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The Stomatogastric Nervous System: A Formal Approach

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Abbreviations: DG, dorsal gastric; GM, gastric mill; PD, pyloric dilator; STG, stomatogastric ganglion; STNS, stomatogastric nervous system; VOR, vestibulo-ocular reflex.

Running title: The STNS: A Formal Approach

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Abstract–A discrete mathematical formalism (d-space) which is specifically designed to investigate discrete aspects of behavior is applied to the foregut of decapod crustacea. This approach differs from continuous modeling techniques in that the analysis determines a structure in which the observed behavior of the foregut is constrained. A notation for the implementation of the formalism is developed as well as a coordinate system natural to the functioning of the gastric mill. The formalism is used to organize previous observations that suggest potential courses of further experimental investigation. A detailed analysis of observed chewing modes of the gastric mill is presented, along with a discussion of the overall organization of the interrelationships between these modes. The investigation also addresses the relationship between behavioral modes of a pyloric muscle found in the shrimp *Palaemon*.

Two alternative hypotheses are presented to describe the relationship of the behavioral components of the gastric mill: an interlaced control scheme in which the components are freely exchanged, and a top-down control system where the chewing modes are rigidly separated into packages. Flow through regions of state space in time is found to be important in determining the relations between the discrete behavioral components. The behavior of the foregut, as that of other motor control systems, is shown to fit naturally into the d-space formalism.

Key words: Stomatogastric, discrete, behavior, state, dynamic, modulation.

Biological systems are known to exhibit rather discrete forms of behavior in dealing with a continuous world. Although one might expect that an optimal strategy for adaptive systems would be to accurately match their behavior to the given task, there is a tendency for organisms to adopt a discrete set of overall strategies and fine tune within the confines of each discrete strategy [7]. Some of this discreteness is parameter dependent such as when gait switches abruptly among different patterns depending on the speed of an animal. In the well-known example of horse gaits, at slow speeds the horse's legs move in a sequence called a walk, and as the horse increases speeds the leg movement patterns move through the sequence from walk to trot to canter on to reach a gallop at the highest speed [3]. The exact speed of the animal may vary considerably during each of these discrete phases, but there are small overlapping regions where the same speed can be maintained with either of two different gaits. It is interesting to point out here that the stabilities of the gaits are not equivalent: the canter is considered to be a trained gait and may be absent in the transition from trot to gallop.

Observations of human postural adjustments point to the existence of a discrete set of responses on which a behavioral repertoire can be built [25]. One finds that if a standing subject is perturbed from an upright position, then the response can be decomposed into two typical strategies: a torsion about the ankles or a counter-rotation of the hip that exerts a restoring shear force on the floor. Although the hip movement may be chosen exclusively if the support base is too small for producing an ankle torque, individual subjects may choose to use it even when standing on a flat floor or in combination with the ankle strategy. The point here is that the continuum of potential strategies available for returning to stable stance after a perturbation is discretized into a limited number of strategies that may then be adjusted in strength to adapt to environmental challenges [20].

Discreteness also arises in the following form: responses such as reflexes may differ depending on discrete behavioral states of an organism [26]. Among the examples of this phenomenon is the phase dependent reflex response in walking spinal cats after cutaneous stimulation of the leg. [5]. When a forward walking cat encounters an obstacle on the front side of the foot during the swing phase of the step, the cat reflexively steps over the obstacle, but the same stimulation elicits a contraction of the antagonist muscles during other phases of the step. This kind of reflex reversal shows that a discrete change in the spinal reflex is caused by moving from one region of limb positions to another. Another related example is found in the observed context dependence of the vestibulo-ocular reflex (VOR) [1]. In cat, it is possible to train a cat to produce a different VOR for each of two orientations of the head: left-side-up or right-side-up. A more common example is the change in VOR when one puts on corrective glasses. In this case, the physical cue is the placement or removal of the glasses, but the result is an automatic change in the VOR that is tuned to the optical distortion learned from previous experience.

Such conditional responses are better described by a discrete logic rather than by continuous methods such as differential equations used in conventional approaches [27]. By a logical implication we mean if condition A is satisfied, then response B is appropriate. (For example, if the cat is left-side-up, then a certain VOR is produced.) When several discrete conditions are to be met (such as if the cat is left-side-up and in the swing phase of walking), this scheme will yield a treelike structure determining the viable response. Although discrete mathematics has not been as thoroughly developed as its continuous counterpart in the context of the neural control of movement, there are aspects of behavior that are simplified in a discrete formalism. The discrete approach to nonlinear complex systems has been referred to as the "infinitely nonlinear approximation" [30]. This language follows from replacing smooth functions used in differential equations with discontinuous functions. Since many aspects of biological systems arise from the nonlinear elements, this is an appropriate approximation to make. Yet once one has opted to take a discrete approach, the formalism forces one to consider such possibilities such as discontinuous biological parameters that the system drives to restricted values in the behaving organism.

The purpose of this paper is to analyze the discrete modes of behavior of the stomatogastric nervous system (STNS) and the foregut in decapod crustacea. The formalism used allows us to present hypotheses for determining the behavioral components of the foregut in terms of their interrelationships. In the next subsection we give a brief introduction to the known facts of the behavior under investigation. The mathematical approach will then be introduced in the following section to show how one applies the formalism to help elucidate the behavior of the stomatogastric system. Examples are given of the components that will be integrated in the Results section to analyze the known behavior of the foregut. This analysis points out ambiguities in published data regarding the stomatogastric system and suggests hypotheses for further experimental investigations. We conclude with discussion of how this approach impacts the present view of the stomatogastric system.

The Behavior of the Foregut

The foregut of decapod crustacea is divided into three parts: a cardiac sac which holds food after swallowing, and allows mixing with gastric juices, a set of teeth referred to as the gastric mill that chew the food of the larger decapods, and a pyloric filtering chamber which sorts out the particles fine enough for absorption (for a more complete introduction to the subject, see [15]). The pyloric and gastric mill musculature is primarily innervated by neurons in the stomatogastric ganglion (STG). This neural network consists of fewer than thirty cells, yet can produce several distinct rhythms required for the chewing and filtering of food. The present study concentrates on the activity of the gastric mill, and investigates how this activity is influenced by interactions among the neurons in the STG, the muscles that drive the teeth, and the observed chewing modes.

The gastric mill consists of two opposing lateral teeth and a central medial tooth. The three most stable and commonly observed modes of chewing that are observed in both the lobster [9] and the crab [11] are: squeeze, cut and grind, and cut and squeeze (Figure 1). In the squeeze mode the three cusps of the teeth meet to pinch any food that is between the cusps. The cut and grind mode begins with the lateral teeth meeting in a "cut" until the medial tooth comes down and is dragged along the length of the lateral teeth to meet the cusps. Less often observed is the cut and squeeze mode that begins as the cut and grind, but before the medial tooth comes down onto the lateral teeth, the latter open again and then meet the medial tooth as in the squeeze. Heinzel [9]

Fig. 1 near here.

emphasizes that these three modes are distinct with respect to the timing of the various muscles' contractions that make up the motor pattern, which is itself generated by the gastric mill neural network in the STG. It is this observation of distinct behavior that suggests the application of discrete mathematics.

Electrophysiological readings from the neurons of the STG that innervate the muscles of the gastric mill [29] have identified the neural firing patterns corresponding the above chewing modes [9, 11]. The STG is capable of switching between these patterns depending on the presence of certain neuromodulators that often affect the cellular properties of target neurons and/or the synaptic strength connecting the neurons of the network [8]. The neural network itself thus exhibits the type of parameter dependent switching between discrete behaviors noted above for motor patterns.

Gastric mill rhythms are not the only patterns that can be generated by the STG. Some of the motor neurons innervate the muscles of the pylorus that operates with its own rhythm to perform filtering tasks. Thus the STG is capable of generating two simultaneous rhythms that respectively drive the gastric mill and the pylorus, where the gastric rhythm completes a cycle in 5-20 seconds, and the pylorus follows a faster rhythm with a period of 1-3 seconds. In fact, many of the neurons that innervate the gastric mill can switch rhythms and burst in time with the pylorus. These shorter bursts do not appear to be long enough to close the teeth in any meaningful chewing mode, but rather are assumed to help move food into the pylorus and mix the contents of the cardiac sac [11].

The behavior of the foregut is driven and constrained by four components. The most obvious is the overall anatomical structure of the foregut. The cardiac sac and pylorus are suspended in the thorax, and the gastric mill resides in between the two (Figure 1). The teeth of the gastric mill are attached to a set of ossicles that are hinged in a complicated manner restricting the movement of the teeth so that the medial tooth moves in a plane perpendicular to the lateral teeth.

The second component of the system is the muscular structure that moves the various parts of the foregut. Most of the muscles are bilaterally symmetric and can be divided into two groups: extrinsic muscles that attach the foregut to the thoracic wall, and intrinsic muscles that run between different parts of the foregut itself. These muscles can exhibit a variety of properties that complicate the behavior of the foregut. For instance, in the shrimp the pyloric dilator muscle (cpv1) has been shown to display three states of behavior [21, 22]. (*i*) The muscle can act as a passive follower, its tension being an approximately linearly function of the spike frequency of the motor neurons that innervate it. (*ii*) It can also behave as an endogenous oscillator that can be entrained by spike trains at frequencies near its natural oscillation frequency. (*iii*) The muscle has a sensitized state where it returns all-or-none responses to spike activity from its driving motor neuron. Thus, here is another parameter dependent series of discrete states controlled by chemical modulators. The muscles of the foregut also exhibit facilitation and depression so that even in the follower mode they may not always follow an exactly linear relationship to the neuronal input.

The neurons of the STNS make up the third component of the system; they limit the behavior of the foregut and contribute to determining the available states of operation. The STG is a subset of the STNS and contains the motor neurons that innervate the muscles of the foregut. Because the axons of the STG motor neurons bifurcate to innervate the muscles of the foregut bilaterally symmetrically, the movements of these muscles are constrained to move symmetrically. This implies that the lateral teeth of the gastric mill meet in line with the movement of the medial tooth. The properties of the STG's neurons are numerous and varied. The neurons show modulator dependent bursting properties due to their plateau potentials, and they exhibit postinhibitory rebound that in combination with plateau properties can induce strong bursts of spike activity after synaptic inhibition from other neurons. Many of the neurons are also modulator dependent conditional oscillators, and thus can also contribute to a particular behavioral state with their own endogenous rhythm.

The final component we will discuss is the network based properties, i.e. the synaptic connectivity of the STNS neural networks. The synaptic connectivity of the STG comprises about 50% of all possible connections, and rhythm generation is based to a large extent on inhibition among neurons. The network's distributed structure endows it with discrete collective properties that do not arise from either its component neurons or its synaptic connectivity alone. Although most of the cells are motor neurons that innervate the muscles of the foregut, each also contributes to the overall pattern generation. The STG contains several important subcircuits that are known to reconfigure their effective wiring, exchange members, or join together to build circuits of different characters [4]. There are many interactions with other parts of the STNS, such as pacemaker neurons found outside the STG that modulate the pyloric rhythm [24, 28]. A few sensory neurons also influence the activity of the STG [14], but *in vitro* studies show that the rhythmic patterns of the STG can be generated in the absence of sensory inputs [4]. As with the other components, the stomatogastric nervous system as a whole exhibits a set of discrete, modulator dependent behaviors that is considerably smaller than the full set of possibilities given the architecture of the stomatogastric system.

