

A peer-reviewed version of this preprint was published in PeerJ on 8 November 2018.

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Yakovenko S, Sobinov A, Gritsenko V. 2018. Analytical CPG model driven by limb velocity input generates accurate temporal locomotor dynamics. PeerJ 6:e5849 <https://doi.org/10.7717/peerj.5849>

Analytical CPG model driven by single-limb velocity input generates accurate temporal locomotor dynamics

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The ability of vertebrates to generate rhythm within their spinal neural networks is essential for walking, running, and other rhythmic behaviors. The central pattern generator (CPG) network responsible for these behaviors is well-characterized with experimental and theoretical studies, and it can be formulated as a nonlinear dynamical system. The underlying mechanism responsible for locomotor behavior can be expressed as the process of leaky integration with resetting states generating appropriate phases for changing body velocity. The low-dimensional input to the CPG model generates the bilateral pattern of swing and stance modulation for each limb and is consistent with the desired limb speed as the input command. To test the minimal configuration of required parameters for this model, we reduced the system of equations representing CPG for a single limb and provided the analytical solution with two complementary methods. The analytical and empirical cycle durations were similar ($R^2=0.99$) for the full range of walking speeds. The structure of solution is consistent with the use of limb speed as the input domain for the CPG network. Moreover, the reciprocal interaction between two leaky integration processes representing a CPG for two limbs was sufficient to capture fundamental experimental dynamics associated with the control of heading direction. This analysis provides further support for the embedded velocity or limb speed representation within spinal neural pathways involved in rhythm generation.

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15 *preprint PeerJ doi: <https://doi.org/10.7287/peerj.preprints.26734v1>*

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19 Abstract

20 The ability of vertebrates to generate rhythm within their spinal neural networks is essential for
21 walking, running, and other rhythmic behaviors. The central pattern generator (CPG) network
22 responsible for these behaviors is well-characterized with experimental and theoretical studies, and
23 it can be formulated as a nonlinear dynamical system. The underlying mechanism responsible for
24 locomotor behavior can be expressed as the process of leaky integration with resetting states
25 generating appropriate phases for changing body velocity. The low-dimensional input to the CPG
26 model generates the bilateral pattern of swing and stance modulation for each limb and is
27 consistent with the desired limb speed as the input command. To test the minimal configuration of
28 required parameters for this model, we reduced the system of equations representing CPG for a
29 single limb and provided the analytical solution with two complementary methods. The analytical
30 and empirical cycle durations were similar ($R^2=0.99$) for the full range of walking speeds. The
31 structure of solution is consistent with the use of limb speed as the input domain for the CPG
32 network. Moreover, the reciprocal interaction between two leaky integration processes
33 representing a CPG for two limbs was sufficient to capture fundamental experimental dynamics
34 associated with the control of heading direction. This analysis provides further support for the
35 embedded velocity or limb speed representation within spinal neural pathways involved in rhythm
36 generation.

37 Introduction

38 The mechanism of spinal rhythmogenesis is an integral part of the mammalian locomotor system
39 that fuses descending and sensory feedback signals with body's dynamics (Dickinson et al., 2000).
40 The theoretical description of this element, termed the central pattern generator (CPG), has been
41 the focus of research with diverse aims. Previous computational studies introduced a variety of
42 models to describe inter- and intra-limb coordination (Yakovenko et al., 2005)(Schöner et al.,
43 1990) and the rhythm generating network dynamics (Daun et al., 2009; Barnett and Cymbalyuk,
44 2014). Other models tested the organization of spinal interneuronal circuitry (Bashor, 1998; Rybak
45 et al., 2006) and the dynamic interactions between the mechanical system and the CPG (Taga et
46 al., 1991). The elusive mechanism of locomotor pattern generation remains to be poorly
47 understood in the context of its regulation and integration within descending feedforward and
48 sensory feedback pathways. One of the main obstacles is the definition of CPG's essential
49 function. We know that this neural element can compute control commands for the redundant
50 musculoskeletal system (Gritsenko et al., 2016) that, in turn, shapes the activity of hierarchal
51 neural mechanisms (Lillicrap and Scott, 2013) distributed along the neuraxis (Grillner, 1985).
52 Moreover, the spinal motor circuits are known to accommodate rewiring in healthy operation
53 (Vahdat et al., 2015) and injured states (Stevenson et al., 2015; Liu et al., 2017).

54 The computational models of CPG may help to define the role of this element within the
55 sensorimotor hierarchy. What would be the pertinent CPG model for this task? There are multiple
56 models, and their implementation varies in complexity mostly due to the nature of addressed
57 problems. One of the main challenges in computational neuroscience is the choice of appropriate
58 model complexity and the level of abstraction for the theoretical description of complex neural
59 mechanisms. The rule of thumb for an appropriate choice of mathematical model is to match the
60 dexterity of experimental and theoretical descriptions. For example, the experimental data
61 representing cellular mechanisms are captured with Hodgkin-Huxley (H-H) equations that detail
62 the observed changes in membrane properties with the nonlinear dynamics of ion channel
63 conductances. In contrast, the network behavior is assessed most optimally with the relatively
64 simple phenomenological rate models that approximate the details of neural spiking by their
65 discharge rate (Sterratt et al., 2011). Recently, the CPG models with H-H formulations were
66 applied to cross the multiscale and multilevel divide between cellular and network levels at the

67 cost of high parametric dimensionality but describing the underlying mechanisms responsible for
68 neural discharge (Rybak et al., 2015; Danner et al., 2016).

