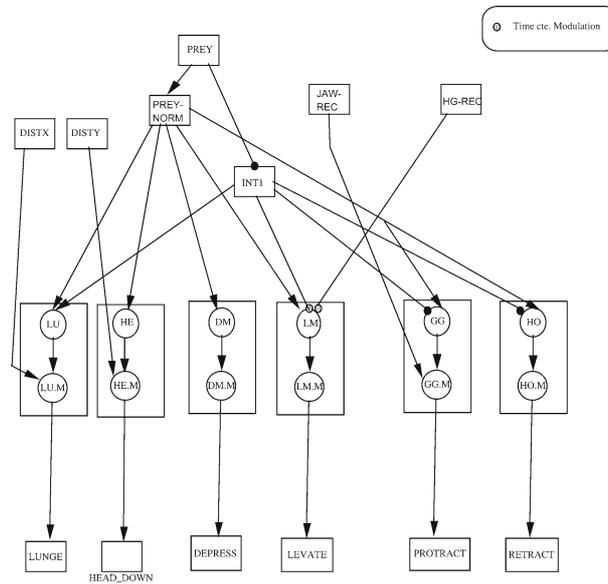


Fig. 6 Overall *schema-based* organization with the main components/connections for prey catching in anurans. Namely, control circuitry for depressor mandibularis, levator mandibularis, tongue protractor, tongue retractor, head ventro-flexion and lunging. Notice the simplified triplets of Fig. 4. Also some of the neural network structure is simplified to allow for inclusion of lunge and head down flexion MPGs as well as the corresponding sensory feedback

responding pathways. Delays are induced by different synaptic properties across the population of synapses between two connected units. The system in newly metamorphosed froglets may have a crude “assignment” for some of the different delays. The parameters may be in the right ballpark with subsequent tuning of the parameters for more optimal performance. For other MPGs the right spatiotemporal relations might have to be learned almost from scratch (e.g. throwing a basketball to the basket).

A variety of *sensory feedback* is also included within the overall architecture. For instance, we introduced *sensory feedback* about the state of the jaw by muscle spindles in the jaw muscles through the trigeminal nerve. It has already been shown that muscle spindles from the jaw muscles project to the cerebellum (Lund and Enomoto 1988). We now **hypothesize** that they also project to the reticular formation. This is also analogous to HG (Hypoglossus) which projects to the granular layer of the cerebellum but also to the reticular formation. Also the lunging motor schema LU.M receives input from DISTX coding the distance from the animal’s snout to the prey; and the tongue protractor motoneurons receive input from JAW_REC about the status of the jaw.

4.4 Basic schemas implementation

In this section we introduce the formal definition of schemas, as well as *neuroschemas* as schemas specifically implemented by neural networks. We described a **schema** as a unit of concurrent processing corresponding to a domain of interaction. We will follow the notation introduced by (Lyons and Arbib (1988).

Definition a basic schema description is

```
Basic – schema ::= [Schema – name : < N >
Input – Port – List :           (< Iplist >)
Output – Port – List :          (< Oplist >)
Variable – List :               (< Varlist >)
Behavior :                      (< Behavior >)]
```

where, N is an identifying name for the schema,

< Iplist > and < Oplist > are lists of <Portname>: <Porttype> pairs for input and output ports, respectively.

< Varlist > is a list of <Varname>:<Vartype> pairs for all internal variable names, and

< Behavior > is a specification of computing behavior.

In the rest of the paper we will use the notation $i_k^x(t)$ to represent the pattern of activity in the i is used to represent the pattern of activity in the k th input port of schema X at $timet$ and $o_k^x(t)$ for the analogous output port. All along this paper when the schema has a single output port, then this output port takes the name of the schema in lower case, that is, we will use the notation $dm(t)$, $lm(t)$ and $jaw(t)$ to name the output port activity pattern from the DM, LM and JAW_REC schemas respectively.

Lyons and Arbib (1988) provide a formal semantics based on port automata and Corbacho (1997) extended this definition to include schema activity variables along with their corresponding dynamics. It is simple to extend the automaton-based scheme to a neural net specification by making it possible, in the basic schemas, to define the behaviour directly in terms of a neural network rather than, let us say a C-like program. That is, neuroschemas correspond to mappings between layers of neurons. In particular neuroschema mappings are implemented by leaky integrators. These leaky integrators “integrate” a variety of inputs from other

schemas to compute the membrane potential of the neurons. The membrane potential may then be passed through an activation function, in this instance a simple threshold to obtain the firing rate. Neuroschema instances correspond to spatio-temporal patterns of activity in the neural layers. This pattern could correspond to a simple activity level in one unit or a whole pattern over an array of units. Other basic schemas are defined as functional units that may receive inputs from *layers* of neurons (e.g. LUNGE) or may affect layers of neurons by projecting their outputs (e.g. PREY_REC). Hence integrating schemas with neural networks within the architecture of the prey catching system.

