# Effect of individual spiking activity on rhythm generation of Central Pattern Generators

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**Abstract**

Central Pattern Generators (CPGs) are highly specialized neural networks often with redundant elements that allow the system to act properly in case of error. CPGs are multifunctional circuits, i.e. the same CPG can produce many different rhythms in response to modulatory or sensory inputs. All these rhythms have to be optimal for motor control and coordination. In this paper, we use a model of the well-known pyloric CPG of crustacean to analyze the importance of redundant connections and individual spiking activity in the generation of its rhythm. In particular, we study the effect of different individual spike distributions on the network behavior.

*Key words:* Central Pattern Generators (CPG), spiking activity, neuron signatures, Interspike Intervals (ISI), triphasic rhythm.

## 1 Introduction

Central Pattern Generators (CPGs) are neural networks that acting alone or together with other CPGs generate rhythmical patterns of activity that drive different motor systems. Member neurons of a CPG have a regular and rhythmical firing sequence. This sequence controls the contraction of muscles in a system that has to repeat a set of movements in time. For example, CPGs are responsible for activities like chewing, walking or swimming (5). CPGs are multifunctional circuits that modify their behavior in response to modulatory or sensory input. The shape and phase relationship of the rhythm induced by each input is different. However, not only the input is responsible for the

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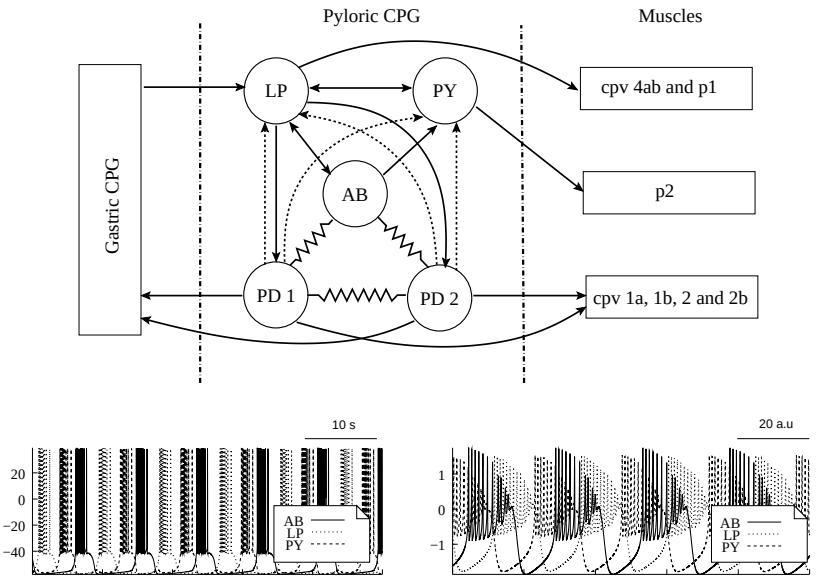


Fig. 1. Top panel (center): Network topology used to model the pyloric CPG of crustacean. Resistors represent electrical synapses, dotted lines represent slow chemical synapses and solid lines represent fast chemical connections. We have simplified the 14 cell living CPG (6), by modeling one PY neuron (which represents the eight electrically coupled PY neurons), and excluding from the circuit the IC and VD neurons which are not essential in our study. In our analysis we used an intact circuit with all the connections shown above and a damaged circuit without slow chemical synapses. The figure also displays schematically the connectivity between the pyloric and gastric CPGs, and the connectivity from the motoneurons to the muscles (see discussion). Bottom panels: Examples of triphasic rhythms produced by the pyloric CPG with the two types of neuron models used in this study: KK type neurons (left) and HR type neurons (right). Units are $s$ and $mV$ for KK and dimensionless for HR. Models and parameters used are described in (3; 4).

generation of a particular CPG rhythm. The intrinsic properties of the circuit, i.e. the individual neuron dynamics and the network topology, determine the collective activity of the system. One of the best known CPGs is the pyloric CPG of the stomatogastric ganglion (STG) of crustacean (6) (see an schematic representation in Fig. 1, top panel). The pyloric CPG generates a characteristic *triphasic rhythm* of spiking-bursting activity that controls the muscles of the pylorus. In each pyloric rhythm cycle, the AB and PDs neurons fire first, then the LP neuron follows, and finally, the PYs burst and the sequence starts again (see Fig. 1, bottom panel).