Mathematical Methods

The basic tool of this analysis is the d-spaces formalism; a d-space consists of a discrete set of regions described by physiologically relevant parameters, the regions being connected according to two relations, inclusion and contiguity ([17, 18] has further details, and [19] has formal definitions). Often, the regions belong to a linear space formed by the direct product of parameters. Inclusion is used in the same sense as set inclusion such that a large region in the parameter space may include smaller regions. Contiguity between two regions implies that a path exists from one of the regions to another. A contiguity may be directed or not, depending on whether there is some underlying biological mechanism or physical constraint that inhibits movement in one of the directions.

We will use of these concepts in our analysis of the movements gastric mill's teeth. In order to denote regions, we must introduce a coordinate system to report the positions of the teeth so that the regions can be clearly defined. The coordinates shown in Figure 2 are chosen for precision in analyzing tooth movements and ease in distinguishing chewing modes. Unlike standard Cartesian coordinates [9], they include all parameters

Fig. 2 near here.

relevant to the positions of the teeth with respect to each other.

Fig. 3 near here.

Figure 3 gives a formal d-space of gastric mill positions. The minimal regions shown in the figure are not given as points because functionally equivalent movement sequences can arise over a range of tooth positions. The lower left panel shows the region of tooth positions that corresponds to the "open resting position" that the teeth assume between bites and while the gastric mill is inactive [9]. The lateral teeth are nearly parallel ($\theta_L \approx 0$) and the tips of the teeth are far apart ($r_L \neq 0$), although other positions have been observed (Mary Boyle, personal communication). The medial tooth is retracted in this state so that r_M is large. This region is depicted by the sphere in the graph (where the hairline that pierces the sphere is for perspective). The next panel to the right represents the squeeze state. The tips of the lateral teeth are touching ($r_L = 0$) and thus "slant" inward ($\theta_L > 0$), but are otherwise constrained only by the foregut's mechanical structure and the intervening medial tooth. The cusp of the medial tooth is in contact with the tips of the lateral teeth ($r_M = 0$). This leaves a small region (shaded) on the θ_L axis that represents the remaining unrestrained movement of the lateral teeth. The horizontal dashed lines between these panels represent contiguity between behavioral states. A contiguity between the open resting and squeeze states means that there is an allowed transition between these states in the behaving animal.

The solid lines that connect the regions from top to bottom denote inclusion of the lower levels in the upper levels. This treelike structure forms a partially ordered set, or poset, that is used for constructing a d-space. Thus, the resting (sphere) and squeeze (shaded line) states shown individually in the left most lower panels are both included in the region shown in panel A on the second level, as is the transition region that the teeth repetitively pass through in the squeeze mode of chewing. The second level of this d-space thus represents the behavioral modes that organize the states of the bottom level into movement patterns, and the arrows show the movement in the transition region between states. In panel A, the double headed arrow implies that the squeeze mode consists of an oscillation between two states: resting and squeeze.

The middle panel (B) represents the cut and grind mode. This includes all four of the states on the first level. Taking the resting state as a starting point (spherical shaded region near top of figure), Heinzel [9] reports that the cut and grind mode usually begins with a slight opening of the teeth as shown in the third panel on the bottom level, the "spread" state. The positional region of this state is smaller than the resting state and the distances between the tips of the lateral teeth (r_L) and the distance from them to the cusp of the medial tooth (r_M) is generally greater than in the resting state although there may by some overlap. Although Heinzel [9] does not remark on the relative angle between the lateral teeth, we assume that they are nearly parallel ($\theta_L \approx 0$) as in the resting state. The contiguity line joining the resting to the spread state is directed (note arrow) because Heinzel reports that the appearance of this state is a clear indicator that the system will proceed through the sequence of the cut and grind (or cut and squeeze modes) before returning to the resting state. The next state in the cut and grind sequence is the cut where the lateral teeth meet along their lengths so that $\theta_L = 0$ and $r_L = 0$, and the medial tooth may assume all positions (r_M is not constrained; shaded area on r_M axis). After the cut state, the system makes a transition to the squeeze state, but if the lateral teeth do not open, the transition manifests itself as the grind movement of the cut and grind mode. This transition is seen in the middle panel of the second level as a band in the $r_M - \theta_L$ plane. Finally, the pattern ends by a transition back to the rest state. Panel C shows the other gastric chewing mode (cut and squeeze [31]), which consists of transitions from rest to cut, cut to rest, rest to squeeze, and squeeze to rest.

The top of the pyramid in Figure 3 is a panel representing all possible tooth movements consistent with the mechanical restrictions of the foregut. The second level lists behavioral modes of the gastric mill, and the contiguity relations show the allowed transitions between these modes. Each mode consists of a restricted set of behavioral states that reside on the bottom level. Inclusion is indicated by lines connecting the behavioral mode to the behavioral states. The reason for the hierarchical organization is that different modes on the higher levels can share behavioral states of the lower levels. This lends flexibility to the system while minimizing the number of states required to perform a variety of tasks. On each level, it is assumed that the members are quasi-stable elements regardless of whether the members are states or modes, and there is a restricted set of allowed transitions between them. Mechanisms on the higher levels constrain the possibilities on the lower levels as the organism performs its activities.

It should be emphasized that the position of the teeth results from an integrative combination of neural output and stomach anatomy. For instance, in the squeeze mode, if the lateral teeth were not touching at the cusps before the medial tooth moved into position, the system would require fine control to exactly place the medial tooth in a precise position (i.e. at $r_M = 0$). As it is, the medial tooth is simply protracted until it bumps into the lateral cusps. Thus, the form and structure of the gastric mill is as important in insuring the behavior as the output of the neural circuit.

Turning now to the muscles, the second behavioral component mentioned above, we first take a look at the pyloric dilator muscle (cpv1) in the shrimp *Palaemon*. This example is investigated here because the cpv1 muscle is a conditional oscillator with three modes of activity. The cellular properties of the neuromuscular junction yield the directed contiguities in the d-space representing this behavior. In Meyrand and Marder (1991) [22] the three activity modes of cpv1 were induced *in vitro* by a bath application of FMRFamide-like peptides. The muscle is innervated by two electrically coupled pyloric dilator (PD) motor neurons that reside in the STG. To depict the behavior of the neuron-muscle system under the influence of FMRFamide-like peptides, a d-space with a minimum of three parameters is required: the burst length of the motor neuron PD, the tension of the muscle cpv1, and the concentration of the appropriate peptides.

Fig. 4 near here.

Figure 4 shows a d-space for the bath application of FMRFamide-like peptides in [22]. The neuromuscular response graphs have been divided into nine regions in anticipation of using the same regions in a study of movements of the gastric mill. It suffices to say here that a long burst is on the order of the bursts that drive the gastric rhythm, a moderate burst is closer to the scale of a pyloric burst, and the shortest burst represents either a series of single spikes or silence from the PD motor neuron. The tension is also divided into three regions to relay the most relevant structure. The lower left panel shows a neuromuscular state where there is little or no neural input and minimal tension in the muscle. The lower right panel shows a state where there is a moderate burst and the muscle has responded with a moderate tension. Note that this is an unstable state because over time it must proceed to either a long burst, or the burst ends and there is a transition to the state represented by left bottom panel. The response to a long burst is not included here because in the normal functioning of the pyloric circuit, the PD neuron does not fire in long bursts.

The panels of the second level show the transition between states of the bottom level in this d-space. The implicit assumption here is that the response of the muscle follows the initiation of the burst. Thus the PD neuron commences a moderate burst in the far left panel that is followed by a moderate response of the cpv1 muscle in the next panel to the right. The directed lines of contiguity connect these flows in their proper temporal ordering. The third panel represents the end of the burst that is followed by a relaxation of the muscle in the far right panel. All of these response flows are included in the low peptide activity mode of the muscle as shown by the lines of inclusion connecting them to top left panel. The peptide concentration needs to be explicitly shown only on this level. This panel shows the overall flow pattern of the activity mode associated with a low peptide concentration and the normal activity of the PD neuron. The top right panel shows the flow pattern for another peptide concentration where the muscle tension is maximal for a moderate burst length. This depicts the all-or-none activity mode. The flows and states included in this mode follow as under the top left panel (follower mode) with some overlap.

The contiguity relations between these activity modes of Figure 4 follow from the observations of Meyrand and Marder (1991) [22]. When the peptides are applied to the bath, the muscle jumps from the passive follower state to the endogenous oscillator state (shown in Figure 5, bottom row), and then drops down to the all-or-none state during the wash. Although it is anticipated that one may move directly from the passive follower state to the all-or-none state without passing through an oscillator phase, the limitations that this behavior would impose on the behavior at lower levels of inclusion are made explicit in the present formalism to help guide *in vivo* studies.

Fig. 5 near here.

In order to draw the d-space related to the activity mode that results from a high peptide concentration in the bath, the addition of another variable is required (Figure 5). Because the oscillations of the muscle may be entrained by the PD neuron if the frequency of the input is close to the endogenous frequency of the muscle, the frequency input is added to the d-space under this condition. These two activity modes are shown in Figure 5 on the top level. The panel to the right shows the activity flow if the input frequency is restricted to the entrainment region. Included in this activity is the sequence of flows as in the follower activity mode of Figure 4. The top left panel shows the situation when the input frequency lies outside the region of entrainment (note that the "slab" shown in the right panel is missing from the "block" on the left). Here there are simply endogenous oscillations of the muscle with no relation to PD neuron input.

Results

Unified Analysis of Neural-Muscular-Behavioral Activity in Chewing Modes.

The method can now be applied to unify neural, muscular, and behavioral aspects of the gastric mill in one mathematical object. Although some components will be omitted for simplicity, this approach affords a multi-level analysis in which no level alone determines the behavior of the whole. Three of the motor neuron types in the STG that innervate the muscles of the gastric mill will be considered in the present example. The reason for displaying a subset of the motorneurons is that we may more easily display the full d-spaces in the figures. The neurons chosen are the minimum necessary for the description of the mechanism of the gastric mill following Heinzel 1988 [9]. It is appropriate here to give a brief description of these motor neurons and the mechanical function of the muscles that they innervate (see [31] for further details).

The medial tooth is controlled by two motor neuron types; the gastric mill (GM) neurons and the dorsal gastric (DG) neuron. These function as antagonists where the GM neuron brings the medial tooth down into the plane of the lateral teeth and DG retracts the medial tooth. Because they work in opposition and are strongly mutually inhibitory, these neurons generally burst in antiphase, although co-contraction of the muscles innervated by these do contribute to the behavior of the gastric mill in the cut and grind mode [9]. However, a coarse grained approach is appropriate here; we therefore show here only the action of the GM neurons, and assume where possible that the DG neuron fires in antiphase. The muscles responsible for protraction of the medial tooth are called “gm1” and “gm2” and are innervated by the GM neurons. In the crab, the GM neurons also innervate muscles of the lateral teeth, but in our coordinates contractions of these muscles decrease r_M as do gm1 and gm2 contractions, and thus the contractions of these lateral teeth muscles need not be explicitly included.