Perceptual schemas

Perceptual schemas are modeled as simple functions of environmental parameters which deploy an objective, e.g. PREY_REC and PREY_NORM are triggered by the presence of prey in the animal's visual field. As already mentioned above PREY_REC codes the size of the prey by their firing frequency (smaller prey corresponding to higher frequencies), and PREY_NORM which is equally active if there is a prey in view, no matter what its size is ("normalized" within the boundaries of "prey"). Others are modeled by a simple function of internal states of the animal, e.g., JAW_REC which corresponds to the state of the animal's jaw, being more active the more open the jaw is. Instead of modeling all inner jaw mechanisms we have opted for approximating JAW_REC by a function of the state of the LEVATE and DEPRESS.

Specifically, HG_REC is modeled by a sinusoid simulating the effect of the respiratory cycle. It signals optimal positioning of the tongue within the respiratory cycle for optimal protraction. The position is signaled by mechanoreceptors activated when the tongue presses up against the roof of the mouth. The HG_REC schema is specified by:

$\langle N \rangle:$ HG_REC
 $\langle Iplist \rangle:$ $\langle (f : R), (t : R) \rangle$
 $\langle Oplist \rangle:$ $\langle (hg(t) : R) \rangle$
 $\langle Behavior \rangle:$ implemented by the mapping

$$S^{HG_REC}(t, f) = \sin(2\pi ft) \quad (2)$$

where f is the frequency of the respiratory cycle.

On the other hand, the activity of the muscle spindles in the jaw is approximated by the schema JAW_REC,

$\langle N \rangle:$ JAW_REC
 $\langle Iplist \rangle:$ $\langle (depressor(t), R), (levator(t), R) \rangle$
 $\langle Oplist \rangle:$ $\langle (jaw(t) : R) \rangle$
 $\langle Behavior \rangle:$ implemented by the mapping

$$S^{JAW_REC}(X, Y) = \begin{cases} X - Y + \rho & \text{if } X > Y \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

where $depressor(t)$ and $levator(t)$ represent the state of the depressor mandibulae muscle and the levator mandibulae muscle respectively (described later in the motor schemas section) and ρ is white noise.

Analogously for the muscle spindles in the tongue, the schema TONGUE_REC is defined by

$\langle N \rangle:$ TONGUE_REC
 $\langle Iplist \rangle:$ $\langle (retractor(t), R), (protractor(t), R) \rangle$
 $\langle Oplist \rangle:$ $\langle (tongue(t) : R) \rangle$
 $\langle Behavior \rangle:$ implemented by the mapping

$$S^{TONGUE_REC}(X, Y) = \begin{cases} X - Y + \rho & \text{if } X > Y \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

Analogously GP_REC detects prey contact by comparing the positions of the roof of the mouth with the position of the prey to compute whether there has been prey contact represented in $gp(t)$. And analogously $distx(t)$ and $disty(t)$ represent the distance from the x and y coordinates of the tip of the tongue to the coordinates of the prey respectively.

Sensorimotor neuro-schemas

The schema INT1 corresponds to the neural program controlling the interneuron *int1* which gates the perceptual input about prey to the reticular formation in turn giving rise to different patterns of activation in the premotor neurons. From now on we are going to use the following notation for the leaky integrator mappings implementing neural dynamics: $X_m(t)$ denotes the membrane potential for neuron X , and $X(t)$ denotes its corresponding firing rate. The INT1 neuro-schema specification follows

$\langle N \rangle:$ INT1
 $\langle Iplist \rangle:$ $\langle (prey(t) : R), (t : R) \rangle$
 $\langle Oplist \rangle:$ $\langle (int1(t) : R) \rangle$
 $\langle Varlist \rangle:$ $\langle int1_m \rangle$
 $\langle Behavior \rangle:$ implemented by the following two mappings:

$$\tau_{INT1} \frac{dint1_m(t)}{dt} = -int1_m(t) - \alpha_{INT1} \cdot DELAY_{INT1}(prey(t)) + int1_tonic \quad (5)$$

where $int1_m(t)$ has constant tonic activity $int1_tonic$ (set to 0.5 in the model) and the firing rate

$$int1(t) = \Theta(int1_m(t)) \quad (6)$$

where

$$\Theta(x) = \begin{cases} x & \text{if } x > 0 \\ 0 & \text{otherwise} \end{cases} \quad (7)$$

Next we describe the control of lunge and head ventroflexion by the premotor neuro-schemas LU and HE respectively.

$\langle N \rangle:$ LU
 $\langle Iplist \rangle:$ $\langle (prey_norm(t) : R), (int1(t)), (t : R) \rangle$
 $\langle Oplist \rangle:$ $\langle (lu(t) : R) \rangle$
 $\langle Varlist \rangle:$ $\langle lu_m(t) \rangle$
 $\langle Behavior \rangle:$ implemented by the following two mappings,

$$\tau_{LU} \frac{dlu.m(t)}{dt} = -lu.m(t) + \alpha_{LU} \cdot DELAY_{LU}(prey_norm(t)) + \beta_{LU} int1(t) \quad (8)$$

where premotor $lu(t)$ onset activity is delayed with respect to $prey_norm(t)$ and in turn $he(t)$ onset activity is delayed with respect to $lu(t)$ (i.e.). The firing rate $lu(t)$ is in turn calculated by

$$lu(t) = \sigma(lu.m(t), \theta_{LU}) \quad (9)$$

where

$$\sigma(x, \theta) = \begin{cases} x & \text{if } x > \theta \\ 0 & \text{otherwise} \end{cases} \quad (10)$$

Analogously for schema HE, the neuro-schema mapping is implemented by

$$\tau_{HE} \frac{dhe.m(t)}{dt} = -he.m(t) + \alpha_{HE} \cdot DELAY_{HE}(prey_norm(t)) + \beta_{HE} int1(t) \quad (11)$$

and the firing rate $he(t)$ is calculated similarly to $lu(t)$.