69 The multiscale problem of representing input-output relationships using different physical laws
70 and mathematical implementations to capture physical phenomena at different scales is not
71 commonly addressed in the context of CPG models. Yet, there is a long-standing history of varied
72 techniques for simulating CPG dynamics that span physical simulations of reciprocal integrators
73 with inhibition (Verzár, 1923), nonlinear oscillators and rate models (Patla et al., 1985; Pribe et
74 al., 1997), and models based on spiking neurons with varied complexity of computational dynamic
75 (Selverston et al., 2000; Rybak et al., 2006). The scope of questions addressed with these models
76 is also surprisingly wide, e.g., quantifying the role of ionic currents shaping the bursting activity
77 of single neurons (Kueh et al., 2016) or identifying the role of specific network elements within
78 the CPG simulated with either the H-H models (Ausborn et al., 2017) or the rate models (Sobinov
79 and Yakovenko, 2018).

80 In our previous studies using a rate CPG model, we used data-driven parameter optimization to
81 describe locomotor phase modulation (Yakovenko et al., 2005) and then applied the inverse
82 solutions from empirical data to identify limb speeds as the modality of computed CPG inputs
83 (Yakovenko, 2011). Unlike in classical Marr's top-down analysis (Marr, 1982), the CPG structure
84 was used as a "wetware" implementation in the bottom-up analysis to identify the nature of neural
85 computation in locomotor tasks. Similar results were also found using H-H type CPG models, i.e.,
86 the monotonic relationship between the input strength and the frequency of locomotion (Rybak et
87 al., 2006) or limb speed (Danner et al., 2016) were identified.

88 Using an analytical CPG model, we have demonstrated previously that the asymmetric gait can be
89 represented with the strengths of connections between intrinsic elements of a relatively simple
90 bilateral CPG (Sobinov and Yakovenko, 2018). In contrast, our focus in this study was to test the
91 prediction that the elements of a single limb CPG are sufficient for the implementation of the
92 relationship between speed and step cycle duration. For this purpose, we derived the analytical
93 solution for the single limb model consisting of two coupled integrators. Then, we hypothesized
94 that the general form of the solution is consistent with the velocity command input that modulates
95 appropriately the timing of locomotor phases. Since limb-dependent phase modulation was also
96 implicated in the control of heading direction (Courtine et al., 2006), we used the analytical

97 solution to demonstrate, for the first time, that single-limb velocity command signals are capable
98 of appropriate phase modulation necessary for the control of heading direction.

99

100 Methods

101 A. CPG structure and function

102 The observations of neural activity in the absence of descending signals or sensory feedback led
103 T.G. Brown to formulate the principle of intrinsic rhythmogenesis of spinal networks, the half-
104 center oscillator hypothesis (Brown, 1911). Brown posited that “... *the centres are paired, and*
105 *that each pair consists of antagonistic opposites.*” The intrinsic rhythmogenesis opposed the
106 established view that the locomotor pattern is generated and shaped only by supraspinal and
107 sensory feedback pathways. The bilateral CPG model in Fig.1 was developed from a numerical
108 model of a single-limb oscillator to describe phase dominance in fictive cat locomotion, which is
109 a type of experimental behavior with diminished sensory contribution (Yakovenko et al., 2005).
110 This model controlling two limbs consisted of two dedicated oscillators made of two reciprocally
111 coupled half-center elements (gray area in Fig.1). It can generate bilateral rhythm using the
112 interactions within and between the half-center elements. Only the rhythm generating mechanism
113 is captured by this feedforward rate model with time-varying inputs. The pattern formation
114 mechanism responsible for the generation of motoneuronal input signals can be computationally
115 decoupled from the temporal dynamics of rhythm generation (McCrea and Rybak, 2008).

116

117

118 Fig. 1. **The schematic of bilateral CPG.** Each locomotor phase T_i is generated by the transformation of low-feature
119 inputs (desired velocity) with the intrinsic interactions between the half-centers (weights r_{ij} , see Eq.2). The outputs in
120 the form of phase durations define the pattern of flexor and extensor motoneurons responsible for the activity of
121 muscles during swing and stance for each limb.

122

123 The process of controlling locomotor phase durations is based on the ability of the network to
124 integrate inputs until reaching a critical threshold causing a phase resetting within CPG network,
125 Fig. 2. We have previously developed the bilateral model (Yakovenko, 2011; Sobinov and
126 Yakovenko, 2018) and describe it in brief here. The model was expressed as the system of
127 differential equations consisting of two parts in Eq.1: *i*) the largely extrinsic signals (right side)
128 and *ii*) the intrinsic interactions (left side). The offset term (x_0) could combine both intrinsic and

129 extrinsic influences on the background excitability of spinal cord. The bilateral CPG model
130 consists of a system of differential equations for four intrinsic states ($x = (x_1, x_2, x_3, x_4)^T$) that
131 represent flexor and extensor locomotor phases for each limb. The single limb CPG would consist
132 only of two reciprocal states:

$$133 \quad \dot{x} - G_x^{UL}x = x_0 + G_u u \quad (1)$$

134 where G_u matrix represents gains of input signals u , x_0 are constant offset values, G_x^{UL} matrix
135 represents the strength of unilateral connections between the CPG half-centers (shown as arrows
136 with weights r_{ij} in Fig.1, the connections across the midline were removed). G_x^{UL} matrix has the
137 following form:

$$138 \quad G_x^{UL} = I * r_{leak} \quad (2)$$

139 where I is the identity matrix, r_{leak} is the constant that determines intrinsic state-dependent
140 feedback.

141 The internal states are limited to positive values with the switching threshold set to 1. Only one
142 state from a pair, 1-2 (Fig.2), is set to be active $x \in (0, 1]$ to impose the reciprocal relationship
143 between half-centers. This implementation assumes robust reciprocity between antagonistic states
144 and enforces zero overlap between them. The single limb CPG would consist only of two
145 reciprocal states ($x = (x_1, x_2)^T$).