The operation of the lateral teeth is more complicated and requires a minimum of two motor neurons to describe their behavior; the lateral gastric and the lateral posterior gastric neurons. [We have omitted the medial gastric neuron because it is electrically coupled to the LG neuron and generally bursts in phase with it.] The lateral gastric motor neuron innervates muscle gm6 that acts to close the lateral teeth, and the lateral posterior gastric neurons innervate gm3 that opens the lateral teeth, but these muscles do not work as antagonists unless activated in antiphase. When co-contracted in the lobster, they tend to pull the cusps of the lateral teeth together in a squeeze position and pull them forward against the medial tooth if it is protracted [9].

All of these motor neurons can also fire bursts in time with the pyloric rhythm even though they innervate gastric mill muscles because neurons of the gastric circuit can switch roles and participate in the pyloric circuit [4]. However, as noted in Heinzel *et al.* [11], when the gastric neurons are participating in the pyloric rhythm, the bursts are not long enough to close the teeth of the gastric mill. This leads us to represent the regions of the neuromuscular interaction in terms of burst length vs. tension. The functional difference between the gastric and pyloric bursts leads us to divide the burst length axis into three regions; gastric, pyloric, and single spikes or resting. The tension axis is also appropriately divided into three regions so we display the three neuromuscular subspaces along with the position space of the teeth as in Figure 6. Assuming that the muscles are in the follower activity mode, the input frequency axis that was necessary in Figure 5 will be suppressed in the following. Figure 6 will be used as a key to the succeeding d-spaces. Notice that by displaying the three burst-tension subspaces separately, we are leaving out the neuron-neuron interactions in the STNS. Such regions can also be included into the formalism and would possess their own flow between states depending on cellular and ensemble properties. For the purpose of exhibiting the d-space formalism in the context of stomatogastric research, we will take the phase relations of the neuron bursts from the literature [9, 11] for the chewing modes and apply that information to the construction of the relevant d-spaces.

Fig. 6 near here.

The d-space depicted in Figure 7 represents the squeeze chewing mode as reported in [9]. The lowest regions are referred to as the atoms of the d-space, and in this figure they represent momentarily static positional regions of the movement. Note that the movement sequence is cyclical. The bottom left panel represents a state where the teeth are in a resting phase (note that in the resting state, the lateral posterior gastric neurons are firing, and hence gm3 has high tension), and is therefore a convenient point to punctuate the movement. The next level up shows a more dynamic picture of the neuromuscular activity. The flows of the neuromuscular junctions must be included because these include larger regions in the burst length vs. tension subspaces. This flow restricts our contiguities to the directions given so that in the first panel the neural bursts have begun for lateral gastric and GM neurons, but the respective muscles have not yet responded. In the next panel to the right, the muscles contract (or, in the case of gm3, relax), and the teeth come in contact at their cusps in the "squeeze" position (compare to squeeze panel in the bottom row of Fig. 3). The next two panels along the direction of contiguity reverse the process in that the motor neurons return to their states in the resting phase. Since the far right state can lead to the far left state, there is a directed line of contiguity closing the cycle.

Fig. 7 near here.

The top level shows an explicit representation of the transitions between the behavioral states of the bottom level. The left panel displays the transitions from the resting to the squeeze state including the flow at the neuromuscular junction. The return transition is given on the right, and the two panels are connected by an undirected line of contiguity expressing the fact that the system can oscillate between the two states. Another level could be added above this level with one panel including all the states and transitions in the squeeze mode. At this next higher level the transitions between contiguous chewing modes would be displayed, but since we are only considering one mode at a time in Figures 7, and 9, these transitions have been left out.

The d-space of Figure 7 was constructed by first determining the states, and with a knowledge of the flows, building up to the larger regions that include the states and connect them together. In this way one can explore the interplay of the relevant components of the stomatogastric system. Another possibility is to start at the top of the d-space with the major regions and transitions and search for subregions where the behavior under study may be included. Then it is a matter of adding restrictions to these large regions and working towards the atoms. The d-space of Figure 7 should not be thought of as a complete description of the squeeze mode because there is always room for the elaboration of d-spaces [19] by including more details. The addition of more parameters such as other motor neurons and muscles would be illuminating, as well as the inclusion of a more detailed description of the bursting phases in the middle level. Here we have opted for the simplest possible description of the chewing mode to demonstrate the method of d-space analysis.

The cut and grind mode presents a more complicated picture and reveals some ambiguities in the published data. Although the movement pattern of this mode is well documented, not all the parameters that are included in the d-space have been pinned down. Since the open and squeeze states appear to be quite stable, the representations of the neuromuscular aspects shown in Figure 7 are reasonably convincing. The ambiguity lies in the sequence through the spread and cut states. Some of this difficulty was expressed in [9] and updated in [10], although this issue was not directly addressed in [11]. The d-space formalism may be used as a tool to investigate the nonlinear aspects of the transfer function in this case, and three alternatives are given in Figure 8. The procedure used here is referred to as "solving" the d-space [13, 19]. If one has a high degree of confidence about some of the states in the sequence, then those states may be used as boundary conditions where the remaining states represent the possible trajectories given the constraints of our knowledge about the system.

The sequence in Figure 8A shows a pattern most closely aligned with the proposal by Heinzel and Selverston (1988) [10]. In this sequence, the spread is a transient state between the resting (open) and cut states. Before the lateral teeth have a chance to begin closing in a cut, the DG neuron fires (not shown) and thus holds back the medial tooth and partially inhibits the GM neuron. This occurs almost simultaneously with the bursts fired by the lateral gastric and GM neurons. Because the GM neuron also innervates gm3, a muscle that opens the lateral teeth, the net result would be a slight opening of the gastric mill teeth before tension increases in gm6 result in a cut. Finally, the DG neuron would release the GM neuron from inhibition, simultaneously releasing the antagonist of gm2, allowing the medial tooth to move through the grind to the squeeze state. One problem with this scenario is that it is dependent on precise timing of the muscle tension following the bursts of the motor neurons. Although this may explain why the spread state is not always observed to initiate the cut and grind mode [9], the cut state requires a complicated interaction among several muscles and could not be considered as a stable behavioral state.

Fig. 8 near here.

A second alternative is given in Figure 8B were the cut state is more stable than above. Here the neuromuscular configuration is the same for both the squeeze and the cut states, the difference being the intervention of the medial tooth in the squeeze. These two alternatives may be distinguishable by recording the relative angle between the lateral teeth and comparing the difference between how tension on gm6 and gm3 affects this parameter. The results reported in [11] for the crab suggests that the IC neuron may be important in determining the relative angle between the cut and squeeze modes.

The final alternative given (Fig. 8C) is less sensitive to the relative timing of muscle tensions than Figure 8A, and assumes that the spread state is a well defined, stable state. The new assumption is that some other mechanism is responsible for the state than the muscles and motor neurons included here. An important unaddressed issue in all the above schemes is the necessity of medial tooth motor neuron (GM and DG) participation in the cut state. This is unexpected because the lateral teeth close independently of any medial tooth movement [9]. The subcircuit controlling the lateral teeth can generate a pattern without the participation of the medial tooth subcircuit [23], but one would anticipate this behavior in the d-space. One possibility is that there are at least two cut states differing in their neuromuscular aspects, but equivalent in their behavioral output.

The d-space for the cut and grind mode is given in Figure 9 based on the sequence shown in Figure 8A. The cycle presented in the previous figure makes up the lowest level. As in the squeeze d-space, the middle level shows the neuromuscular flows required for the transitions that determine the contiguities of the bottom level. The top level gives the flows between the position states and the associated neuromuscular flows. Note that the top left panel shows a flow in the movement subspace without an accompanying change in muscle tension. This implies that there is a missing mechanism responsible for this movement. As stated above, we assume that the flow is due to increased tension of the part of gm3 innervated by the GM neuron (gm3c), while the tension remains the same in the part shown, which is innervated by the lateral posterior gastric neuron (gm3a). The third panel from the left on the top level represents the grind of the cut and grind mode. This panel shows an extensive movement associated with a small change in tension. In this case the most likely cause is the relaxing of the gm4 muscle innervated by the DG neuron, which releases the medial tooth. As can be seen here, the construction of a d-space can reveal missing mechanisms and point to holes in the existing data.

Fig. 9 near here.

Organizational Hypotheses on the Functional Logic of Chewing Modes

In a dynamical biological network such as the STG, the modes of operation can switch due to the influence of modulatory substances. The patterns of mode changes can be investigated by further nesting of the d-spaces for chewing modes into a larger d-space. Figures 10 and 11 show two alternative hypotheses for the interplay of three chewing modes in the gastric mill. Using the atoms from the above d-spaces as behavioral components, the functionally relevant interconnections can be made using the inclusion and contiguity relations.

The case where these components are freely interchanged is constructed in Figure 10. The components are shared by each chewing mode and the active mode is determined by the route taken through the contiguities. This can be called an interlaced control method where the mode of operation emerges from the linking of behavioral components. Not all the conceivable contiguity relations are found in the interconnections of this d-space; some are directed and others are not, and the cut and the squeeze atoms can only be linked by passing through the resting atom. The d-space displays the functional logic of the system by giving the behavioral rules of the discrete operation, and how the modes of operation are related to one another.

Fig.10 near here.

A top-down control scheme is depicted in Figure 11. Here the chewing modes are rigidly separated into packages, and switching between modes takes place after a return to the resting state. The pyloric rhythm has been included because gastric motor neurons have been observed participating in that rhythm and thus may have some functional significance in the switching of modes. Here the functional logic derived from the d-space

Fig.11 near here.

differs from the first case in that the atoms are linked in cycles but the modes pass to one another only through the resting state.

The concept of a central pattern generator would seem to favor this control scheme, but in the stomatogastric system there has been observed a gradual change from the cut-and-grind to the cut-and squeeze mode [9] where both modes appear to be active simultaneously. Another observation that would be useful in deciding between these control schemes is whether chewing modes can switch midstream, or if the teeth always return to the resting state before switching between modes. A detailed analysis of these questions would begin with a careful study of gastric mill movements and STG activity to find a consistent set of behavioral components. These components could then be linked by contiguity relations observed in movement recordings to build up d-spaces of chewing modes and show how these modes are linked.

Discussion

Functional Logic Analyzed by Means of a Discrete Formalism

The analysis presented in this paper raised specific questions and hypotheses about neural-behavioral interactions in the chewing modes of the gastric mill. The sequence of behavioral states was linked with probable activities of muscles and neurons to yield several hypotheses as to the exact mechanisms that generate the movements of the gastric mill. The constraints of the functional logic defined relationships between variables that limited the possibilities to a limited solution set (Figs. 8, 9). Also, hypotheses about the overall functional logic of the control mechanisms involved in the expression of various chewing modes was presented. These are seen as extreme examples of control schemes for shifting between chewing modes (Figs. 10, 11). The methods demonstrated here can be expected to help link the information gathered in *in vitro* studies with recent neural and endoscopic recordings in intact animals [2, 12].