In this paper we want to study the dependence of the CPG rhythm on several intrinsic properties of these circuits. In particular we are interested in the study of the role of redundant connections and individual spiking activity on the triphasic rhythm generation. Recently the presence of a characteristic signature in each neuron has been revealed in CPG preparations (7). These individual signatures consist of characteristic interspike intervals (ISIs) in the activity of the CPG cells. Using a computer model, we discuss the ability of the pyloric CPG to generate triphasic rhythms with different neuron signatures.

## 2 Neuron and networks models

Both the individual neuron behavior and the connection topology will be analyzed in this study. To model the pyloric CPG we have used the network architecture shown in Fig. 1. In order to analyze the dependence on the connection topology, we have studied the behavior of two different circuits: intact circuits, with all the connections, and damaged circuits, without the slow chemical connections (dotted lines in Fig. 1). To validate the generality of our results and to study their dependence on individual neuron dynamics, we have also used two different models of spiking-bursting neurons, both with a very rich individual dynamics: Hindmarsh-Rose (HR) type neurons (1) and Komendantov-Kononenko (KK) neurons (2). We have previously discussed the ability of these models to generate neuron signatures in pyloric CPG network architectures (3; 4). Parameters and model descriptions used in our simulations can be found in these references.

## 3 Free and forced spike dynamics

Our main goal is to study the dependence of the rhythms on the individual spiking activity of the CPG cells. Thus, in some simulations we modify the fast dynamics (the particular ISI distribution on top of the slow waves) of the spiking-bursting behavior of the cells. To analyze the role of the neuron signatures in the rhythm generation, we have chosen to modify LP neuron dynamics. LP is the only neuron in the network that does not belong to pacemaker group –AB and PDs neurons, for details see (6)– and is connected to the muscles and also to the gastric CPG. Furthermore, the LP neuron sends and receives signals to/from the rest of the cells in the CPG. Consequently, LP neuron is the best candidate because it has full connectivity with the rest of the system.

We call forced LP simulations to those simulations with modified spiking dynamics for this cell. Free LP dynamics in this context means simulations with normally evolving LP spiking activity described by the differential equations of the model at any time. In the next section we will present simulations with free and forced LP spike dynamics in intact and damaged circuits.

Forced LP simulations are performed as follows. The activity of the LP neuron in several circuits with free LP spike dynamics is recorded to obtain different ISI distributions. These distributions are used later to generate the actual spike timings in forced LP simulations. In all cases the number of spikes and width of the bursts are kept as in the equivalent free LP simulations. The forced spiking activity is clamped on top of the slow waves, which always has