146 Even this simple model had many parameters that were largely undefined. Using an error-driven
147 search algorithm in our previous study (Yakovenko, 2011) we found a set of optimal parameters
148 (Table 1 in Appendix). These parameters were resolved by the minimization of the objective
149 function with terms related to the errors in simulating swing and stance phases and the rate of their
150 modulation for different overground speeds (Goslow et al., 1973; Halbertsma, 1983).

151 Results

152 The relationship between step cycle duration and the input “drive” to the analytical model was
153 investigated in two complimentary solutions that rely on different assumptions: *i*) the assumption
154 of constant integration rate in a single limb model of CPG, and *ii*) the expansion of function with
155 the common Taylor series method.

156

157 Figure 2. **The temporal schematic of two reciprocal states with integration and resetting.** The integration process
 158 in flexor half-center (blue) described by Eq.3 and 7 is reset to 0 (minimal value) after reaching 1 (maximal value) and
 159 the reciprocal extensor state (red) is initiated with the same state-switching constraints.
 160

161 A. Solution using constant rate assumption

162 First, let us express explicitly all the term in Eq.1 to describe only flexor and extensor states
 163 controlling a single limb. Here, x_1 and x_2 are the reciprocal state variables as shown in Fig. 1. The
 164 system of equations can then be stated as:

$$165 \begin{cases} \dot{x}_1 = x_{01} + g_{u1}u + r_{leak}x_1 \\ \dot{x}_2 = x_{02} + g_{u2}u + r_{leak}x_2 \end{cases} \quad (3)$$

166 Since r_{leak} is a small negative number (Table 1) the rate of state (\dot{x}) can be further approximated
 167 without this term using phase duration quantities as the difference of states for a given phase
 168 duration, i.e., the inverse of phase duration. Even for the time-variable input (u), the rate of state
 169 for a full phase duration can be simplified as:

$$170 \dot{x} = \frac{max - min}{\tau} = \frac{1}{\tau} \quad (4)$$

171 Figure 2 shows an example for this formulation based on Eq.1 for a single limb with the assumption
 172 of the constant rate of integration (g_{u1} and g_{u2} are scalars, as in our previous studies). Each state
 173 (x_1 and x_2) integrates an input (u) only when active. The integration rate per step cycle can then be
 174 stated as in Eq.4. This formulation is possible due to the removal of midline crossing connections
 175 (green in Fig.1) between CPG states that complicate the relationship. Then the expression for cycle
 176 duration can be described as a sum of the antagonistic phases in the simplified system, Eq.5:

$$177 T_c = \tau_1 + \tau_2 = \frac{1}{\dot{x}_1} + \frac{1}{\dot{x}_2} = \frac{\dot{x}_1 + \dot{x}_2}{\dot{x}_1 \dot{x}_2} \quad (5)$$

178 Since the cycle duration, T_c , is a constant for a given constant input (u), the only time-varying
 179 variables are the states of the system, x_1 and x_2 . In phase transition points, at $t = \tau_1$ or $t = \tau_1 + \tau_2$, x_1
 180 and x_2 are zero or a small value close to zero. We can further expand this equation with Eq.3 and
 181 simplify it to all the known terms:

$$182 T_c = \frac{x_{01} + x_{02} + (g_{u1} + g_{u2})u}{(x_{01} + g_{u1}u)(x_{02} + g_{u2}u)} = \frac{a + bu}{\tilde{a} + \tilde{b}u + \tilde{c}u^2} \quad (6)$$

183 where the step cycle duration is expressed as a function of input (u) and all parameters $a, b, \tilde{a}, \tilde{b}, \tilde{c}$
 184 are constants determined by the coefficients in the system of equations Eq.3.

185 **B. Solution using Taylor series**

186 The same solution Eq.6 was found by integrating the differential equations (3) between 0 and t .
 187 For this, Eq.3 can be rewritten with the assumption of independent limb control:

$$188 \quad \dot{x} - rx = x_0 + G_u u \quad (7)$$

189 where variables are as defined for Eq.1, and $r = r_{leak}$. Note that the right-hand side can be assumed
 190 to be time-independent for constant input (u) and this type of equations has a general solution of
 191 the form e^{kx} . The left side of the above equation can be expressed as

$$192 \quad (xe^{-rt})' = \dot{x}e^{-rt} - rxe^{-rt} = (\dot{x} - rx)e^{-rt} \quad (8)$$

193 Hence, Eq.7 can be integrated and evaluated between 0 and t using

$$194 \quad (xe^{-rt})|_0^t = \int_0^t (x_0 + G_u u)e^{-rt} dt \quad (9)$$

$$195 \quad x(t)e^{-rt} - 0 = \frac{x_0 + G_u u}{-r}(e^{-rt} - 1) \quad (10)$$

$$196 \quad x(t) = \frac{x_0 + G_u u}{r}(e^{rt} - 1) \quad (11)$$

197 The exponential function can be further expanded with Taylor series and some components can be
 198 dropped since r is a number close to zero, so that $rt \approx 0$ in the expansion:

$$199 \quad x(t) \approx \frac{x_0 + G_u u}{r}(1 + rt + \dots - 1) \approx (x_0 + G_u u)t \quad (12)$$

200 Then, the full phase of each integrated state is

$$201 \quad t = \frac{1}{x_0 + G_u u} \quad (13)$$

202 Finally, the full cycle duration consisting of two reciprocal phases ($t_1 + t_2$) has the same form as
 203 Eq.6

$$204 \quad T_c = t_1 + t_2 = \frac{a + bu}{\tilde{a} + \tilde{b}u + \tilde{c}u^2} \quad (14)$$

205 where $a, b, \tilde{a}, \tilde{b}, \tilde{c}$ are constants defined by the examination of algebraic terms from Eq. 13.