In this study, the stomatogastric system of decapod crustacea was analyzed using a mathematical formalism based on d-spaces. The behavior of the gastric mill was analyzed in terms of the inclusion and contiguity relations between regions of d-space. The formalism analyzes the interrelation between the various subsystems of the stomatogastric system, and clarifies the functional logic of the system as a whole. Detailed analyses of observed chewing modes in the lobster and neuromuscular interaction in the shrimp were presented in this paper. By putting together discrete subsets of the known behavioral modes of the foregut, hypotheses can be developed to identify essential information needed to further clarify the behavior of the stomatogastric system. An essential task for the investigator when using the d-space formalism is to identify the natural behavioral components of the movement under study. When embarking on a study using this formalism, one must identify physiologically relevant discrete regions from which to build the space. This does not imply that all behavior ought to be broken into discrete units; some behavioral problems can be well understood in terms of continuous parameters and state variables. Yet, by restricting our thinking about a particular problem to continuous approaches, it is likely interesting phenomena of importance to the functioning of the organism will be overlooked.

The study of functional circuits in central pattern generators can be aided by viewing the system in terms of discrete behavioral modes rather than as anatomical circuits. The latter approach will inevitably lead one to a large system of nonlinear differential equations as a continuous description of the system. In this age of powerful computers, it is now possible to numerically solve very complicated systems, and this kind of modeling can surely lead to insights and test certain hypotheses. On the other hand, such complex systems tend to exhibit behavior that can be very sensitive to the values of state variables; simply following trajectories through time does not give a clear picture of the overall behavior of the system. Furthermore, any digital computation involves some discretization of the system, so it would be advantageous to first analyze the natural discreteness of the behavior before attempting further modeling efforts.

Another aspect of the d-space formalism that differs from modeling approaches to understanding motor behavior is in the concept of causation. Temporal sequencing of steps was seen in the constructions of chewing mode d-spaces from the bottom-up procedure (Figs. 7 and 9). In those examples, the inclusion levels ranged from the simplest behavioral components to the highest levels of inclusion that gave the biological mechanisms leading to the transitions between the states. In contrast, Figure 11 was based on a top-down structure where there was an overall purpose to each of the chewing modes, and it was the switching between the command choices that changed the behavior. A third alternative concept of causation was presented in Figure 10 in the interlaced control method. Here the behavior would be determined by obstacles and opportunities that it encountered along the way. This last example is neither deterministic nor goal directed, rather the behavior emerges from the interaction of the system with its environment.

The insights obtained from the d-space formalism arise from the interplay between the two relations: inclusion and contiguity. The inclusion relation alone generates a treelike structure, a partially ordered set, that specifies the available discrete states among which the organism can maneuver. At any given level of inclusion, there is measure of distance between states and possible mechanisms for transitions between states. The contiguity relations then show the allowed transitions between the states. This is where the dynamics of the logical structure lie, and the contiguities find their foundation in the physiological mechanisms underlying the behavior. Thus, a d-space may be regarded as a theory of states (inclusion relations) combined with a theory of transitions (contiguity relations), which together fully describe the behavior of an organism managing a specific task.

An obvious omission in the present study is a detailed analysis of the stomatogastric ganglion as a network of neurons. This is a very rich topic and will be presented in a future publication. Preliminary results suggest that the relations of inclusion and contiguity find a very natural interpretation in general ensembles of neurons. The differences between the rhythms form a treelike structure, and the contiguities express the transitions between rhythms. The formalism presented here has already been applied to the process of children learning to walk [16] and rehabilitation of stroke patients [13, 18]. We expect that there is a natural explanation in terms of d-spaces for many motor control problems in which discreteness plays a salient role.

Consequences of the d-space formalism for the stomatogastric system.

The basic building blocks that have been used in this investigation are the behavioral states. These are understood to be regions in position space where the teeth of the gastric mill tend to remain, or return to on a regular basis under various conditions. Since this study was based on published accounts of observations, the data sets used were quite limited. A more detailed study would begin with digitized endoscopic recordings of the movements of the gastric mill. A scoring could then be given to position regions over time to measure regions of the behavioral states. This is similar to the method used in [31] to separate the cut and grind from the cut and squeeze modes.

It would be interesting to understand the biological mechanisms that underlie each of the behavioral states. The first question to be asked is whether there is a one-to-one correspondence between the behavioral states and the neural states generated by the STG. Here we define neural state in the sense of Getting (1993) [6] as the state of the circuit at any given time. The forgoing study leads one to expect that this question is likely to be answered negatively. The behavioral states seem to emerge from more than the motor pattern generated by the STG, rather as the interaction of all the elements of the system. Although one could define a behavioral state to be the motor output corresponding to a given neuronal burst pattern, such a definition would probably be limited and even misleading when trying to understand the organizational principles of behavior. Thus the mechanisms responsible for each state would not be limited to membrane properties that maintain the bursts and their phase relationships, but include the properties of the neuromuscular junction, the activity states of the muscles, the mechanical constraints in the gastric mill, and the relative position of the teeth during the expression of the state.

Once the behavioral states are established, the transitions between these states could be investigated to find the contiguity relations on the lowest level. A similar analysis to the above for assessing the states could be used to find the most common transitions and exclude any forbidden transitions. The transitions can be categorized into two groups: transitions that join states into behavioral modes, and transitions that result from perturbations. The first group has been considered in the previous sections, but not all the mechanisms responsible for these transitions have been addressed. Although the muscle response to neuronal input and the relative positions of the teeth are very important in shaping the behavioral outcome, the progression of the burst pattern generated by the STG is of overriding importance in determining the transition structure. The mechanisms responsible most likely have a longer time scale than the those maintaining plateau potentials because the transition mechanisms are responsible for burst termination. An example of the second group is the transition from the resting to the squeeze state upon injecting seawater into the cardiac sac [9]. Another example is found in [11] where the MG neuron is depolarized to elicit a closure of the lateral teeth. These kinds of experiments applied during different states can help to discover the possibilities for transitions from each state and uncover the mechanisms responsible.

There seems to be a tendency in complex systems for simple states to cluster into higher level states. In the stomatogastric system this phenomenon is expressed as the behavioral states clustering into behavioral modes. On their own level, the modes are really higher level states that have their own transition structure. In the stomatogastric system it appears that the hierarchy stops at this level, but in the behavior of the intact animal the chewing modes become elements included in feeding behavior. It should be emphasized that this hierarchy is not created out of a chain of command directed by descending signals such as those generated in the commissural ganglion or brain, but a result of distributed mechanisms throughout the organism. There may be some central organization of many of the elements, but most likely only to trigger mechanisms on lower levels of the "feeding d-space" that carry out the various activities.

In the analysis of the cut and grind mode, two results suggested further experimental study. First, several solutions to the d-space were found to be consistent with the published data. This kind of analysis is quite constrained once several of the elements are included in the d-space, severely limiting the possible solutions. Closing such holes in the literature will help further our understanding of the transfer function under different conditions. The second result showed that the same positional state could result from different neural activity. This kind of multifinality is not unexpected in nonlinear systems, but in the d-space formalism it is possible to be explicit about the differences between degenerate states.

Conclusions

The d-space formalism emphasizes the extreme nonlinear limit of the stomatogastric system, breaking up the behavior into simple units of states and transitions. This makes the formalism simple to use, but the structure can contain sufficient complexity to constrain possible solutions such that predictions can be made about behavior. By carefully choosing the parameters in a d-space, the biological mechanisms responsible for a given state or behavioral mode can be tested by stating alternative hypotheses as we have in the previous sections. The d-spaces for different subsystems can be connected using knowledge of the transitions (contiguities). Eventually, the overall organization of the system emerges as lower levels cluster into higher modes of behavior by the relation of inclusion. The final result is a behavioral map of the system embedded in a unified logic of neural, muscular, and behavioral states and transitions.

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Figure captions:

Figure 1. The foregut and three chewing modes of the gastric mill. (A) The position of the gastric mill in the foregut of the lobster in a lateral cross-section. (B) Two views of the gastric mill teeth in the squeeze chewing mode. The left side of each panel shows a top view of the relative positions of the two lateral teeth. The right side is a view in the sagittal plane of the medial tooth and one lateral tooth. Each panel gives a three dimensional representation of the teeth in the gastric mill. The squeeze mode is punctuated by 2 positions: the resting position of the left panel where there is no contact between the teeth, and the squeeze position where the teeth meet at the cusps. The broken line with arrows shows the movement between these two positions. (C) The cut and grind chewing mode is punctuated here by four positions. Beginning at the resting position on the left, the movement follows the arrows. First the lateral teeth close in a "cut," then the medial tooth comes down and "grinds" across the lateral teeth in the next two panels. Finally, the teeth return to the resting position. (D) The cut and squeeze mode has two panels in the resting position. From the resting position at the far left the lateral teeth close in a cut, but before the medial tooth comes down, the lateral teeth open again returning to the resting position. Finally the teeth meet in a squeeze in the panel on the right before repeating the cycle.

Figure 2. The coordinate system to be used in the following figures. (A) The position of the lateral teeth are given by the relative distance between the cusps and the angle of the teeth with respect to the midline. Bilateral symmetry is assumed. Below is the coordinate plane showing the region of possible positions of the lateral teeth. (B) The position of the medial tooth is given relative to the lateral teeth. The radial coordinate is defined as the distance from the cusp of the medial tooth to the intersection of the line between the cusps of the lateral teeth and the sagittal plane on the midline. The angular coordinate is taken relative to the line along the crest of the lateral teeth, but this component is functionally unimportant in the following and will be left out of further discussion. Below is the region containing the full range of medial tooth positions relative to the lateral teeth.

Figure 3. A formal d-space of the positions of the gastric mill. The bottom row shows the position atoms, the smallest functionally relevant regions that are used to build the d-space. The position of the teeth are given in the bottom row for reference. The bottom left two panels are contiguous because there is a behavioral transition between them. The second level displays the behavioral modes of this system. These are from left to right, the squeeze, the cut and grind, and the cut and squeeze chewing modes. The top level contains all of the possible position of the teeth in the gastric mill. See text for further explanation.

Figure 4. This figure investigates the neuromuscular junction between the pyloric dilator (PD) motor neuron and the muscle that controls the cardiopyloric valve (cpv1). The response of the muscle to burst length of the PD motor neuron is found to be dependent upon the bath application of a FMRFamide-like peptide. At the top of the d-space is shown responses with two peptide concentrations. The arrows give the flow

through the regions which describe the response of the muscle to neural input. The second level shows how the flows for the low peptide condition are linked in a temporal sequence. The bottom row gives the neuromuscular states for this configuration. See text for further explanation.

Figure 5. The muscle is in the oscillatory mode under high peptide bath concentration. The activity of the neuromuscular is dependent upon the input frequency in this case so that an extra axis is required. The muscle can be entrained to the bursts if the input frequencies are in a restricted range as show in the top right graph. The top left graph shows the situation when the muscle oscillates without coupling to the input. The bottom level shows the contiguities between the flows. See text for further explanation.