Analogously the activity dynamics of the motoneurons associated to LU and HE (denoted $lu.m$ and $he.m$ respectively) are defined by the following mappings

$$\tau_{HE.M} \frac{dhe.m.m(t)}{dt} = -he.m.m(t) + \alpha_{HE.M} \cdot disty(t) + \beta_{HE.M} \cdot he(t) \quad (12)$$

$$\tau_{LU.M} \frac{dlu.m.m(t)}{dt} = -lu.m.m(t) + \alpha_{LU.M} \cdot distx(t) + \beta_{LU.M} \cdot lu(t) \quad (13)$$

In Liaw et al. (1994) the motoneurons only served to scale the output of the premotor circuitry. In this paper we also include other inputs to the motoneurons. For instance, we have included the sensory feedback for the horizontal distance ($distx$) between the snout and the prey to control the lunging, as well as the sensory feedback for the vertical distance ($disty$) to control the head ventroflexing. The motor neurons may also receive *resetting* input (cf. discussion on medullary M4 neurons).

Modeling control of jaw

We hypothesize that both DM as well as LM are triggered by PREY_NORM in parallel and equally delayed with respect to LU, hence, influencing the onset of mouth opening with respect to lunging. The other alternative of direct input from LU to DM and LM requires the activation of LU (lunging) in order to open the mouth—which is not the case. For instance, the timing of mouth opening must be controlled even when there is little or no activity in LU, as in the case of Tongue Prehension. The premotor schemas LM is defined by

$$\begin{aligned} < N >: & \quad LM \\ < Iplist >: & \quad < (prey_norm(t) : R), (t : R) > \\ < Oplist >: & \quad < (lm(t) : R) > \\ < Varlist >: & \quad < lm.m(t) > \\ < Behavior >: & \quad \text{implemented by the following mapping,} \end{aligned}$$

$$\tau_{LM} \frac{dlm.m(t)}{dt} = -lm.m(t) + \alpha_{LM} \cdot DELAY_{LM}(prey_norm(t)) \quad (14)$$

and in an analogous manner for schema DM,

$$\tau_{DM} \frac{ddm.m(t)}{dt} = -dm.m(t) + \alpha_{DM} \cdot DELAY_{DM}(prey_norm(t)) \quad (15)$$

where $DELAY_{LM} = DELAY_{DM}$, and $DELAY_{DM} > DELAY_{HE}$ for the temporal coordination of motor synergies. The firing rates $lm(t)$ and $dm(t)$ are calculated similarly to $lu(t)$ by the transfer function (10).

Nishikawa and Gans (1992) have shown that $lm(t)$ activity is delayed with respect to $dm(t)$ activity if the mouth is to open. On the other hand, in XII nerve transected anurans, DM and LM are excited simultaneously. We hypothesize two different mechanisms responsible for the delay of LM (Fig. 6): 1) premotor LM's time constant is modulated (increased) by *HG* sensory feedback so that before the *HG* transection, LM is delayed with respect to *DM*; and 2) LM's time constant is modulated (increased) by *INT1*. We will later show that mechanism 1) gives rise to *TP* whereas mechanism 2) gives rise to *JP*.

Figure 7 displays a more detailed organization for some of the circuitry for motor pattern generation for snapping in anurans to emphasize the underlying circuitry giving rise to *JP* vs. *TP* under different input conditions (i.e. control circuitry for Lunging and Head ventroflexion has not been included). This circuit will also be the basis for learning after the *HG* lesion (refer to companion paper). We have implemented the dynamics of the time constant by a leaky integrator as well. It receives input from *HG* and *INT1*. In the absence of input the time constant resets to its resting value.

$$\tau \frac{d\tau_{LM}(t)}{dt} = -\tau_{LM}(t) + hg.rec(t) + int1(t) \cdot Y(t) + \tau_{rest} \quad (16)$$

where $Y(t)$ corresponds to the efficacy of the pathway connecting *INT1* to *LM*. In the discussion section we will discuss the effect of $Y(t)$ strength on biasing *JP* vs. *TP*. As a concluding remark we may point out that in general, simultaneous activation of antagonists may be very common (as in fish swimming, for example) and, thus a major function of premotor circuits may be to generate a pattern primarily through modulation and inhibition.

