The Metastability of the Double-Tripod Gait in Locust Locomotion

\[
\frac{d\varphi_n}{dt} = \sum_{m=1}^{6} \Gamma A_{nm} H(\varphi_m - \varphi_n) + k H(f_n(\varphi) - \varphi_n)
\]

HIGHLIGHTS

- Isolated in vitro locust preparations indicate that idling is a stable fictive gait.
- This is in contrast to the dominant in vivo locomotive pattern (i.e., double tripod).
- Hence functional locomotion behavior is dependent on descending and sensory inputs.
- The presented model generates intermittent double-tripod bouts as seen empirically.

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The Metastability of the Double-Tripod Gait in Locust Locomotion

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SUMMARY
Insect locomotion represents a fundamental example of neuronal oscillating circuits generating different motor patterns or gaits by controlling their phase coordination. Walking gaits are assumed to represent stable states of the system, often modeled as coupled oscillators. This view is challenged, however, by recent experimental observations, in which in vitro locust preparations consistently converged to synchronous rhythms (all legs oscillating as one), a locomotive pattern never seen in vivo. To reconcile this inconsistency, we developed a modeling framework to capture the trade-off between the two competing mechanisms: the endogenous neuronal circuitry, expressed in vitro, and the feedback mechanisms from sensory and descending inputs, active only in vivo. We show that the ubiquitously observed double-tripod walking gait emerges precisely from this balance. The outcome is a short-lived meta-stable double-tripod gait, which transitions and alternates with stable idling, thus recovering the observed intermittent bouts of locomotion, typical of many insects' locomotion behavior.

INTRODUCTION
Six-legged locomotion is exceptionally effective, making, together with other traits, the insect family one of the most successful groups of organisms. One reason for this prominence is their remarkable capacity for dynamic stability: insects can rapidly generate adaptable movement in changing environments, employing multi-level adaptations while incorporating adaptive control mechanisms (Aminzare et al., 2018; Ayali et al., 2015b; Graham, 1985; Ritzmann and Büschges, 2007). Such locomotion patterns are driven by the insects’ central nervous system, specifically its thoracic ganglia, which contains the basic circuitry for generating movement via networks of central pattern generators (CPGs) (Arshavsky, 2003; Bucher, 2009; David et al., 2016; Hooper and Weaver, 2000; Marder and Bucher, 2001; Marder and Calabrese, 1996). The movement is further coordinated through dynamic interactions between the central nervous system and sensory inputs from the rest of the body and the environment (Ayali et al., 2015a; Borgmann et al., 2009; Büschges et al., 2011; Friesen and Cang, 2001; Fuchs et al., 2011; Puhl and Mesce, 2010; Skinner and Mulloney, 1998; Yu and Friesen, 2004; Zill et al., 2009), as well as descending inputs from the head ganglia that mediate initiation, maintenance, and modification of locomotor motor patterns (Bender et al., 2010, Gal and Libersat, 2006, Guo and Ritzmann, 2013, Kien, 1990a,b, Kien and Altman, 1984, Kien and Williams, 1983, Knebel et al., 2019, Martin et al., 2015, Mu and Ritzmann, 2008, Ridgel and Ritzmann, 2005). The relative importance of these different complementary components, central versus descending and sensory, in generating adaptable locomotion behavior is still largely an open question (Ayali et al., 2015a,b, Büschges et al., 2011, Cruse, 2002, Knebel et al., 2017, Mantziaris et al., 2017).