Figure 6. The axis labels for subsequent figures with the flows for the neuromuscular junctions. The three neurons to be investigated are the lateral posterior gastric (LPG), the lateral gastric (LP), and the gastric mill (GM) neurons. These neurons control the following muscles: *gm3* which opens the lateral teeth, *gm6* which closes the lateral teeth, and *gm2* which protracts the medial tooth. The 3-dimensional axis in the lower left show the relative positions of the teeth in the gastric mill with the greatest allowed region of the tooth positions.

Figure 7. The d-space for the squeeze chewing mode (see Fig. 6 for axes labels). The bottom row contains two distinct atoms: the open resting state where the teeth are not in contact, and the squeeze state where the teeth meet at the cusps. The middle level of inclusion shows the flows that take the teeth from one position to the other. The elements of the top row include the movement patterns such that the region in the position subspaces cover the transition regions, and the full flow for excitation or relaxation of the muscles is shown. See text for further details.

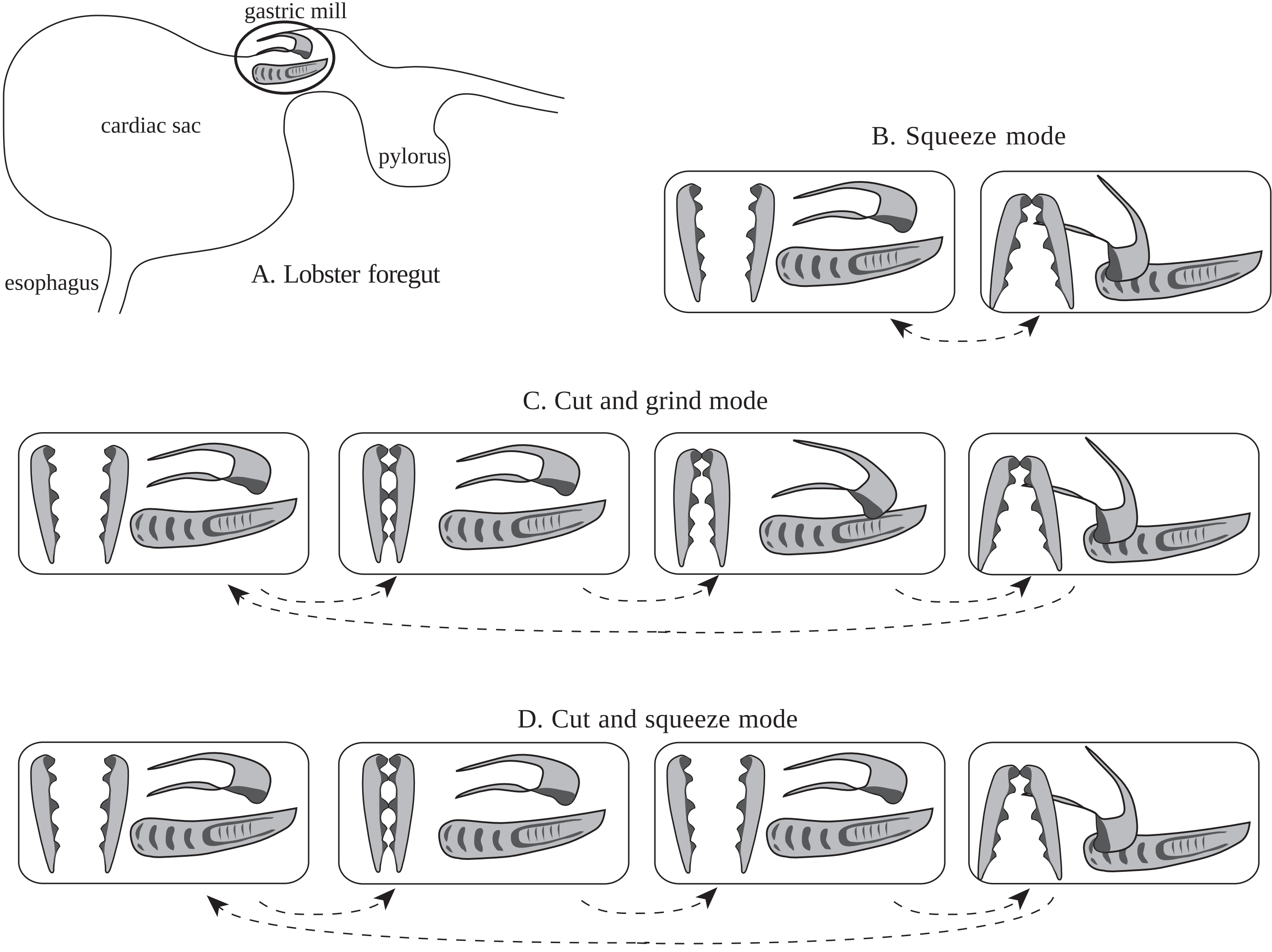
Figure 8. Three possible solutions for the transitions through the states of the cut and grind mode of chewing. (A) Following the resting state on the left, the DG neuron (not shown) fires a burst to hold the medial tooth before the cut in the third panel. (B) The neuromuscular configuration is the same for the cut and squeeze states, the difference arises from the position of the medial tooth between the lateral teeth in the squeeze state. (C) In this case it is assumed that there exists an unknown mechanism responsible for the spread state that is not displayed in the graphs. See text for further details.

Figure 9. The d-space for the cut and grind chewing mode based upon the states and transitions of Figure 8A (see Fig. 6 for axes labels). The bottom row contains four distinct atoms: the resting state, the spread state that initiates the mode, the cut, and the squeeze state. The middle level of inclusion shows the flows that take the teeth from one position to the other. The elements of the top row include the movement patterns and the regions that the teeth pass through during the transitions. The full flow for excitation or relaxation of the muscles is also shown on this level. See text for further details.

Figure 10. Interlaced control method (see Fig. 6 for axes labels). Each element is an atom from the previous chewing mode d-spaces. This depicts how the atoms may be connected by contiguity relations to partic-

ipate in three chewing modes: squeeze, cut and grind, and cut and squeeze. Under the squeeze mode, the system oscillate between the squeeze and the resting states. The cut and grind mode cycles through the spread state on the far right, the cut, to the squeeze atom, and on to the resting atom. The cut and squeeze mode cycles through the cut atom, to the resting state, on to the squeeze atom, and back to the resting state. In this d-space, the elements are freely exchanged. See text for further details.

Figure 11. Top-down control method (see Fig. 6 for axes labels). An alternate control scheme to be contrasted with Fig. 10. The three chewing modes are independent cycles of movements which can be interchanged in bulk by passing through the resting state. When the gastric motor neurons are participating in the pyloric rhythm, they do not come in contact with each other so that the mode is within the region of the parameter space contained in the resting state. See text for further details.

