Modeling Quadruped Gait Bifurcations

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Introduction

As quadrupeds have complex movement patterns termed gaits, developing related models can help identify movement pathologies when data deviates from the model and inform robotic movement. These models are Central Pattern Generators (CPGs): where various cells, each a system of ODEs, generate a dynamical system that spatiotemporally resembles gait patterns. While much theoretical work has been done (Golubitsky et al., 1998), they have been heavily abstracted without biological basis. Additionally, they focus on reproducing all gait types, but not if the model properly bifurcates, namely transition between gaits, in a smooth, stable way. We expand on the properties of the Golubitsky et al. (1998) model: while the model likely doesn't reflect biological mechanisms that generate gaits, it does reflect many biological properties that generate gaits, namely spatiotemporal limb coordination, gait stabilization, and gait transitions.

Methods

A critical assumption is that the CPG model reflects gait symmetries. Bilaterally symmetric organisms usually has underlying bilaterally symmetric biology, hence any left-right nodes from the model should be interchangeable. For quadrupeds, a "rule" applied to the back legs should also be applied to the front and vice versa. So if the back legs move out-of-phase, so too is the front (like pace or trot). Per Golubitsky et al. (1998), an 8 cell cube generates all known quadruped gaits (Fig. 1D). So in algebraic notation, relabeling the nodes say (12)(34)(56)(78) or (1357)(2468) doesn't change any model findings e.g. gait type and stability.

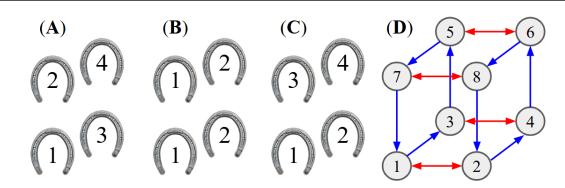


Figure 1: Spatiotemporal pattern of relevant gaits. Numbering is limb movement order when the quadruped faces North, starting with left hind. (**A**) Walk. (**B**) Pace. (**C**) Transverse Gallop. (**D**) Bottom cells controls the limbs, where 1 to 4 are paired with the left and right hind, left and right front, respectively. Blue and red are ipsilateral and contralateral couplings, respectively. By bilateral and translational symmetry, the gaits stay the same regardless of cube face and orientation chosen.

All the assumptions are borrowed from the Golubitsky et al. (1998) paper with another assumption: each cell is simplified to a neuron. Then a common model for neuronal spiking is the FitzHugh-Nagumo Equations:

$$\dot{x} = c(x + y - \frac{x^3}{3})$$
 $\dot{y} = -\frac{1}{c}(x - a + by)$

x is the membrane potential, y the recovery variable, a the excitability threshold, b the recovery strength, and c the x-y speed (which increased c hastens the spikes and slows recovery). As gait generation depends more on how the limbs are coupled together rather than how each individual leg moves, fix (a, b, c) = (0.02, 0.2, 0.44) per the Golubitsky et al. (1998) paper for reproducibility unless stated otherwise. Assume x_1, x_2, x_3, x_4

spiking has a 1-1 map to their respective leg flexing. By symmetry, all cells have the same internal dynamics \dot{x} and \dot{y} . Then add the external dynamics to each cell with $i=1,\cdots 8$ taken modulo 8:

$$\dot{x}_i := \dot{x} + \alpha(x_{i-2} - x_i) + \gamma(x_{i+\epsilon} - x_i)$$

$$\dot{y}_i := \dot{y} + \beta(x_{i-2} - x_i) + \delta(x_{i+\epsilon} - x_i)$$

$$\epsilon := \begin{cases} +1 & i \text{ odd} \\ -1 & i \text{ even.} \end{cases}$$

While $(\alpha, \beta, \gamma, \delta)$ are dimensionless, they model coupling strengths between limbs, where α, β and γ, δ are for ipsilateral and contalateral couplings, respectively. Thus, generating gaits should depend on their relative strengths. Initial conditions were fixed $(x_1, y_1) = (0.06, 0.04), (x_i, y_i) = (0, 0), i = 2, \dots, 8$, except during sensitivity analysis where they're perturbed by uniformly randomly sampling $(x, y) \in \times_{i=1}^{16}[-0.1, 0.1]$.