To address this, in our recent study we conducted a thorough investigation of the central neuronal mechanisms that control leg motor patterns in locust, a leading insect model (Knebel et al., 2017). In this study, we observed the insect’s emergent locomotion patterns, by tracking the locomotive rhythms exhibited by the insect’s nervous system in vitro; namely, we isolated the thoracic nerve chord and measured the activity of the depressor motor neurons following pharmacological activation with the muscarinic agonist pilocarpine (Knebel et al., 2017). We observed three main results (Figure 1): (1) CPGs controlling the left and right legs in the two rostral ganglia (i.e., the pro- and mesothoracic ganglia) have an inherent bilateral synchrony, whereas the CPGs in the caudal, metathoracic ganglion show an anti-phase bilateral preference; (2) each ganglion can recruit the other ganglia to adopt its own bilateral preferred coordination; (3) when all ganglia are activated simultaneously, CPGs in all ganglia tend to show synchronous oscillations, representing a spurious gait in which all six legs oscillate as one.
These results were obtained, as noted, in the absence of sensory or descending inputs and thus reflect the endogenous wiring diagram of the locust CPG network. Depending on the animal models (Hughes and Wiersma, 1960; Roberts et al., 1998; Wallén and Williams, 1984; Wilson, 1961), this network is assumed to play an important role in shaping locomotion behavior (Ayali et al., 2015a,b, Büschges et al., 2011). Although our findings agree with patterns observed in other insects (Büschges et al., 1995; Mantziaris et al., 2017), they seem to defy the common perception of the insect's hard-wired locomotive patterns, as, indeed, these recorded motor patterns do not correspond to any functional coordination pattern, or gait, of in vivo walking insects. For instance, a common gait demonstrated by many walking insects (including the locust) is the double-tripod gait: two extreme legs on one side are in phase with the middle leg of the other side, and in anti-phase with the other three, resulting in two alternating tripods (Figure 2B, right). This gait is considered extremely stable and is assumed to be partly responsible for the outstanding fast locomotion of some insects and their ability to negotiate different terrains. However, our in vitro locust preparations failed to exhibit this locomotion pattern, instead showing synchronous oscillations among all ganglia, suggesting that the locust endogenous network is, in fact, not adapted to enable double-tripod locomotion.

The study described herein was motivated by these discrepancies between the consistent, robust, functional gait seen in walking locust and the non-functional, yet seemingly consistent and stable, coordination patterns observed in the isolated in vitro preparations. To settle this disparity we use mathematical models of coupling between CPGs, to uncover the trade-off between the two driving forces of locust locomotion: (1) the natural wiring of the insect’s nervous system, which drives it toward synchronous oscillations and (2) the sensory feedback mechanisms, and their processing by higher motor centers, which correct for noise and help sustain temporarily stable bouts of locomotion. The first is present both in vitro and in vivo, whereas the second is only featured by live insects, explaining the discrepancy between the gait observed in live insects and isolated preparations. Interestingly, this balance retrieves several frequently encountered features of in vivo locomotion, specifically, the time-limited locomotive bouts (Ariel et al., 2014; Bazzazi et al., 2012; Kramer and McLaughlin, 2001), whose empirically observed distribution emerges as a natural prediction of our experimentally motivated model.

RESULTS

Modeling Locust Locomotion

Mathematical models of insect locomotion are based on data acquired by both observation and experimental manipulation of intact animals and, to a large extent, on fictive motor patterns recorded in vitro.
under isolated, controlled conditions. Early models of insect CPGs used relaxation and delay oscillators (Graham, 1977), with several more detailed descriptions subsequently developed (Cruse, 1990; Schilling et al., 2013). Other approaches span the space of central–decentralized and feedforward-feedback control (Koditschek et al., 2004, Kukillaya et al., 2009, Tóth et al., 2013a,b), but their complexity makes analysis...
difficult. Indeed, a complete insect model, with 18 joint CPGs, muscles, and sensory pathways would contain over 500 differential equations, severely limiting our ability to extract analytical insight. Hence, here we revert to a phase-reduced model (Proctor and Holmes, 2010) that collapses the complexity of the biophysical details into an effective description of a six-node coupled oscillator network, representing a highly efficient modeling scheme that can be compared directly with data (Ayali et al., 2015b; Borgmann et al., 2011; Fuchs et al., 2012; Ghigliazza and Holmes, 2004; Holmes et al., 2006; Tóth et al., 2015). Within this framework we treat each of the six legs (nodes \( n = 1, \ldots, 6 \)) as an oscillator, whose phase \( \varphi_n(t) \) is driven by

\[
\frac{d\varphi_n}{dt} = \sum_{m=1}^{6} A_{nm} H(\varphi_m - \varphi_n) + k H(\varphi_n - \varphi_n) + \nu(t). \tag{Equation 1}
\]