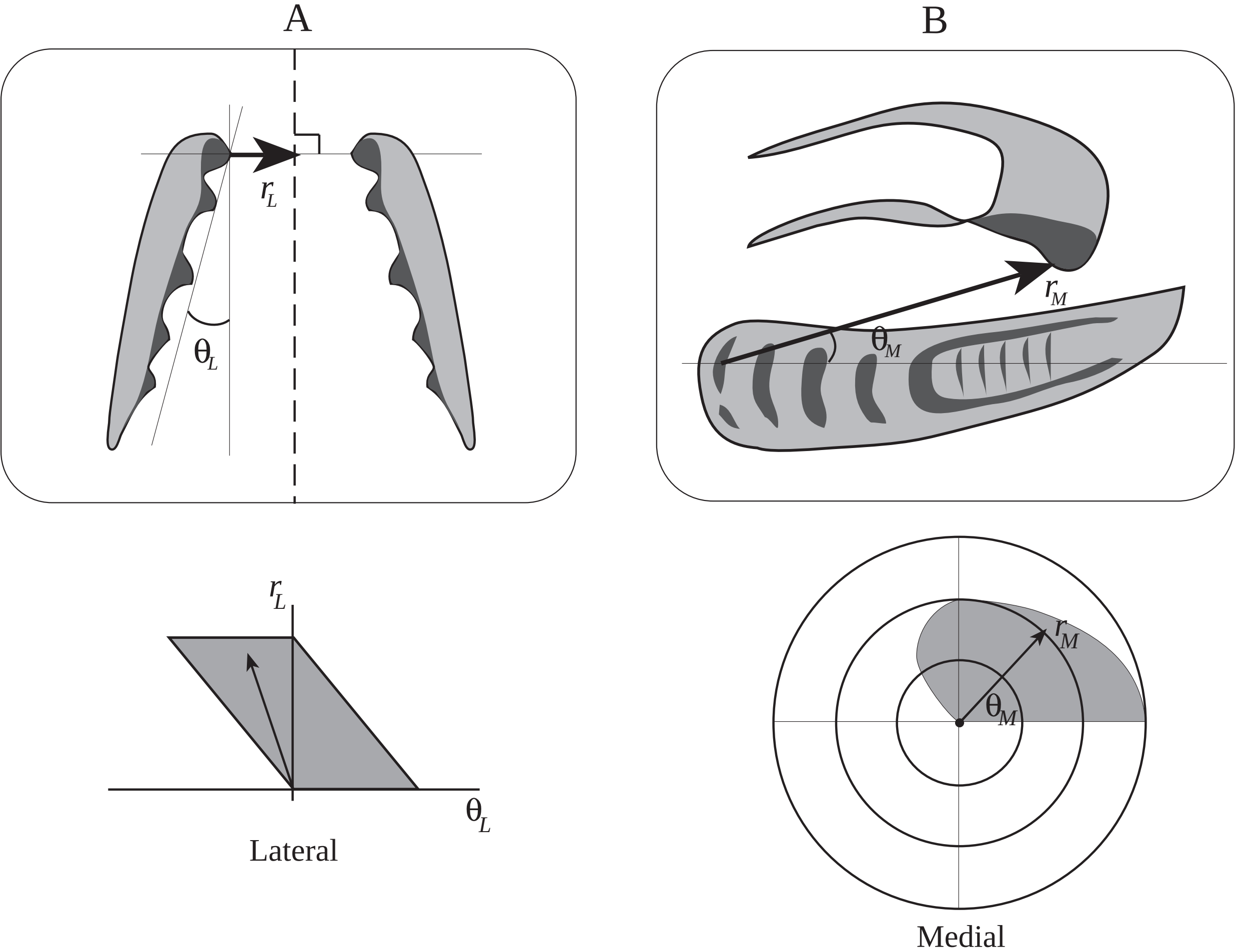

A. Lobster foregut

B. Squeeze mode

C. Cut and grind mode

D. Cut and squeeze mode

Figure 1



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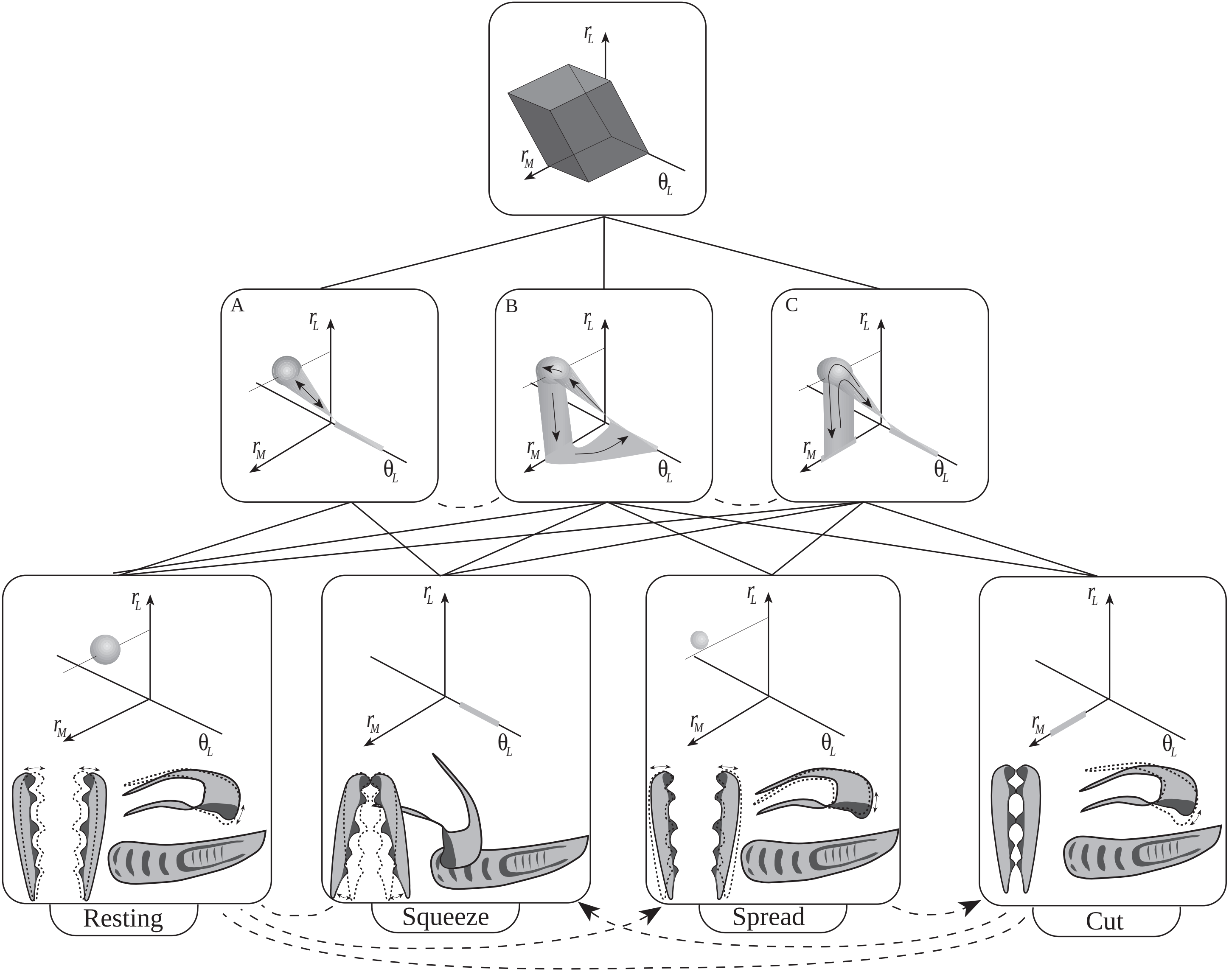

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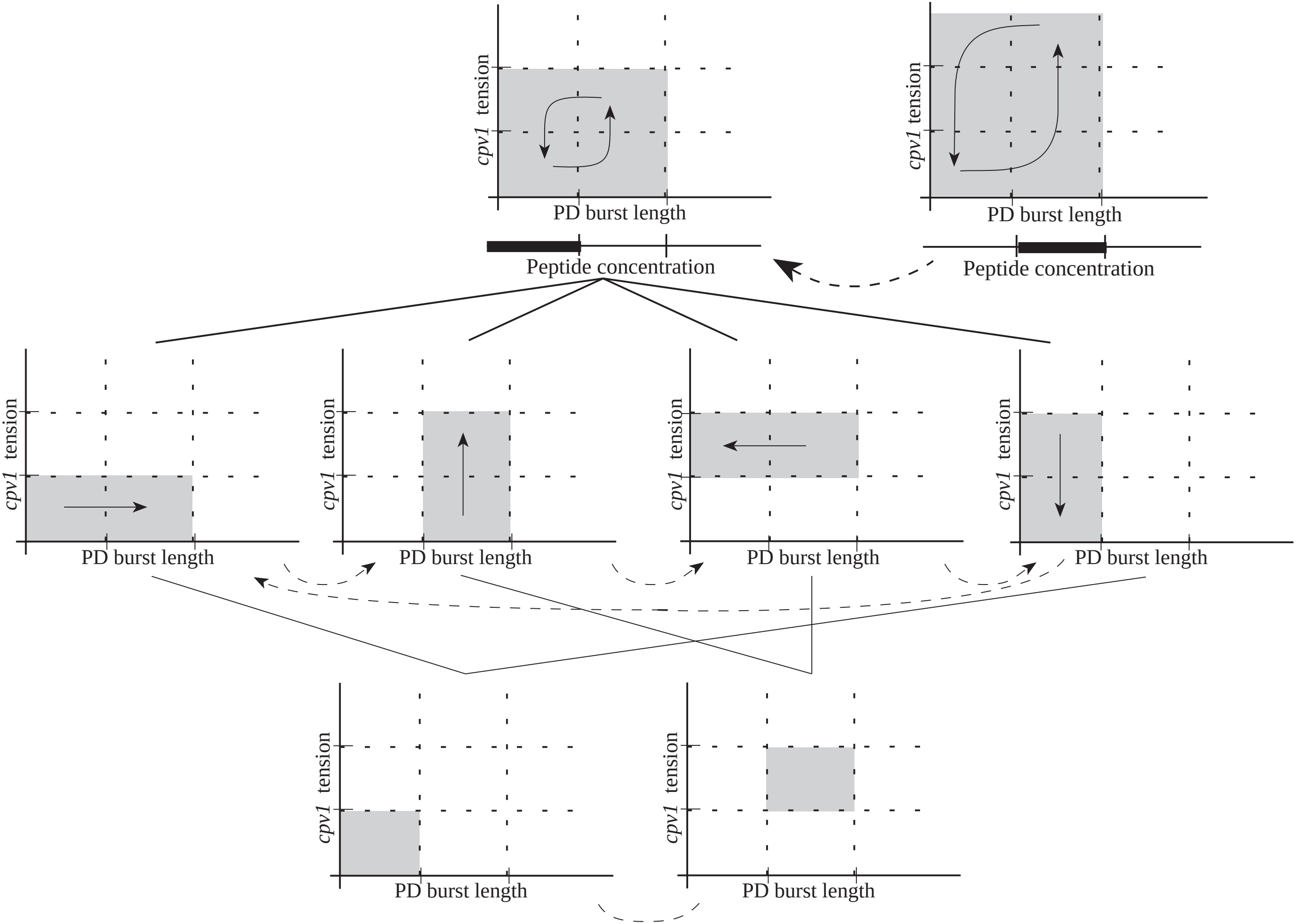
cpv1 tension
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Figure 4

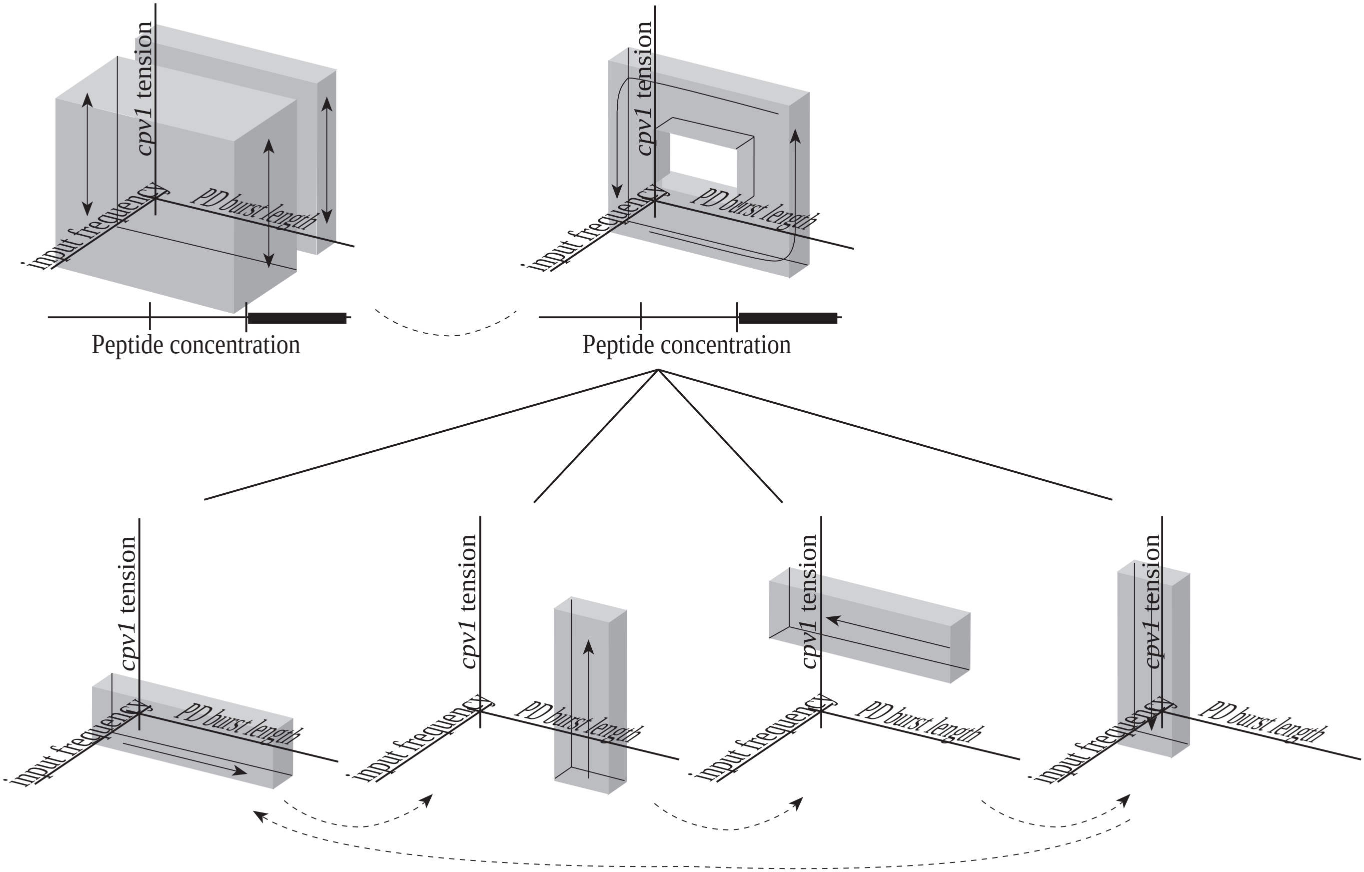
cpv1 tension
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Figure 5