HG modulation: alternative hypotheses

A first hypothesis by Weerasuriya (1989) was that inhibition of *LM* by *HG* allows the mouth to open. A refinement of that hypothesis formulated in Liaw et al. (1994) proposed the *modulation* of *LM* time constant by feedback from *HG*. They also had to modulate the threshold and the amplitude to overcome the decrease in activity due to the slower time constant. Weerasuriya (1991) proposed that the lack of jaw opening and closing has to be attributed to an inhibition of jaw movement arising from the absence of tone in the lingual muscles. He

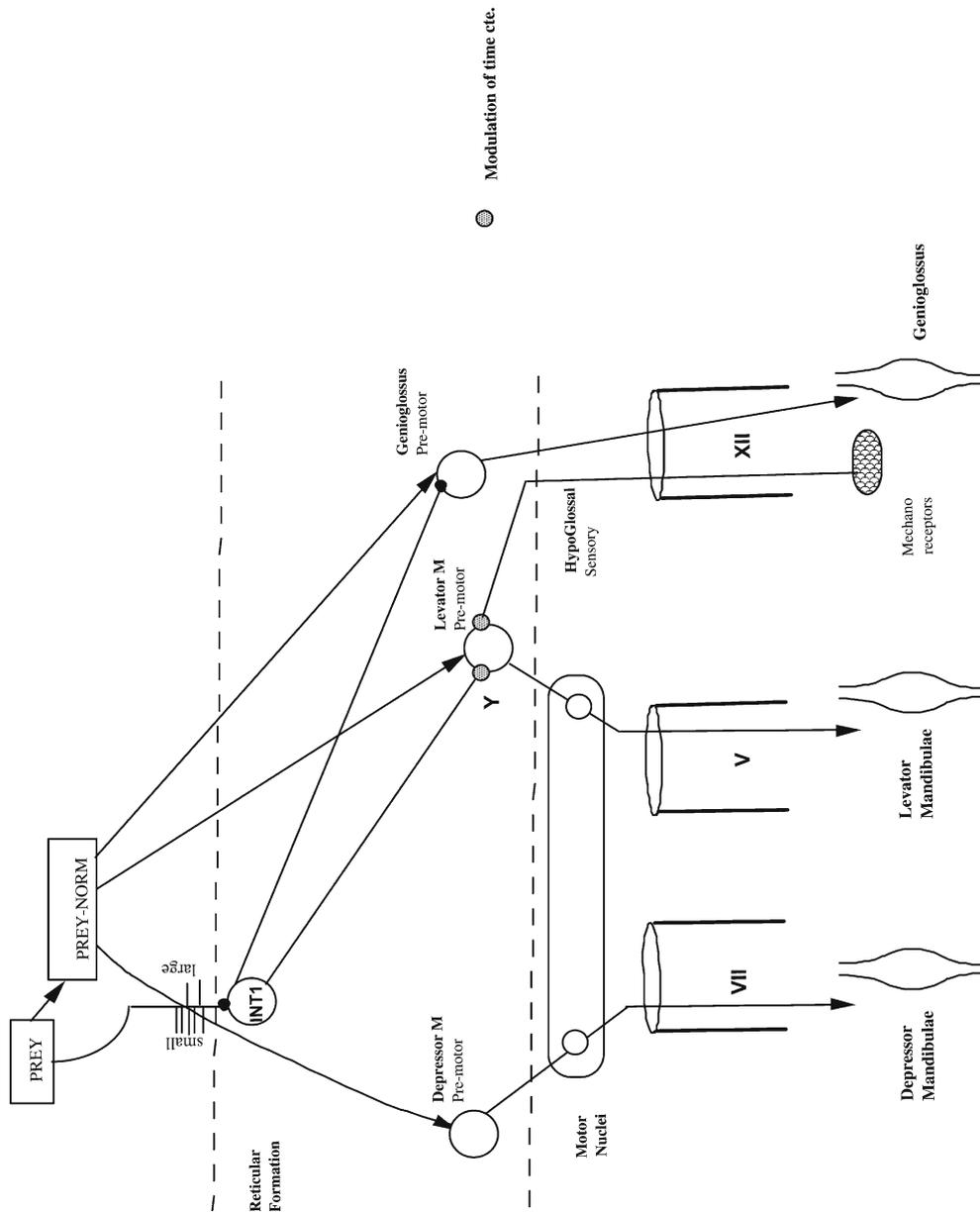


Fig. 7 More detailed organization for some of the circuitry for motor pattern generation for snapping in anurans (i.e. circuitry for tongue retraction, lunging and head downflexion has not been included). This figure emphasizes the circuit that gives rise to the JP vs. TP under different input conditions including the biological notation to ease the comparison with the anatomical data (e.g. control circuitry for *Depressor mandibularis*, *Levator mandibularis*, and tongue protractor *Genioglossus*)

further claimed that the results suggested a potential hierarchical organization of the subsynergies involved in snapping. The components lower down in the hierarchy (tongue and jaw movements) can be uncoupled less easily than those further up (lunge vs. tongue and jaw movement) in the hierarchy.

The question remains as to what is the behavioral advantage (role) of HG feedback modulation: Nishikawa (personal communication) suggests that it allows the animal to control its long tongue more precisely, signaling optimal positioning of the tongue within the respiratory cycle for optimal protraction. The position is signaled by mechanoreceptors

active when the tongue is pressing up against the ceiling of the mouth.