206 C. Validation

207 Both methods converged on the same form, Eq. 6 and 14, supporting the consistency of solutions
 208 with different assumptions. The relationship between step cycle duration and CPG input (T_c and
 209 u) is of the form $T_c = a * u^b$. This simple analytical solution has a similar form to the
 210 phenomenological relationship between cycle duration and the velocity of overground forward
 211 progression $T_c = 0.5445 * V^{-0.5925}$ (Goslow et al., 1973). Figure 3 shows the comparison of solutions
 212 with our analytical and the previous phenomenological model for the step cycle duration and
 213 velocity values. The simulated T_c data values were calculated with Eq.7 using optimal parameters
 214 and u values selected with the regression equation $u = (V + 0.1272) / 0.2357$ (from Fig.4 in our
 215 previous work (Yakovenko, 2011)) and plotted in Fig.3C. The analytical solution (red) for leg
 216 speed was closely related to the empirical curve (*black*) calculated with the phenomenological
 217 functions that were calculated as the best-fit expressions for the experimental measurements
 218 (Goslow et al., 1973; Halbertsma, 1983) (Fig. 3A). Since the swing duration remains nearly
 219 constant as a function of either step cycle duration or the velocity of forward progression in cats
 220 (Halbertsma, 1983; Frigon et al., 2014), it can be approximated as a constant (~ 0.25 s). Then, the
 221 stance duration is the same as in Eq. 6 and 14 with the negative constant. This relationship may
 222 not be preserved for gaits with the large differences in limb speeds as those used in split-belt
 223 experiments (D'Angelo et al., 2014) and may require the consideration of bilateral inputs as in our
 224 previous study (Sobinov and Yakovenko, 2018). The analytical and empirical step cycle durations
 225 were highly correlated (Fig.3B) for the linear relationship between CPG inputs (u) representing
 226 scaled forward velocity values (Fig.3C).

227
 228 Figure 3. **The comparison of analytical and empirical values.** A. The solution of cycle durations is shown for both
 229 the analytical (red) and empirical (black) values. B. The analytical cycle durations (T_c) are plotted as a function of
 230 empirical T_c ($R^2 = 0.9946$, $p < 0.001$). C. The relationship between input signals and empirical forward velocity.
 231

232 The implementation of CPG with the limb speed inputs is expected to generate spatiotemporal step
 233 modulation appropriate for the locomotion on a curved path. We used the following equation to
 234 compute the relationship between the heading direction (γ) and limb speeds (V_R , V_L): $\gamma = T_c (V_R -$
 235 $V_L) / W$, where W is the interlimb step width (≈ 0.15 m in cat) and T_c is the step duration from Eq. 6.
 236 This equation was previously derived for the experimental and theoretical kinematics of
 237 locomotion along a curved path (Courtine et al., 2006; Sobinov and Yakovenko, 2018). Fig. 4A

238 shows the monotonic relationship with extremes occurring for large interlimb speed difference
239 (∂V) at slow speeds. This range may be consistent with the “spin turning” when body spins around
240 a supporting limb (Hase and Stein, 1999). Examples of simulated kinematics for three speeds (a,
241 b, c = 0.5, 1, 2 m/s) with increasing interlimb speed differences in each consecutive step are shown
242 in Fig. 4B. The green vector indicating the heading direction demonstrates the dependency not
243 only on the interlimb speed difference (∂V), but also the overall magnitude of body’s velocity (V).
244 The parsimonious analytical CPG model that includes computations for two limbs can generate
245 steering.

246
247 Figure 4. **The simulated relationship between CPG inputs (limb speeds) and the heading direction.** A. The change
248 in the heading direction is shown as a function of two parameters — mean speed and limb speed differential. B.
249 Examples of asymmetrical walking trajectories simulated for the ranges marked (a-c) in A. The heading direction
250 (green) was scaled with the mean stride length in 5 simulated steps. C. Schematic summarizing the heading direction
251 control based on the velocity command hypothesis. The desired heading direction (γ^*) can automatically generate the
252 CPG speed commands appropriate for steering body (γ).

253 Discussion

254 Here, we have investigated an extreme example of the structural feedforward rate model with time-
255 varying inputs and its ability to capture general CPG function. We have developed an analytical
256 solution for a reduced CPG model to test if the basic structure of reciprocal interactions between
257 integrating and leaky network elements can generate appropriate input-output relationship between
258 limb speed and locomotor cycle duration. The analytical solution of the reduced CPG model
259 recreated the empirical data very closely, despite model simplicity and assumptions in deriving the
260 solution. This was not clear *a priori*.

261 The minimalistic implementation of CPG required significant assumptions about morphology and
262 function in the model. Both, flexor and extensor half-centers were assumed to be capable of
263 generating rhythm based on the reciprocity of two integrating circuits. The ability for
264 rhythmogenesis of each half-center is the current consensus among multiple groups (see reviewed
265 in (Frigon, 2017)), but it has been under some scrutiny, see discussion of “swing-phase” CPG
266 below. In the model, the switching to the antagonistic phase is triggered by the state signal crossing
267 the threshold ($x_i=1$). The process responsible for maintaining activity in one phase is similar to the
268 dynamics arising from the slowly inactivating persistent sodium current in CPG models using H-
269 H dynamics.