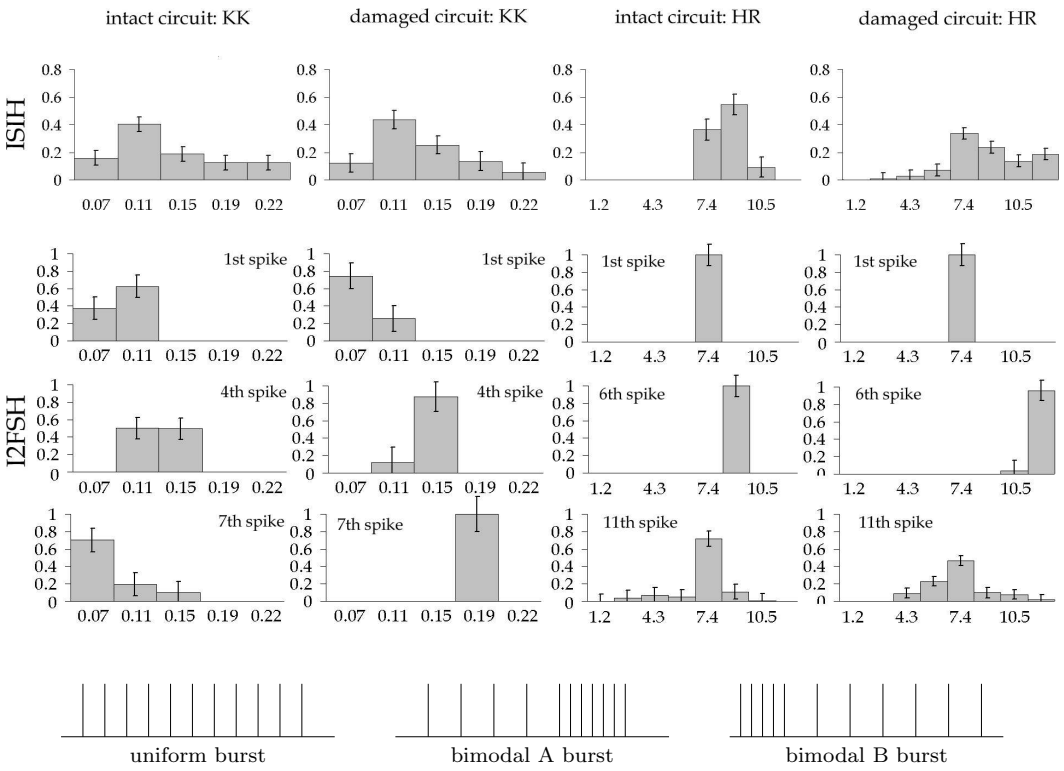


Fig. 2. Spike distributions used to force LP neuron grouped in columns by neuron model (KK and HR) and network circuit (intact and damaged without slow connections). Top row: LP ISI histogram (ISIH) obtained with the free dynamics for LP neuron. Middle panels: LP interval to the first spike histogram (I2FSH) for three different spikes with free dynamics. Bottom panel: computer generated uniform and bimodal bursts used to force LP neuron dynamics. Units are *s* for KK and dimensionless for HR.

a free dynamics. Consequently, in these simulations we alter the LP neuron signature and this allows us to test its role in the generation of the CPG rhythms. The distributions of spike timings used in forced LP simulations are listed below with the acronyms used to display our results:

- LP spike probability distributions (ISI histogram, *ISIH*) corresponding to intact and damaged topologies (first row of Fig. 2).
- Interval to first spike histograms (*I2FSH*) characterizing the distribution of distances of a given spike to the first spike within the burst. In this case we have one distribution for each spike in the burst. As an example we show the distribution of spikes at the beginning, at the middle and at the end of the bursts (second, third and fourth rows of Fig. 2). Note the increasing dispersion of the distributions at the end of the burst.
- Computer generated uniform and bimodal distributions of spikes (bottom row of Fig. 2).

To validate our method to force spike timings we have performed simulations with forced LP dynamics with exactly the same ISIs as in the free dynamics simulations. In all trials the triphasic rhythm was properly generated.

| | Uniform | Bimodal A | Bimodal B | ISIH int. | ISIH dam. | I2FSH int. | I2FSH dam. |
|---|---|---|---|---|---|---|---|
| KK intact | no | no | no | 0.411 | 0.430 | 0.390 | 0.405 |
| KK damaged | no | no | no | no | no | 0.418 | 0.420 |
| HR intact | no | no | no | 0.453 | no | 0.419 | 0.426 |
| HR damaged | no | no | no | 0.453 | 0.478 | 0.428 | 0.442 |

Table 1
Ability of several circuits with different LP neuron signatures to generate the triphasic rhythm. Rows describe the circuit and model neuron used in the simulations. Columns describe the criterion used to modify neuron signatures with forced LP dynamics. In the cases where the rhythm is correctly generated, numbers show the precision of the rhythm calculated as in (4) (lower values mean higher precision).

