

# Competing Sensory Neurons and Motor Rhythm Coordination

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## Abstract

The marine mollusk *Clione limacina* has a peculiar hunting behavior characterized by a complex sequence of loops and turns. We have developed a model of the receptor network of *Clione*'s gravimetric organ to explain this behavior. In this paper we discuss the possible role of an activation phase lock among the statocyst receptor neurons to coordinate the motion during hunting. As a result of a winnerless competition among receptor cells, an apparent intricate but coordinated sequence of signals emerges. This sequence can drive complex but, at the same time, organized movements.

*Key words:* Statocyst receptor network, winnerless competition, motor coordination.

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## 1 Introduction

The marine mollusk *Clione limacina* is a predator whose only prey is another mollusk, *Limacina helicina*. *Clione* does not have a visual system and although its chemosensors can detect the presence of *Limacina*, they are presumably nondirection-sensitive. When hunting behavior is triggered, *Clione* loops and turns in a complex trajectory trying to locate its prey. *Clione* has several neural structures involved in the control of the orientation of its body during

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normal and hunting behavior (6; 4). The statocysts, a pair of spherical gravimetric organs located in the pedal ganglia, contain a stone-like structure –the statolith– that moves under the effect of gravity. The statolith exerts pressure on the internal wall of the sphere which is lined with statocyst mechanoreceptor cells. Information about the orientation of the body is sent from the mechanoreceptors to several groups of cerebro-pedal interneurons. These interneurons control the central pattern generators that move *Clione*’s wings and tail. *Clione* uses the statocyst to maintain its preferred head-up orientation (see panel *A* in Fig. 1). The statocyst receptor cells (SRC) also receive input from a pair of cerebral hunting interneurons (CHI) (6), which are presumably activated in the presence of *Limacina* by signals from the chemoreceptors.

We have previously developed a model to suggest the hypothesis that the SRCs actively participate in the organization of the complex hunting behavior of *Clione* (7). Several predictions of the model have been confirmed and tested with neurophysiological experiments (5). In this paper we discuss the ability of the model to establish a coordination between the SRCs while producing a complex signaling sequence.

## 2 Statocyst Receptor Network Model

The model of statocyst receptor network consists of six neurons (see Fig. 1, panels *C* and *D*). Each receptor neuron follows a Lotka-Volterra type dynamics given by:

$$\dot{a}_i = a_i(\sigma(\mathbf{H}, \mathbf{S}) - \sum_{j=1}^N \rho_{ij} a_j + H_i(t)) + S_i(t) \quad (1)$$

where  $a_i > 0$  represents the instantaneous spiking rate of the neurons,  $H_i(t)$  represents the excitatory stimulus from the cerebral hunting interneuron to neuron  $i$ , and  $S_i(t)$  represents the action of the statolith on the receptor that is pressing. When there is no stimulus from the hunting neuron ( $H_i = 0, \forall i$ ) or the statolith ( $S_i = 0, \forall i$ ), then  $\sigma(\mathbf{H}, \mathbf{S}) = -1$  and all neurons are silent;  $\sigma(\mathbf{H}, \mathbf{S}) = 1$  when the hunting neuron is active and/or the statolith is pressing one of the receptors.

It is known that the SRC inhibitory connections are non-symmetrical and have different strength (6). In our model we consider three different values for the coupling strength as reflected in panel *D* of Fig. 1. Specifically, we used the following connection matrix ( $\rho_{i,j} \neq 0$ ):