Modeling control of tongue

The Genioglossus premotor schema GG receives input from PREY-NORM and INT1. We are also using the parallel model of activation described in Liaw et al. (1994), that is, the premotor schema HO receives the same input as GG but delayed due to its different synaptic connection properties. The premotor neuro-schema GG is defined by

$\langle N \rangle$: GG
 $\langle Iplist \rangle$: $\langle (prey_norm(t) : R), (int1(t) : R), (t : R) \rangle$
 $\langle Oplist \rangle$: $\langle (gg(t) : R) \rangle$
 $\langle Varlist \rangle$: $\langle gg_m(t) \rangle$
 $\langle Behavior \rangle$: implemented by the following mapping,

$$\tau_{GG} \frac{dgg_m(t)}{dt} = -gg_m(t) + \alpha_{GG} \cdot DELAY_{GG}(prey_norm(t)) - \beta_{GG} int1(t) \quad (17)$$

and in an analogous manner for schema HO,

$$\tau_{HO} \frac{dho_m(t)}{dt} = -ho_m(t) + \alpha_{HO} \cdot DELAY_{HP}(prey_norm(t)) - \beta_{HO} int1(t) \quad (18)$$

The firing rates $gg(t)$ and $ho(t)$ are calculated in the same manner as for the other premotor units (by the transfer function (10))

The associated motoneurons $gg.m(t)$ and $ho.m(t)$ dynamics are described by the following mappings,

$$\tau_{GG.M} \frac{dgg.m_m(t)}{dt} = -gg.m_m(t) + \alpha_{GG.M} \cdot jaw(t) + \beta_{GG.M} \cdot gg(t) \quad (19)$$

$$\tau_{HO.M} \frac{dho.m_m(t)}{dt} = -ho.m_m(t) + \alpha_{HO.M} \cdot jaw(t) + \beta_{HO.M} \cdot ho(t) \quad (20)$$

To protract the tongue the mouth must be open. Nevertheless, sensory feedback from the jaw may be too delayed in most cases to have any effect on the control of the tongue since tongue movements occur very quickly. So tongue activation is mainly a *feedforward* activation yet under certain conditions (e.g. lesions) this sensory feedback may be important.

Motor schemas

Some motor schemas are functional units which update the environmental and agent parameters. We do not simulate the final muscle dynamics for the different motor synergies. Besides, in most cases, the mapping from motor neuron activity to muscle dynamics is not known to any good degree of precision. For instance lunging is itself a motor program involving the spatio/temporal coordination of several muscle synergies. We have simplified it by modeling the effects of the lunging motor program rather than its inner dynamics. Hence, we have implemented lunging by a schema mapping from the motor neurons $lu.m$ to the parameters of the animal within the environment, in this case the animal's coordinates. So the schema LUNGE reduces the horizontal distance between the snout and the prey x_s , namely

$\langle N \rangle$: LUNGE
 $\langle Iplist \rangle$: $\langle (lu.m(t) : R), (x_s(t) : R) \rangle$
 $\langle Oplist \rangle$: $\langle (x_s(t+1) : R) \rangle$
 $\langle Behavior \rangle$: Currently implemented by the following mapping,

$$S^{LUNGE}(a, b) = \begin{cases} b - \alpha_{LUNGE} \cdot \alpha + \rho & \text{if } b > \alpha_{LUNGE} \cdot \alpha \\ 0 & \text{otherwise} \end{cases} \quad (21)$$

whereas the schema HEAD_DOWN reduces the vertical distance y_s between the snout tip and the prey (in an analogous manner).

Regarding the jaw motor schemas, in the model the activation state of each muscle is represented by a variable e.g. $levator(t)$. In turn LEVATE is a simple function of the activity of the motor neuron $lm.m$. In the current model it is simply a scaling function but it is open to further refinements by changing the schema's specification.

$\langle N \rangle$: LEVATE
 $\langle Iplist \rangle$: $\langle (lm.m(t) : R) \rangle$
 $\langle Oplist \rangle$: $\langle (levator(t) : R) \rangle$
 $\langle Behavior \rangle$: Currently implemented by the following mapping,

$$S^{LEVATE}(x) = \theta(x, \Theta_{LEV}) + \rho \quad (22)$$

where

$$\theta(x, \Theta) = \begin{cases} x & \text{if } x < \Theta \\ \Theta & \text{otherwise} \end{cases} \quad (23)$$

where Θ is the threshold beyond which the levator saturates and is white noise. We have implemented analogous dynamics for DEPRESS with respect to $dm.m$; and PROTRACT and RETRACT with respect to their respective motoneurons $gg.m$ and $ho.m$.

4.5 Model dynamics

We have simplified the representation of visual input by coding large prey by lower firing frequency than small prey. This corresponds to the intuitive notion of less "prey like" as the prey gets larger (e.g. becoming "snake like"). The neural mechanisms that can "implement" this notion are both pretectal cells with larger RF inhibiting the prey cells and RF size of prey cells so that large prey get into the IRF. In this regard, Ewert (1987) defined a neural interaction model of prey-catching and avoidance behavior in toads and Ewert et al. (1992) further described the discrimination activity towards geometrical stimuli by a co-processing of tectal and pretectal structures. As already stated, *INT1* has tonic activity (set to 0.5) and is inhibited by PREY_REC. HG_REC has sinusoidal tonic activity due to respiratory cycle causing pressure of the tongue epithelium upon the upper floor of the mouth cavity.