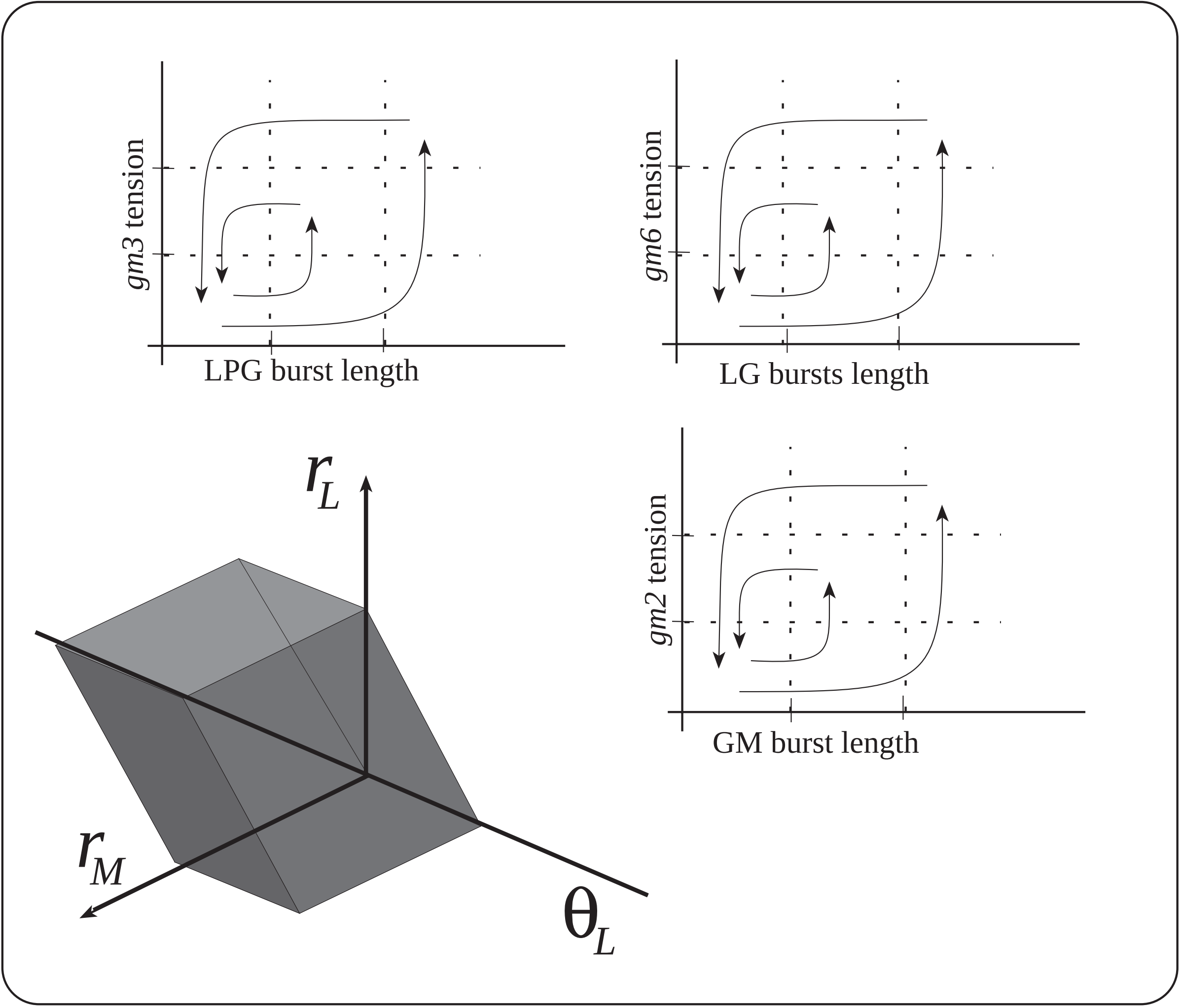

gm3 tension
LPG burst length
gm6 tension
LG bursts length
gm2 tension
GM burst length
r_L
r_M
θ_L

Figure 6

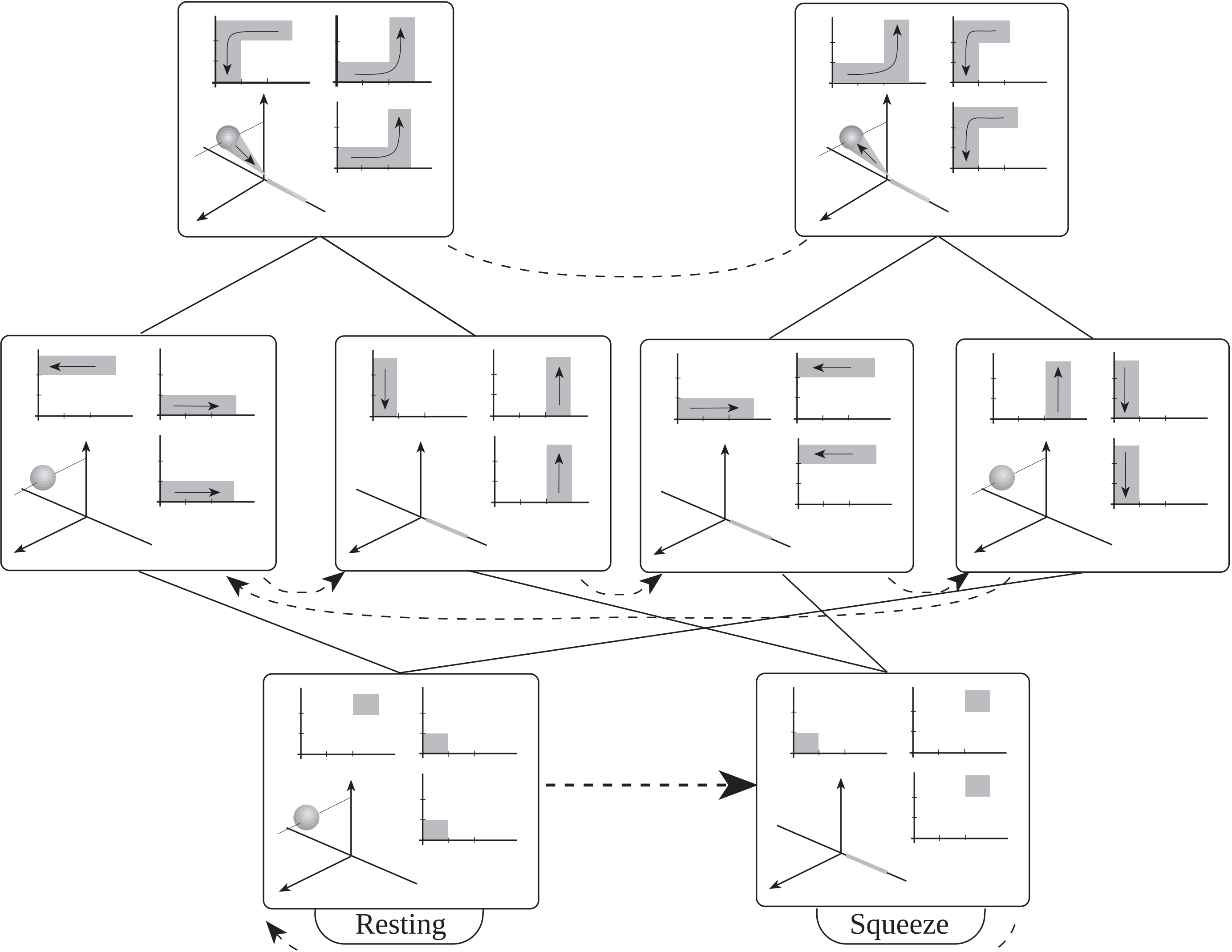
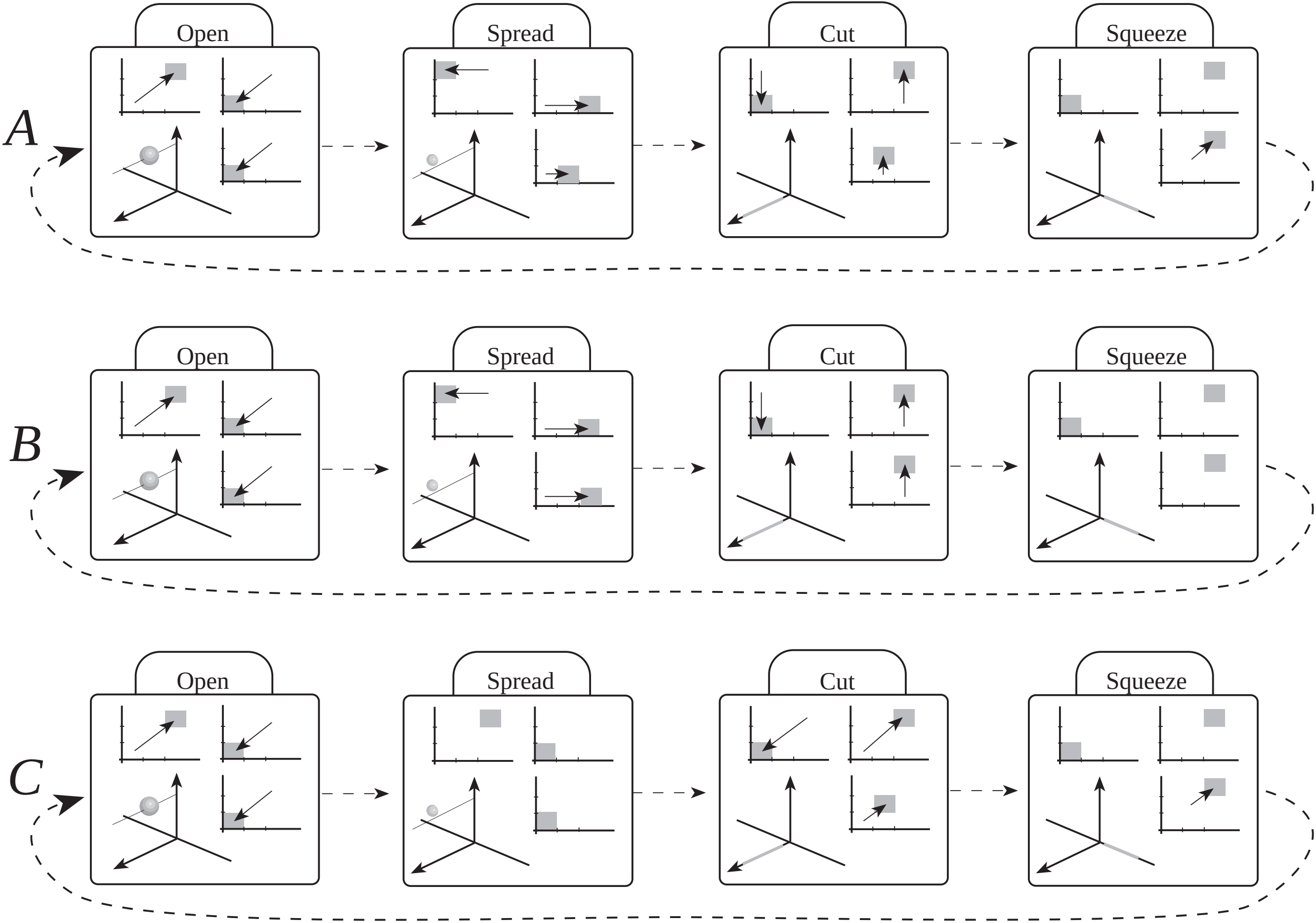