## 4 Results

We have performed several simulations forcing the LP neuron signature in intact and damaged circuits without the slow connections. Our results are summarized in Table 1. The triphasic rhythm (AB-LP-PY burst sequence) cannot be generated in all configurations. In those cases where the rhythm is generated, its particular shape and frequency is different in each case. This fact points out a possible role of the signatures for fine tuning of the rhythms. When the rhythm is not produced (marked as "no" in Table 1), in some cases the phase relationship among the neurons is inverted (AB-PY-LP burst sequence), and in other cases each neuron fires nearly independently.

Forcing the LP neuron signature affects the CPG's behavior in different ways depending on the kind of ISI distribution used and the network topology. When we use the circuit of Fig. 1 forcing LP spikes with an artificial burst, with uniform or bimodal spike distributions, the rhythm is never produced. On the other hand, when we force LP with bursts generated using ISIH of previously recorded free spike dynamics of other circuits, the rhythm is produced only in some cases, mainly in the intact circuit. Finally, when we use I2FSH distributions to force LP spiking dynamics, the rhythm is always correctly generated and with a higher precision (see Table 1). Additional simulations were carried out with a reduced version of the circuit shown in Fig. 1 –see reduced network description in (3)–. The results of these simulations are not showed in Table 1, but they all emphasize the importance of redundant connections to generate the triphasic rhythm. However, we have to point out that the intact circuit produces a triphasic rhythm only if the LP neuron signature is within a reasonable margin of coherence for the network.

## 5 Discussion

CPG rhythms depend mainly on the network topology. We have seen that the presence of slow connections in the intact CPG provides a stable triphasic rhythm (AB-LP-PY burst sequence). Less redundant networks –damaged and reduced (3) circuits– are not always able to produce the same rhythm. However, the topology of connections is not the only factor shaping the collective activity. Our analysis shows that a particular CPG rhythm also depends on the fast dynamics of individual neurons. If this dependence would not exist, the rhythm could always be generated with forced spike dynamics. We have shown several cases that contradict that hypothesis. The neuron signature of each CPG cell must be within a range of coherence (cf. I2FSH vs ISIH or computer generated distributions) for the circuit to generate the triphasic rhythm.

Recent experiments show that modulatory inputs can modify CPG neuron signatures (7). In our simulations we have seen that the triphasic rhythm evolves to other types of rhythms when signatures are changed. Thus, changes in the neuron signatures can have functional meanings for the CPG. Furthermore, individual spiking activity is also seen outside the pyloric circuit (see Fig. 1). The gastric CPG receives signatures from several pyloric cells, and so do muscles innervated by pyloric motoneurons. Neurons and muscles can read these signatures to perform different tasks in response to the multifunctional signals from each pyloric CPG cell.

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## References

[1] J.L. Hindmarsh, R.M. Rose, A Model of Neuronal Bursting Using Tree Coupled First Order Differential Equations, Philos. Trans. Royal Soc. London. B221 (1984) 87-102.

[2] A.O. Komendantov, N.I. Kononenko, Deterministic Chaos in Mathematical Model of Pacemaker Activity in Bursting Neurons of Snail, Helix Pomatia, J. Theor. Biol. 183 (1996) 219-230.

[3] R. Latorre, F.B. Rodríguez, P. Varona, Characterization of Triphasic Rhythms in Central Pattern Generators (I): Interspike Interval Analysis, Lect. Notes Comput. Sc. 2415 (2002) 160-166.

[4] F.B. Rodríguez, R. Latorre, P. Varona, Characterization of Triphasic Rhythms in Central Pattern Generators (II): Burst Information Analysis, Lect. Notes Comput. Sc. 2415 (2002) 167-173.

[5] A.I. Selverston, What invertebrate circuits have taught us about the brain, Brain Research Bulletin, 50(5-6) (1999) 439-40.

[6] A.I. Selverston, M. Moulins, The Crustacean Stomatogastric System: a Model for the Study of Central Nervous Systems, Springer-Verlag, Berlin, New York, 1987.

[7] A. Szücs, R.D. Pinto, M.I. Rabinovich, A.I. Selverston, H.D.I Abarbanel, Synaptic modulation of the interspike interval signatures of bursting pyloric neurons, J. Neurophysiol. 89(3) (2003) 1363-1377.