The next two figures display the temporal activity corresponding to: PREY_REC(t), PREY_NORM(t), HG_REC(t), JAW_REC(t), TONGUE_REC(t), DISTX(t), DISTY(t); the interneuron INT1(t), and the different *premotor* neurons activity: LU(t), HE(t), DM(t), LM(t), GG(t), HO(t) under the following feeding conditions: Small prey (TP), Large prey (JP), and both small and large prey after the Hypoglossal nerve

transection. For small prey (Fig. 8 Left), PREY_REC inhibits INT1 a lot, hence INT1 becomes inactive, so that HG tonic activity modulates LM time constant causing no change in LM onset activity but delay in peak activity, thus allowing mouth opening (as DM is active). This gives rise to the TP motor pattern described in Sect. 2. Notice the large activity of GG, and HO, as well as the low activation of LU and nearly inactive HE characteristic of TP. Also notice the delay

of JAW_REC with respect to DM and obviously the onset and offset of tongue activation happens while the mouth is still open.

For large prey (Fig. 8 Right), PREY_REC inhibits INT1 much less, i.e. INT1 is still active. In this case LM time constant is modulated by INT1. This gives rise to the Jaw Prehension motor pattern described in Sect. 2. Notice the almost sequential behavior between lunging and mouth opening and the smaller inhibition to INT1. Also notice the high activation of premotor LU and HE, as well as the low activation GG and HO corresponding to the Jaw prehension.

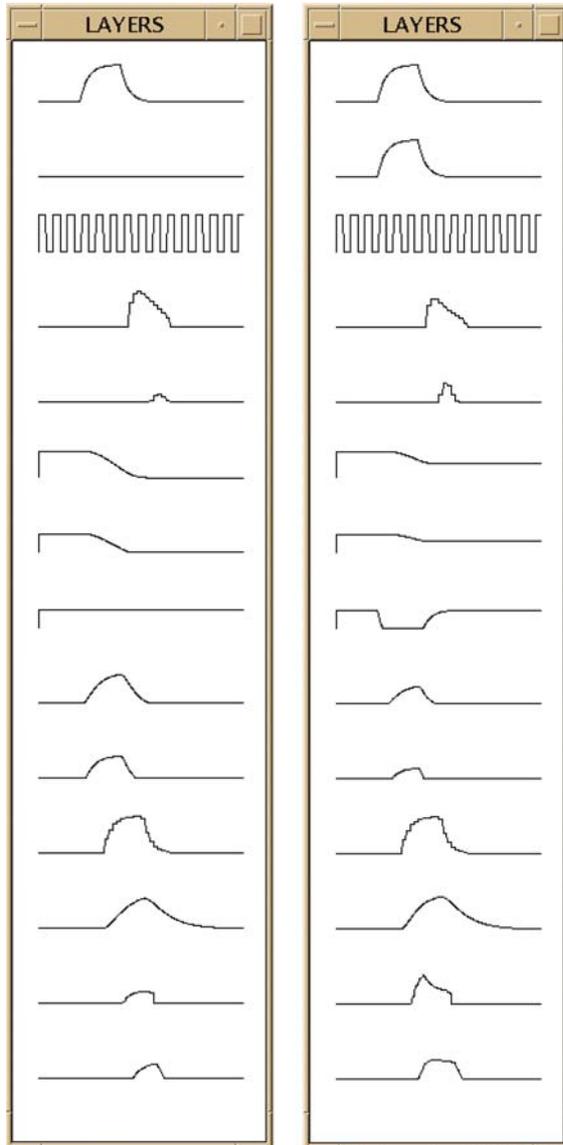


Fig. 8 Temporal pattern of activity for each schema instance. *Right.* Motor pattern when feeding on small prey corresponding to *Tongue Prehension*. *Left.* Motor pattern when feeding on large prey corresponding to *Jaw Prehension*. The *first rows* display the temporal pattern of activity corresponding to the different *perceptual* schemas: PREY_REC, PREY_NORM, HG_REC, JAW_REC, TONGUE_REC, DISTX, DISTY, respectively. The *next row* displays the activity of the interneuron INT1. The *following rows* display the temporal pattern of activity corresponding to the different *premotor* schemas: LU, HE, DM, LM, GG, HO

4.4.1. Lesion phase

As described in the Behavioral observations section, disruption of the nerve innervating tongue muscles abolishes not only tongue movement, but also mouth opening when feeding on small prey, even though the nerve controlling the jaw muscles remains intact (Weerasuriya 1989, 1991). On the other hand, for large prey the animal behaves as before the lesion. So we remove HYPOGLOSSAL from the system and observe the new system dynamics (Fig. 9).

The left pattern in Fig. 9 corresponds to the small prey feeding condition whereas the right pattern corresponds to the large feeding condition. In both, notice the inactivity of GG and HO caused by the lesion. In the small prey preparation notice the absence of delay in LM with respect to DM. Also notice the inactivity of JAW-REC (mouth does not open) and the low activity of LU and nearly inactive HE corresponding to TP. On the other hand for the large prey preparation the activity profiles remain very similar to those of Fig. 8 Right.