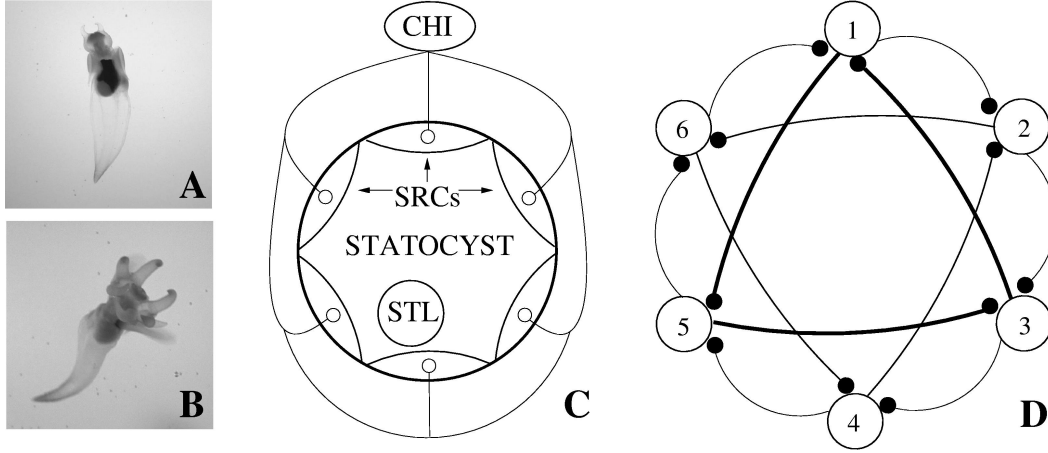


Fig. 1. (A) Picture of *Clione* during normal swimming. (B) Picture of *Clione* in hunting behavior. (C) Schematic representation of the dual excitation of the SRCs: by the statolith (STL) during normal swimming, and by the cerebral hunting interneuron (CHI) during hunting behavior. (D) Model of the SRC network. All connections are inhibitory, thicker traces mean stronger connections.

$$\begin{aligned}
\rho_{1,3} &= \rho_{3,5} = \rho_{5,1} = 5 \\
\rho_{4,6} &= \rho_{2,4} = \rho_{6,2} = 2 \\
\rho_{1,6} &= \rho_{2,1} = \rho_{3,2} = \rho_{4,3} = \rho_{5,4} = \rho_{6,5} = 1.5 \\
\rho_{1,1} &= \rho_{2,2} = \rho_{3,3} = \rho_{4,4} = \rho_{5,5} = \rho_{6,6} = 1
\end{aligned} \tag{2}$$

The Lotka-Volterra formalism allowed us to prove two theorems about the stability of the sequential switching (1). The model of SRC network can also be implemented with more realistic Hodgkin-Huxley type equations with an equivalent connection topology.

### 3 Results

When there is no activation of the sensory neurons by the hunting neuron, the effect of the statolith ( $S_i \neq 0$ ) in the model is to induce a higher rate of activity on one of the neurons (the neuron  $i$  where it rests for a big enough  $S_i$  value). We assume that this higher rate of activity affects the behavior of the motoneurons to organize the head-up position. The other neurons are either silent or have a lower rate of activity and we can suppose that they do not influence the posture of *Clione*. The model displays a winner-take-all situation for normal swimming.

When the hunting neuron is active a completely different behavior arises. We assume that the action of the hunting neuron overrides the effect of the statolith and thus  $S_i \approx 0, \forall i$ . The network described by system (1) with the  $\rho_{ij}$