Lastly, two representative gaits were chosen, namely they differed by only one parameter, say p. As the periodicity of a limit cycle can be represented by the magnitude of oscillation, the average of amplitudes of x_1, \dots, x_4 were calculated after convergence occurred for a given p (namely any error was below 0.002). Then as p slowly varied, the magnitudes were calculated and plotted to test bifurcation type, if the gait stabilizes after the bifurcation, and if the gait chaotically transitions during the bifurcation.

Results

We planned to first reproduce gaits, map out their parameter space, then test their stability after knowing which parameters to fix versus vary where. Though we set c = 2.5 (Fig. 2) as there's a wider diversity of gaits, we focused on c = 0.44 as stand, walk, pace, then transverse gallop reflects the sequence of how many quadrupeds like horses change their gaits as they move faster.

For Fig. 3, we make 5 remarks. (1) Each quadrant of the (β, γ, δ) cube near the origin has mostly 1 gait. (2) Sequencing gaits in increasing speed from stand to transverse gallop involves spiraling near the origin. (3) Uniformly scaling $(\alpha, \beta, \gamma, \delta)$ didn't change gaits. (4) The cube is slightly deviated from origin to get relevant intersections. (5) "Not a gait" means the spatiotemporal pattern fails to match some known biological gait.

For Fig. 4, we makes 3 more remarks. (6) Most gaits on the left-hand side taper as the parameter decreases. (7) As the parameter increases, the slope steepens continuously. (8) At the bifurcation, the oscillation magnitude abruptly flattens to 0 for stand (\mathbf{A} - \mathbf{C}) and > 0 for pace (\mathbf{D}) and transverse gallop (\mathbf{F}). Lastly, of 100 trials total, no different gait was made when slightly perturbing initial conditions around the origin.

Discussion

Fig. 3 is key as relative coupling strengths matches expected gait. With standing, legs on the same and opposite sides are still. Similarly, standing is best made when $(\alpha, \beta, \gamma, \delta)$ are all positive. With $\alpha > 0$, there's some ipsilateral coupling. Indeed, walking moves the left hind and front first, then the right ("ipsi-contraipsi"). Transverse gallop moves the left and right hinds, then the front ("contra-ipsi-contra"). When fixing (β, γ) , transverse gallop is more contralaterally favored as δ increases. Yet walking still temporally separates ipsilateral legs when pace doesn't, reflected by the transition when β increases while fixing $\delta < 0$.

For the remarks made of Fig. 3, (1) suggests relative strengths of coupling parameters is needed to map gaits and (3) is evidenced by the gaits remaining the same when radially dispersed from the origin for some fixed angle. (2) suggests the model is insufficient as the natural gait sequencing when increasing speed isn't naturally reflected by varying (β, γ, δ) and (4) means gaits can't be neatly packed into cube quarters.

A supercritical Hopf bifurcation is when solutions attract from fixed points (stand) to a limit cycle (some gait). This is shown in Fig. 4 for (A-C). This reflects reality as both gaits are stable on the left (concave) and right side (flat) with no chaotic transitions. The bifurcations of (D-F) aren't the same as there's no fixed point, just different limit cycles for different gaits. The transitions are also stable as expected.

Lastly, we note Golubitsky et al. (1998) didn't have y=0.04, but rather -0.04. That could've been the issue why we couldn't reproduce their gaits with their given parameters. The sensitivity analyses disproved that: when performing 100 trials when slightly perturbing initial conditions for some (β, δ, γ) known from Fig. 3, the new gait matched what was expected for all trials, also demonstrating gait stability.

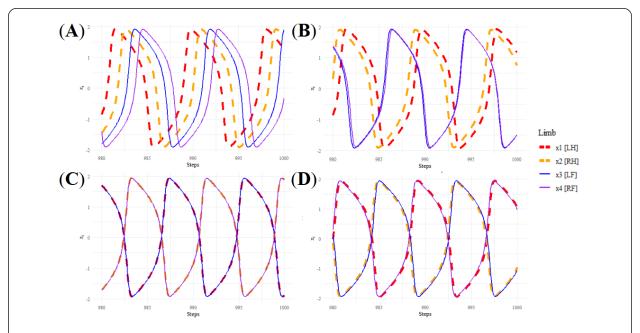


Figure 2: Example gaits for c=2.5. Gaits are classified spatiotemporally: limbs relatively occur at the correct order and time. (A) Transverse Gallop, where $1 \to 2 \to 3 \to 4$ in quick succession, then a pause (the animal being midair). (B) Bound, where it's back legs paired, then front. (C) Pace, where ipsilateral legs are paired. (D) Trot, where diagonal legs are paired. Observe that (B - D) is a 2-beat cycle that's mostly equally spaced.