5 Discussion

In principle, a large amount of information must be integrated in both the planning and implementation stages of motor control, but little is known about how different types of sensory information, such as vision and proprioception, are combined to control movement. In anurans, it is clear from behavioral studies that visual information about the target and proprioceptive information about the animal's starting position interact in feedforward control of prey capture. However, it is unclear where and how these sensory modalities interact in the brain. Anatomical and physiological studies in anurans make the reticular formation a likely location for the integration of this sensory information. Our model tries to find the simplest neural architecture in the reticular formation that can explain the interactions between vision and proprioception in control of prey capture that have been described in behavioral and lesion studies. In the following subsections we sketch a set of observations and begin to provide some preliminary explanations. All these lead the way for ongoing as well as future research.

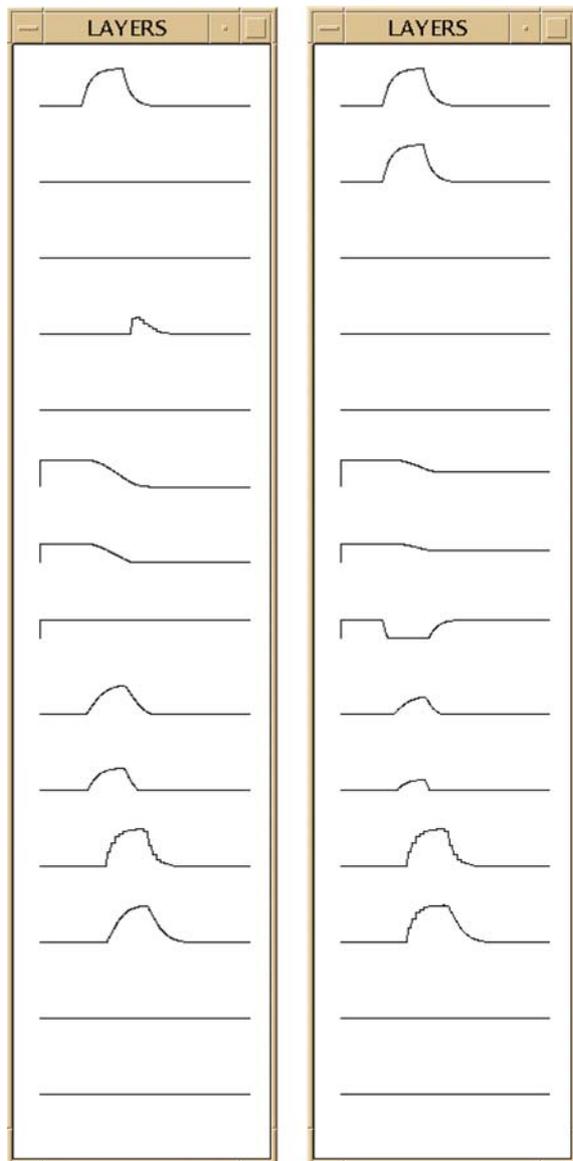


Fig. 9 Left Motor pattern when feeding on small prey after bilateral Hypoglossal transection. Right Motor pattern when feeding on large prey after bilateral Hypoglossal transection. The format of the figure is equivalent to that of Fig. 8

5.1 Motor variability

The present categorization of tongue types in frogs (i.e., discoglossoid, aglossal, hydrostatic and anteriorly attached) is not sufficient to describe the diversity of feeding behavior that frogs exhibit (Anderson and Nishikawa 1993). The behavior patterns used by *Rana pipiens* to catch large and small prey correspond to differences in feeding behavior between primitive and derived frogs, respectively. Primitive frogs have short tongues that can be protracted only a few millimeters, so these frogs must lunge much closer toward prey to catch them. In contrast, derived frogs have highly protrusible tongues and do not need to lunge very close to the prey to catch them. The

similarity between movements used by *Rana* to catch large prey and those used by primitive frogs in general suggests that *Rana* has retained the plesiomorphic motor pattern and uses it to catch large prey, while acquiring a derived motor pattern to catch small prey.

A general model must account for the *variability* across different species (configurations), thus, we propose an *adaptable general framework* with the capability to change not only the parameters but also the MPG structure, based on different anatomical constraints as well as feeding habits. Different species may evolve different configurations and adaptation strategies due to different physical morphology and environmental constraints, in turn giving rise to different patterns of behavior (cf. motor variability). Different motor plants (e.g. longer tongues corresponding to different seed schemas (structure)) would give rise to different MPG. In the companion paper motor variability is also produced by different experience (plastic) changes reflected in internal models and goal schemas. In the companion paper we will also see how SBL explains motor variability beyond simply introducing a range of parameters. That is, SBL also introduces topological changes on the MPGs corresponding to the construction of new schemas.

In particular the model can account for the variability across individuals by varying $Y(t)$ —where $Y(t)$ corresponds to the efficacy of the pathway connecting *INT1* to *LM*. The strength of $Y(t)$ on biases JP vs. TP, i.e. larger $Y(t)$ bias towards JP. The model can also account for the variability across species, for instance toads would have a low value of Y so they mostly use TP, whereas tree frogs would have a high value of Y so they mostly use JP.