270 The dynamical rate models describing the single-limb CPG are sufficient for the description of the
271 relationship between the desired speed and the locomotor phases. The main advantage of simple
272 models is that their parameters can be accurately scaled using empirical data on the timing of
273 locomotor phase transitions. While we have used data from observations of cat locomotion, the
274 general functional homology of the CPG mechanism has been demonstrated in other mammals,
275 including humans (Lam and Yang, 2000; Musselman and Yang, 2007; Dominici et al., 2011). As
276 further anatomical studies detailing the organization and wiring of neurons become available for
277 mammalian CPG (Kiehn, 2016), the inclusion of these details in models is generally left to the
278 intuition. H-H spike-generating models of CPG require multiple estimated parameter values that
279 are often difficult to validate in numerical simulations. These models provide insight into the
280 realistic control challenges and reveal tentative explanations of experimental discrepancies. For
281 example, the discrepancy between the observation of both extensor and flexor phase dominance
282 in locomotor patterns generated by adaptable flexor- and extensor- driven CPG as opposed to only
283 the flexor-driven CPG (see review Duysens et al., 2013) can be reconciled with the consideration
284 of available functionality within underlying single-cell and network dynamic elements (Ausborn
285 et al., 2017). A subset of plausible mechanisms selected from the plethora of unexplored
286 parametric relationships can explain multiple observed states, and other alternative mechanisms
287 generating similar outcomes may exist within the same models.

288 The evidence of underfitting of experimental data by simple models should be the main motivation
289 for the inclusion of additional terms within theoretical representations. As we have observed in a
290 relatively complex dynamical rate model simulating asymmetric bilateral locomotion (Sobinov
291 and Yakovenko, 2018), the same low-dimensional output can be produced by several alternative
292 parameter configurations. What region of the parameter space, which is nine-dimensional for a
293 bilateral rate model, is physiological remains to be established. The potential of dynamical rate
294 models to simulate brain functions also remains an open question. Their utility was demonstrated
295 in a series of studies of motor cortical processing spanning reaching movements and motor
296 learning (Churchland et al., 2012; Gilja et al., 2012; Kao et al., 2015; Sussillo et al., 2015). Our
297 finding suggests that dynamical rate models solve the problem of transforming high-level
298 commands by capturing empirical observations of temporal phase relationships.

299 All parameters in the parsimonious single limb CPG model can be robustly constrained by the
300 corresponding empirical observations. In this model, the inputs are isolated and identified as

301 velocity-dependent based on the observed outputs. For example, it is sufficient to measure the
302 phase and cycle relationship to identify the scalar gain and the offset for each half-center integrator.
303 The excluded connectivity within the CPG model representing propriospinal commissural
304 pathways in the lumbosacral enlargement removes the network rhythmogenic flexibility that may
305 represent different behavioral states intrinsically (Ausborn et al., 2017; Sobinov and Yakovenko,
306 2018). For example, a modeling study using a high-dimensional parameter space model developed
307 with H-H formalism has demonstrated that the interneurons crossing the midline may provide left-
308 right limb coordination (Shevtsova et al., 2015). The reduction of the high-dimensional parametric
309 space reduces inevitably the behavioral repertoire but increases the model robustness and gains the
310 simple expression of the underlying system characteristics. While the utility of simple models can
311 be challenged for problems that require the examination of intricate structural or functional details,
312 the use of simple models conforms to George Box's truism that "*all models are wrong but some*
313 *are useful*" (Box, 1979). The dimensionality of both inputs and outputs in this model's dynamical
314 transformation is equivalent, and all parameters are readily definable by the statistics of
315 observations.

316 The presented solution is based on the analysis of a single limb controller. How does this apply to
317 the behaviors with the interlimb contributions? In a quadruped, the CPG is a network of all four
318 limb controllers that generate patterns with the inputs of all its elements. The analyses of locomotor
319 patterns in split-belt locomotion, when fore- and hind- limbs or left and right limbs were decoupled
320 and allowed to move at different speeds, support the idea that forelimb and hindlimb CPGs are
321 similarly organized without midline asymmetries (D'Angelo et al., 2014). The upper and lower
322 limb CPG networks have been proposed to monitor and to integrate sensory inputs with the
323 ongoing rhythmic activity both in cats and also in humans (Duysens and Van de Crommert, 1998).
324 For example, the cutaneous inputs are similarly modulated in lower limbs during locomotion and
325 in upper limbs during rhythmic, cyclical arm tasks (Zehr and Kido, 2001). The similarity in the
326 structure of the upper and lower limb controllers and their symmetricity across the midline
327 corroborates the idea that the understanding of single limb CPG dynamics is central to the
328 description of inter limb coordination and sensorimotor integration. Thus, this model may be
329 adapted in the future studies to capture, at least partially, upper-limb dynamics in rhythmic
330 movements.

331 Our results have shown that a simple CPG model driven by limb velocities captures the behavior
332 of steering during gait. In studies where subjects were asked to walk on curvilinear paths (Hase
333 and Stein, 1999; Courtine et al., 2006), both amplitude and timing in leg and trunk muscles were
334 modulated. This supports the idea that the descending command interacts directly with the CPG
335 circuitry to change the heading direction and to allow the locomotion along the curvilinear path.
336 The control of turning during locomotion has been described in the context of controlling subject's
337 center of mass (Patla et al., 1999). The dynamics of this problem is typically defined by the model
338 of inverted pendulum (Hof, 2008), which is traditionally used as the basis of neural transformation
339 responsible for the locomotor rhythmogenesis and mechanical stability (Full and Koditschek,
340 1999; Full et al., 2002). The neural circuitry of CPG mechanism coupled to the mechanical
341 dynamics of limbs is thought to anticipate mechanical requirements, a phenomenon termed
342 neuromechanical tuning (Taga et al., 1991; Prochazka and Yakovenko, 2007). Thus, it is logical
343 to hypothesize that the anticipated heading direction signal is processed by the CPG network.
344 However, the operation of this pathway may be limited to the “step turning”, which has no abrupt
345 trunk rotation, as opposed to “spin turning”, which may require stopping the axial leg on the inside
346 of a turn (Hase and Stein, 1999). The step turning is generally stable with wider step width and
347 does not disrupt the gait rhythm. Thus, the limb speed driven CPG may mediate turning through a
348 step turning strategy (Fig. 4). In the task where a subject walks on the same curved path with
349 different limb speeds, the simulations predict an increase in interlimb speed with the increasing
350 velocity – moving along the same heading direction line in Fig.4. Similar increase in the limb
351 stride length asymmetry can be seen in the kinematics of human curved locomotion (see Fig. 4 in
352 (Orendurff et al., 2006)).