Figure 7


A
Open
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C
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Squeeze

Figure 8

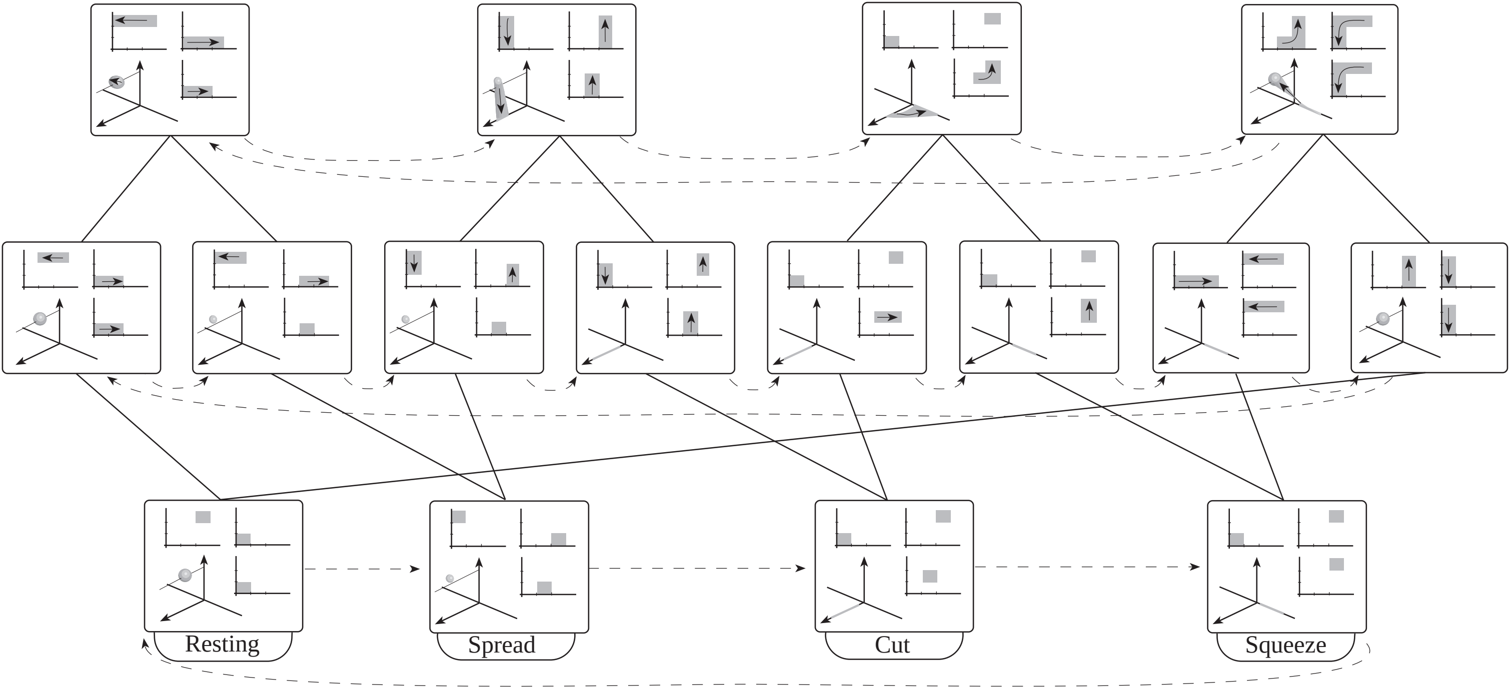

Figure 9

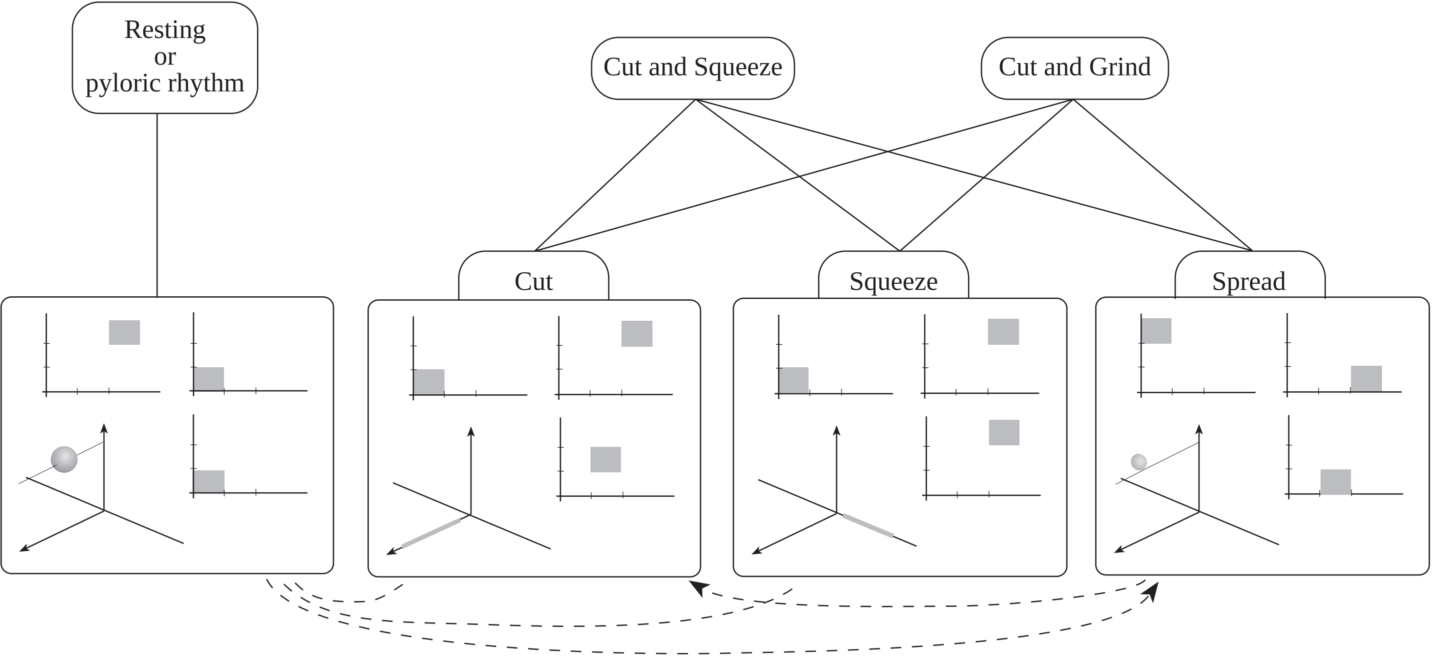
Resting
or
pyloric rhythm
Cut and Squeeze
Cut and Grind
Cut
Squeeze
Spread

Figure 10

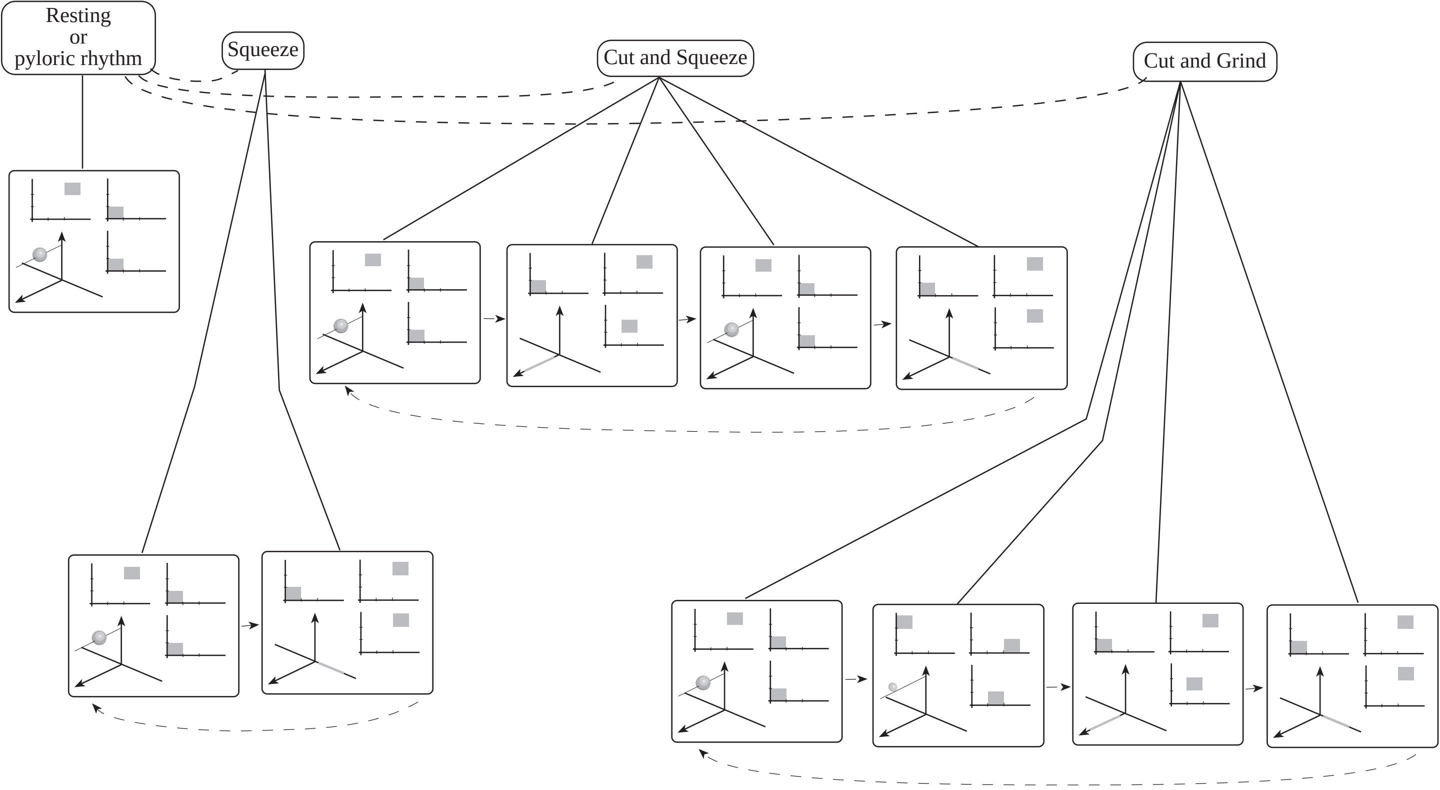
Resting or pyloric rhythm
Squeeze
Cut and Squeeze
Cut and Grind

Figure 11