6 Conclusions

We have extended the model by Liaw et al. (1994) by integrating a number of different *motor pattern generators*, different types of afferent feedback, as well as the corresponding control structure within an adaptive framework we call Schema-Based Learning. A motor action often involves the coordination of several motor synergies and requires flexible adjustment of the ongoing execution based on feedback signals. Neural mechanisms underlying the *construction* and *selection* of motor synergies critically depend on the intricate interaction between different motor synergies, including the interplay of their *afferent* feedback signals with the ongoing motor program. Such data provide insights for the general issues concerning two-way information flow between sensory centers, motor circuits and periphery in motor coordination. In general, simultaneous activation of antagonists may be very common (as in fish swimming, for example) and, thus a major function of premotor circuits may be to generate a pattern primarily through modulation and inhibition. Since the observation that the sequence proceeds to completion once initiated, despite removal of the target (Hinsche 1935), snapping has been regarded as highly *ballistic* with little or no variability based on sensory feedback (Ingle 1983; Ew-

ert 1984). Nevertheless, recent observations by some of the authors (Liaw et al. 1998) have revealed a feedback component in snapping. This paper shows how different afferent feedback signals about the status of the different components of the motor apparatus play a critical role in motor control as well as in learning (refer to the companion paper). Throughout the paper (e.g. in the abstract) we have introduced a set of points/questions that we would like to clarify with this modeling work. In particular the simulations have addressed:

- How do different MPGs dynamically selforganize based on the input? We have presented a model of motor schema selection (i.e. JP vs. TP) where the different motor programs were selected based on the different firing frequencies from the prey-recognition system. Several MPGs (JP & TP) share the same underlying circuitry and yet give rise to different motor patterns under different input conditions.
- What are the characteristic features of the activity of a single muscle? EMG recordings indicate onset, offset and overall dynamics, this model shows this qualitative descriptions to be enough to replicate some behavioral results.
- How can these features be controlled by the premotor circuit? The model shows the role of premotor circuit not only for triggering but also for modulation and inhibition by integrating a variety of signals.
- What are the strategies employed to generate and synchronize motor synergies? We have described the serial model and the parallel model of coordination and demonstrated the larger versatility of the parallel model including different delay lines to coordinate the different basic MPGs.
- What is the role of afferent feedback in shaping the activity of an MPG? Different afferent feedback serve as control signals modulating the overall motor pattern. This include reset signals, “readiness” signals and performance signals (e.g. getting closer to different goals).
- Visual information about the target and proprioceptive information about the animal’s starting position interact in feedforward control of prey capture. However, it is unclear where and how these sensory modalities interact in the brain. The model we propose attempts to shed light on this matter by proposing a specific integration of different sensory modalities (e.g., depth, proprioceptive feedback) and their interplay with different motor commands to achieve both feedforward as well as feedback control.

Future work should include further specificity and variability in both motor patterns and pattern recognition. For instance, Valdez and Nishikawa (1997) have reported different motor patterns for five different prey types (termite, wax, cricket, mice, earthworm). We must introduce more complex spatio-temporal representations. The differences in motor patterns cannot be simply accounted for by changes in prey size. For instance, the relation angle of head/prey type

is similar for all prey types except the one for mice which is much smaller. For other parameters we can also discriminate in this manner. Upon perceiving a prey the brain must dynamically construct the motor pattern for prey capture. Thus, a configuration of schemas must be dynamically assembled on “run time”. We will also study data on the prey-dependency of kinematics of feeding behavior. That is, differences in prey size, shape and mobility may produce differences in the kinematics of feeding motor patterns. On the pattern recognition side we plan to extend the model along several dimensions including more realistic visual input signal (Teeters et al. 1993) for more complex prey discrimination to allow for more diversified motor pattern generation. We will include a more refined model of the retina (R2, R3, R4 cells) providing spatio-temporal signals to a “functional” tectal-pretectal model. The tectal-pretectal circuit is in charge of “refining” the alphabet to be “interpreted” by the motor system in program construction. We also plan to link the model to more realistic biomechanics models (Mallet et al. 2001)

6.1 Predictions and suggested experiments

The predictions here listed also lead the way for future experiments, thus, closing the experimentation-theory cycle. Some of these predictions are directly related to questions listed in the abstract and throughout the paper.

Prediction 1 The same structure gives rise to two different motor patterns under different input conditions. Lesions on the common pathway will affect both motor patterns (although possibly in a different manner).

Prediction 2 By injecting current onto *INT1* we can bias the response towards the Jaw Pattern even though the perceptual input may belong to the other category (i.e. small prey).

Prediction 3 In the model the different sensory feedback interact with the motor commands to achieve optimal performance. For instance it is a prediction of the model that lesion of the input from *JAW_REC* to *GG.M* will cause delay of tongue protraction. In the same fashion lesion of *DISTX* input to *LUNGE* will give rise to overshooting of lunging.

Prediction 4 We have predicted that modulation of *INT1* time constant gives rise to the delay of *LM* activity with respect to *DM* activity. Blocking the modulation will have the effect of synchronous onset of *LM* and *DM* activity, hence causing the mouth not to open for both large and small prey (JP and TP).

Prediction 5 Changing/blocking *Y* will affect the jaw pattern motor program without affecting the tongue pattern (opposite to the effect of the *HG* lesion which only affects the TP).

Prediction 6 By injecting current on *INT1* after performance of the *HG* lesion, *INT1* becomes active thus giving rise to JP even for small prey.

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