353 The desired heading direction may be expressed within limb speed commands that descend to the
354 CPG. Similar to our previous study (Yakovenko, 2011), the simple analytical formulation of the
355 relationship between the heading direction and the CPG inputs can be analyzed bottom-up, where
356 a system producing body reorientation during locomotion is also driven by the desired heading
357 direction originating from the higher levels of the visuomotor pathway. The support for the
358 expression of desired heading direction comes from the observations of anticipatory head
359 orientation in humans walking on curved paths and the existence of dedicated visuomotor cells
360 tuned to the head orientation. The orientation of head relative to the desired locomotor direction
361 (similar to γ^* term in Fig. 4C) may enable the repositioning of body relative to its frame of

362 reference associated with the ongoing forward progression (Hollands et al., 2001). Neurons
363 encoding selectively the head orientation, termed “head direction cells”, have been found in the
364 visuomotor and navigation-related pathways of several mammals (Taube et al., 1990a; 1990b;
365 Knierim et al., 1995; Robertson et al., 1999; Sargolini et al., 2006) and simulated in models (Zhang,
366 1996; McNaughton et al., 2006). The head direction has been shown to influence selection of limb
367 movements (Dancuse and Schieber, 2010) and to anticipate the turning in walking on straight and
368 curved paths (Hicheur et al., 2005). In the system with the desired heading direction control, the
369 left-right limb coordination would be automatically generated within the pathways converging on
370 the CPG network.

371 The current model implementation has both temporal and spatial limitations. It has been validated
372 for the temporal modulation of step cycle duration within the range of walking speeds. However,
373 it may not extend to other locomotion types where stance is shorter than swing, i.e., running. In
374 addition, since the dynamics of single limb CPG model is largely dominated by the modulation of
375 stance phase, the phase modulation has been simplified to the examination of only step cycle
376 duration, where $T_{cycle} = T_{stance} + const$. This is supported by the observations that swing phase
377 remains nearly constant over a wide range of walking speeds (Halbertsma, 1983; Frigon et al.,
378 2015). The speed-related increase in the exerted muscle force is expected to be matched with the
379 increase in the order and size of recruited muscle motor units in accordance with Hennemann’s
380 size principle (reviewed in Taylor, 1978). This quadratically increasing signal has not been
381 represented in the current model because this implementation captures whole limb behavior and
382 not the patterning of individual muscles, which can be achieved with the method of Patla et al.
383 (Patla et al., 1985). In neuromechanical simulations using the single-limb analytical
384 implementation, the velocity-dependent recruitment can be added as the direct command from the
385 descending pathways (velocity signal) to muscle activation (Prochazka and Ellaway, 2012) or as
386 a transformation from the inverse of the corresponding speed-dependent phase duration within the
387 CPG model. The speed-dependent increase in the recruitment of muscles can also be compensated
388 by muscle properties and proprioceptive feedback dependent on muscle dynamics (Yakovenko et
389 al., 2004). For example, the lack of sufficient ankle extensor forces at high speeds would alter gait
390 kinematics forcing ankle extensors to operate at longer lengths, which, in turn, increases both force
391 generation and increases the stretch reflex contribution from Ia and Ib primary afferent pathways.

392 The description of mechanisms responsible for the coordination of phasic activity during
 393 locomotion may be necessary for the development of stroke and spinal cord injury repair and
 394 rehabilitation strategies (Thompson, 2012). The basic mechanistic description of CPG is critical
 395 for the development of robotic and clinical applications that take advantage of this element, and it
 396 is essential for the functional understanding of hierarchical descending and sensory feedback
 397 pathways projecting to it. The fundamental dynamical form of CPG mechanism and its validation
 398 in locomotion with different velocities opens a robust alternative to computationally intensive
 399 models.

400 Conclusion

401 The analytical solution demonstrates that the linear relationship between forward velocity or limb
 402 speed and the CPG model input is an intrinsic property of reciprocal organization between two
 403 half-center oscillators. Moreover, there is a good correspondence between the form of analytical
 404 solution and the previous empirical description of this relationship. The existence of rhythmogenic
 405 neural networks with the reciprocal inhibition makes it possible to use gross signals, i.e. limb
 406 velocity, to specify the nonlinear regulation of locomotor phases. In addition, this model can
 407 describe steering control as the CPG-mediated transformation from the internal representation of
 408 desired heading direction in terms of limb speeds to the executed change in the step cycle of each
 409 limb. Further theoretical description of CPG may provide tools for intelligent prosthetics and the
 410 quantitative metrics of locomotor disabilities.