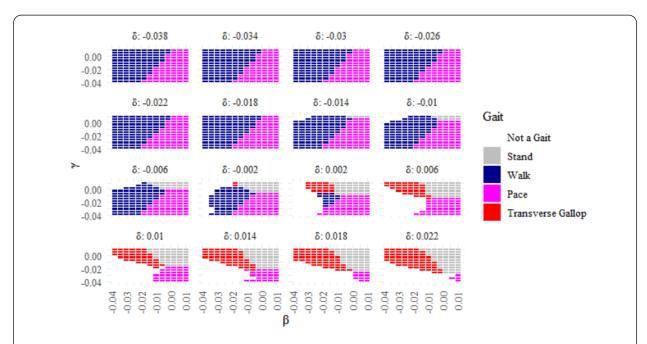


Figure 3: Relative coupling strengths makes one gait. Gaits are mapped onto a cube when varying (β, γ, δ) around the origin and fixing $\alpha = 0.01$, then taking slices for specific δ 's. When $\delta < 0$, walk and pace are made when $\beta < 0$ and $\beta > 0$, respectively. When $\delta > 0$, transverse gallop and standing are made when $\beta < 0$ and $\beta > 0$, respectively, especially when $\gamma > 0$. Standing has all 3 positive.

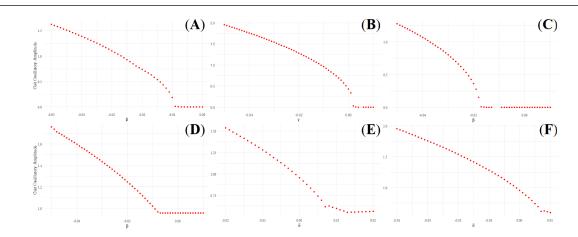


Figure 4: Bifurcations of 6 transitions between gaits. When fixing parameters and varying only one, for the top row, we transition from a (\mathbf{A}) walk, (\mathbf{B}) pace, and (\mathbf{C}) transverse gallop to standing when reading the plots left-to-right. For the bottom row, we transition from (\mathbf{D}) walk to pace as well as (\mathbf{E}) pace and (\mathbf{F}) walk to transverse gallop.

Conclusion

We find varying the relative strengths of cell coupling parameters matched the spatiotemporal coordination of limbs. These areas of stability in Fig. 3, in addition to bifurcation and sensitivity analyses, demonstrates the model is stabilizes gaits with non-chaotic transitions. The model is simplistic, which makes such interpretable, though has a sea of deficits (e.g. there's 7 parameters to vary, there's many coupling types possible, different convergence times when varying parameters).

Thus, we posit some interesting future directions: (I) Strategically Sample. We created $11^4 = 14641$ plots when varying $(\alpha, \beta, \gamma, \delta) \in \times_{i=1}^4 [-0.02, 0.02]$. It was still very hard finding new gaits, yet very easy when $c = 0.44 \rightarrow 2.5$. So varying $(a, b, c, \alpha, \beta, \gamma, \delta)$ for some $H \subset \mathbb{R}^7$ can probe how internal dynamics affect gaits. (II) Add Neurons. Then certain neurons would be receptive to certain gaits. When adding a synchronization parameter, we can test how the model "decides" which gaits to choose.

Most importantly: (III) Incoporate Feedback. Gaits are flexible from hunting wiley prey to walking uneven terrain. We propose propioceptive feedback to cells 1-4 and vestibular for 5-8. That would: (A) Differentiate lower v. higher-order cells. We can't permute any cells, but then cells 5-8 has biological basis and explain why specifically model gaits by x_1, x_2, x_3, x_4 and not say x_6, x_8, x_5, x_7 . (B) Differentiate top-down and bottom-up processes. E.g. the Superior Colliculus integrates multiple sensory modalities and higher-cognitive behaviors to spatiotemporally sequence motor movement (Liu et al., 2022). As a result, both can (C) Explain why gaits are chosen. This model explains how to, but not why we should, produce specific gaits. Internal and external needs can justify parameters beyond an area association.

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