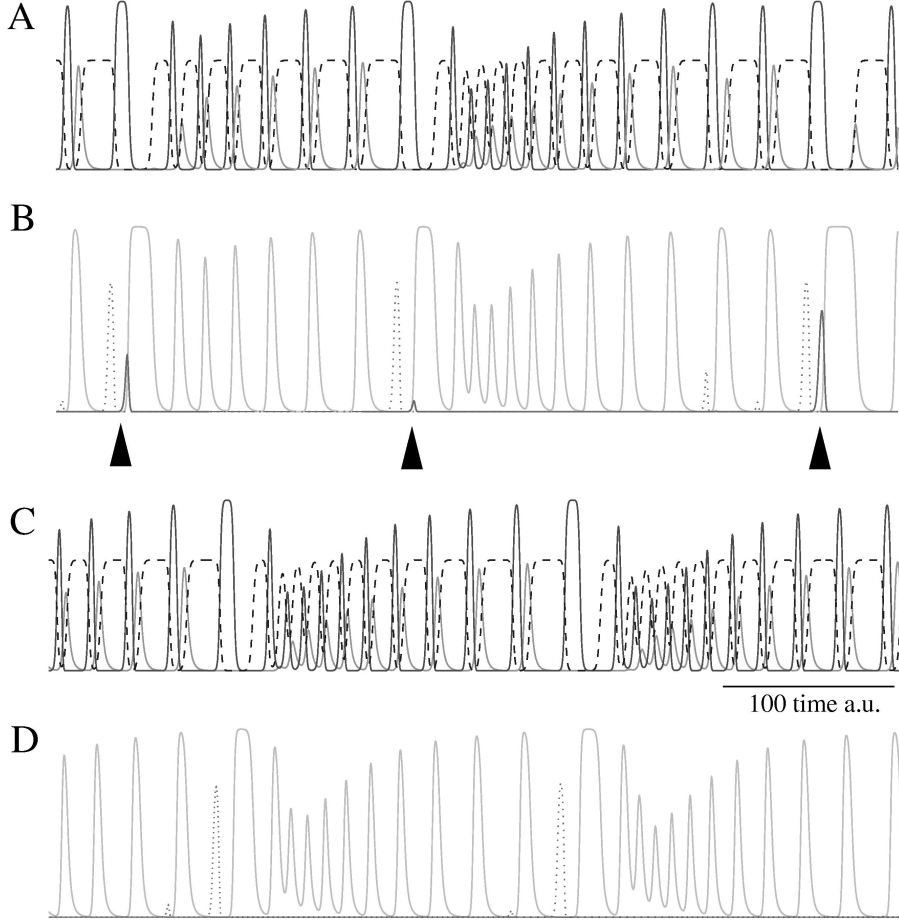


Fig. 2. Irregular switching of activities among the SRCs. Traces represent the instantaneous spiking rate of each neuron  $a_i$  (neurons 1,2,3 are shown in panel *A*, neurons 4,5,6 are shown in *B*). Note that after a neuron is silent for a while, its activity reappears with the same sequence relative to the others (see arrows). Panels *C* and *D* show the dynamics of the same network with neuron 4 inactivated,  $a_4 = 0$ .

values specified above (see also Fig. 1) and with a stimuli from the hunting neuron given, for example, by  $H_i = (0.730, 0.123, 0.301, 0.203, 0.458, 0.903)$  establishes a winnerless competition among the SRCs. As a result of this competition, the SRCs display a highly irregular, and in fact chaotic (7) switching activity. Fig. 2 show an illustration of the non-steady switching activity of the receptors. An interesting phenomena can be seen in this figure. Although the timing of each activity is irregular, the sequence of the switching among the SRC activity (when it is present) is the same at all times. Arrows in Fig. 2 point out this fact for neuron 4 (cf. panels *A* and *B*). The activation phase lock among the statocyst receptor neurons emerges in spite of the highly irregular timing of the switching dynamics. The inactivation of a neuron within the network cannot always destroy this winnerless competition nor the activation phase lock. For example, panels *C* and *D* show the switching activity when neuron 4 is inactivated ( $a_4 = 0$ , arrows point out this neuron in panel *B*). The active neurons adapt to this change by increasing or decreasing their mean

frequencies but still showing an irregular activity and the activation phase lock. However, the inactivation of neuron 5 with the same model parameters turns the network in a winner-take-all mode.

Experimental recordings from the activity of *Clione*'s tail motoneurons during hunting behavior have been reported in (5). In such experiments the activity of individual motoneurons is recorded during fictive –pharmacologically induced– hunting (2; 3). Fig. 3 shows an example of recording from four motor units during 10 successive hunting episodes. As in the model, each episode was different in the timing of the activity of each individual neuron. However, the order of the activation sequence of the different units (when present) was the same in all episodes. This clearly indicated that the apparent irregularity is underlined by an order in the organization of tail motor activity.



Fig. 3. Experimental recordings of tail motoneuron activity during pharmacologically induced hunting episodes (1-10). The figure shows the raster of spike activity of four different tail nerve units (different shades of gray and vertical positions) during 10 successive episodes of fictive hunting behavior. Time (0) is set at the beginning of the activity of the first unit (lighter dots). All other units are aligned on top accordingly for each hunting episode. Note that although the episodes are different, the activation sequence of the units is preserved.

## 4 Discussion

*Clione*'s nervous system has to perform two apparent paradoxical tasks during hunting behavior: i) it has to generate a complex sequence of signals to drive a random-like search for prey; ii) at the same time it has to coordinate *Clione*'s wings and tail to keep swimming activity fast and effective.

We have previously discussed the ability of our model to make a hypothesis about the dual role of a gravimetric organ. In this paper we have emphasized an emerging property of the winnerless competition among the statocyst receptor cells. The complex switching activity among the receptors keeps a coordinated relation in the activation of the signals. This is a desirable property if the statocyst receptor signals are active participants in the control of *Clione*'s tail and wing motion during hunting behavior.

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