411 Appendix

412 Table 1. Optimal CPG parameters from Yakovenko (2011).

Parameter	x_{01}	x_{02}	g_1	g_2	r_{leak}
Value	-0.0007	2.4256	0.6203	0.4882	-0.0094

413 Acknowledgements

414 We thank Jonathan E. Rubin for the discussion of analytical models that led to the development of
 415 this paper. This work was supported by a student fellowship National Institute of Health, T32,
 416 AG052375-01A1 (AS), salary support from National Institute of Health, National Institute of
 417 General Medical Sciences, P20GM109098 (SY, VG), and administrative support U54GM104942

418 (SY). *The funders had no role in study design, data collection and analysis, decision to publish,*
419 *or preparation of the manuscript.*

420 Figure Legends

421 Fig. 1. **The schematic of bilateral CPG.** Each locomotor phase T_i is generated by the
422 transformation of low-feature inputs (desired velocity) with the intrinsic interactions between the
423 half-centers (weights r_{ij} , see Eq.2). The outputs in the form of phase durations define the pattern
424 of flexor and extensor motoneurons responsible for the activity of muscles during swing and stance
425 for each limb.

426 Fig. 2. **The temporal schematic of two reciprocal states with integration and resetting.** The
427 integration process in flexor half-center (blue) described by Eq.3 and 7 is reset to 0 and the
428 reciprocal extensor state (red) is initiated.

429 Fig. 3. **The comparison of analytical and empirical values.** A. The solution of cycle durations
430 is shown for both the analytical (red) and empirical (black) values. B. The analytical cycle
431 durations (T_c) are plotted as a function of empirical T_c ($R^2=0.9946$, $p<0.001$). C. The relationship
432 between input signals and empirical forward velocity.

433 Fig. 4. **The simulated relationship between CPG inputs (limb speeds) and the heading**
434 **direction.** A. The change in the heading direction is shown as a function of two parameters —
435 mean speed and limb speed differential. B. Examples of asymmetrical walking trajectories
436 simulated for the ranges marked (a-c) in A. The heading direction (green) was scaled with the
437 mean stride length in 5 simulated steps. C. Schematic summarizing the heading direction control
438 based on the velocity command hypothesis. The desired heading direction (γ^*) can automatically
439 generate the CPG speed commands appropriate for steering body (γ).

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591

Figure 1(on next page)

The schematic of bilateral CPG.

Each locomotor phase T_i is generated by the transformation of low-feature inputs (desired velocity) with the intrinsic interactions between the half-centers (weights r_{ij} , see Eq.2). The outputs in the form of phase durations define the pattern of flexor and extensor motoneurons responsible for the activity of muscles during swing and stance for each limb.

CPG

MUSCULOSKELETAL

DESIRED VELOCITY

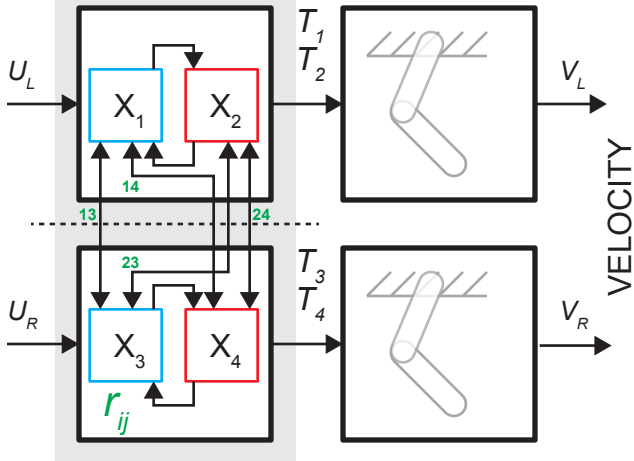


Figure 2 (on next page)

The temporal schematic of two reciprocal states with integration and resetting.

The integration process in flexor half-center (blue) described by Eq.3 and 7 is reset to 0 and the reciprocal extensor state (red) is initiated.

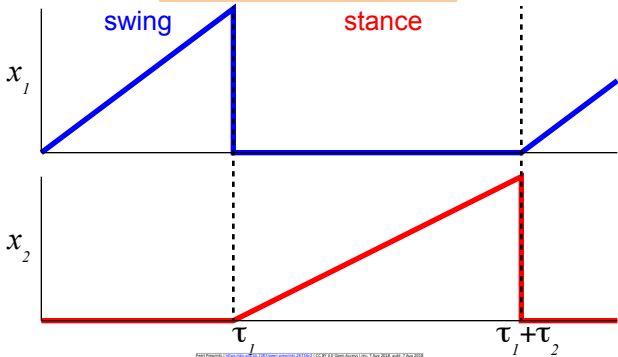


Figure 3(on next page)

The comparison of analytical and empirical values.

A. The solution of cycle durations is shown for both the analytical (red) and empirical (black) values. B. The analytical cycle durations (T_c) are plotted as a function of empirical T_c ($R^2=0.9946$, $p<0.001$). C. The relationship between input signals and empirical forward velocity.

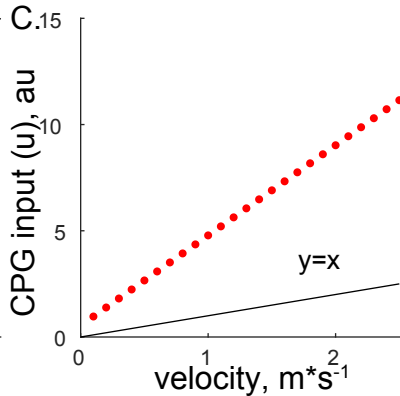
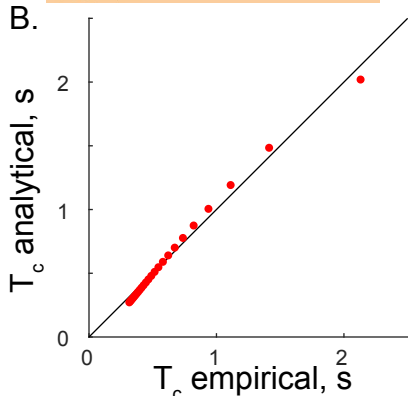
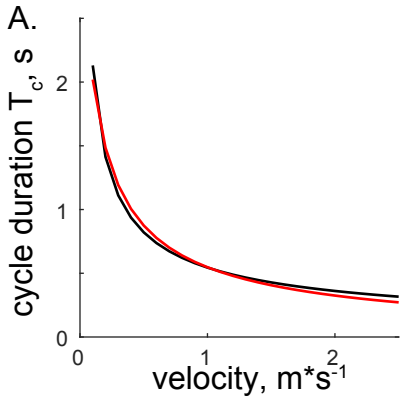


Figure 4(on next page)

The simulated relationship between CPG inputs (limb speeds) and the heading direction.

A. The change in the heading direction is shown as a function of two parameters — mean speed and limb speed differential. B. Examples of asymmetrical walking trajectories simulated for the ranges marked (a-c) in A. The heading direction (green) was scaled with the mean stride length in 5 simulated steps. C. Schematic summarizing the heading direction control based on the velocity command hypothesis. The desired heading direction (γ^*) can automatically generate the CPG speed commands appropriate for steering body (γ).

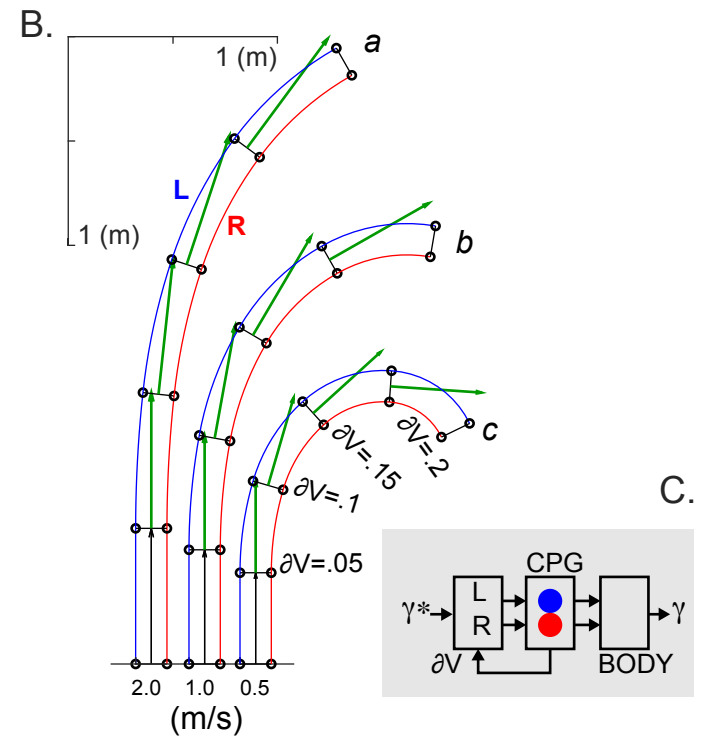
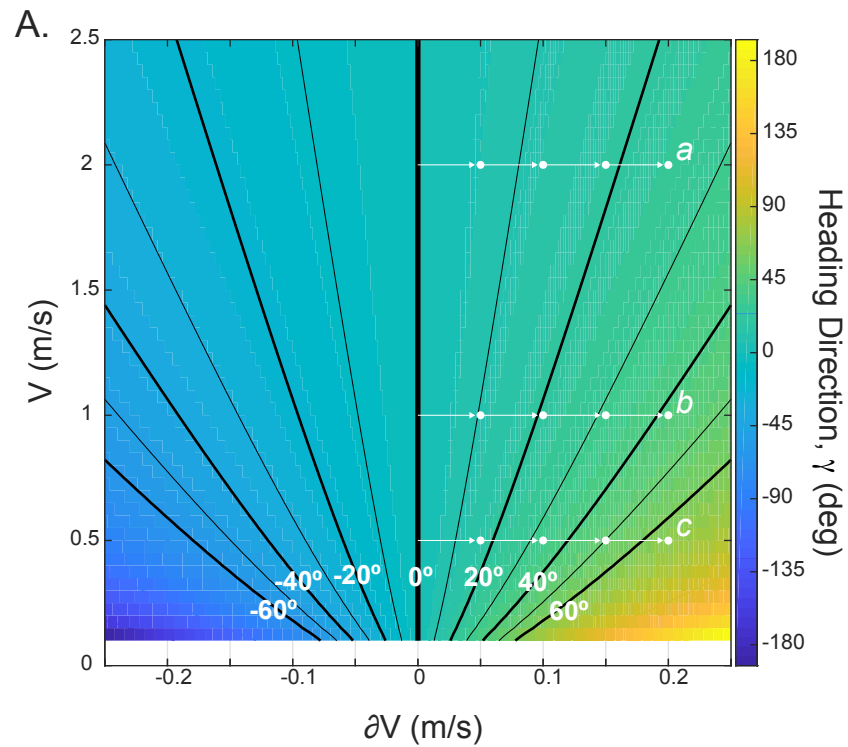


Table 1 (on next page)

Optimal CPG parameters

The parameter values were selected from Yakovenko (2011).

1 Table 1. Optimal CPG parameters from Yakovenko (2011).

Parameter	x_{01}	x_{02}	g_1	g_2	r_{leak}	r_{13}	r_{14}	r_{23}	r_{24}
Value	-0.0007	2.4256	0.6203	0.4882	-0.0094	0.1339	-0.0485	-0.0823	0.0981

2