The matrix \( A_{nm} \) describes the coupling between the oscillating limbs, whose strength (and sign) is governed by \( \Gamma \) (Figure 2A, red), and \( H(x) \) is a 2\( \pi \)-periodic function with \( H(0) = H(\pi) = 0 \) and \( H'(\pi) < 0 < H'(0) \). Hence the first term on the right-hand side captures the impact of the insect’s endogenous wiring diagram, in the absence of any sensory feedback. To introduce feedback we include the second term on the right-hand side, in which each node receives information on the collective state of all other nodes (Figure 2A, green). This feedback is effectively treated as an additional virtual node, whose state is captured by \( f_n(\varphi(t)) = f_n(\varphi_1(t), \ldots, \varphi_6(t)) \), a collective function incorporating the instantaneous states of all other oscillators. In fictive locomotion the in vitro nervous system is isolated, sensory input is suppressed, and hence \( k = 0 \). In live insects, on the other hand, we have \( k > 0 \), allowing each node \( n \) to constantly monitor its state versus that of the virtual \( f_n(\varphi) \). The last term \( \nu(t) \approx \mathcal{N}(0, \sigma^2) \) represents the system’s internal noise, a zero-mean Gaussian noise function, in which the noise levels are controlled by the magnitude of the variance \( \sigma^2 \).

The solutions of Equation 1, \( \varphi(t) \), describe the instantaneous phases of the oscillating limb, capturing the different gaits exhibited by the insect. Note that in Equation 1 the frequency of the oscillations is absent, as, indeed, in realistic gaits, all limbs have identical frequencies, allowing us to transform to the rotating frame, where the common frequency is set to zero. Hence, locomotive gaits are fully characterized by the relative phases, as provided by \( \varphi \), and the parameters of Equation 1. Hence, observing an insect’s stable gaits we can retrieve constraints pertaining to the structure and weights of \( A_{nm} \), the magnitudes of \( \Gamma \) and \( k \), and the functional form of \( f_n(\varphi) \). Below, we use this strategy to analyze two empirically observed gaits: the synchronous oscillations measured in vitro versus the double-tripod featured in vivo.

### In Vitro Fictive Locomotive Rhythms (\( k = 0 \))

The observed rhythms in vitro consistently exhibit stable synchronous oscillations, i.e., \( \varphi_{\text{Idl}} = (0, 0, 0, 0, 0, 0) \). These oscillations have non-zero frequency, distinct from stationary idling; however, in
the context of Equation 1, where only the phases are important, such synchronous oscillations are indistinguishable from the idling state. As explained above, this empirical observation can help us retrieve information on the terms of Equation 1. Clearly, \( \varphi_{\text{Idl}} \) satisfies the criterion in Equation 2, independent of the specific structure of \( A_{nm} \), or value of \( \Gamma \), hence its fixed-point status alone provides limited insight. Its observed stability, however, offers meaningful constraints on \( A_{nm} \) and \( H(k) \), which we investigate below. Therefore, we refer to the system’s Jacobian matrix in Equation 3, which, for \( k = 0 \) and \( \varphi = \varphi_{\text{Idl}} \), takes the form

\[
J_{nm}^{\text{Idl}} = \Gamma H(0) \left[ A_{nm} - \delta_{nm} \sum_{j=1}^{6} A_{nj} \right].
\]

(Equation 5)

and calculate its six eigenvalues \( \lambda_{i}^{\text{Idl}} \), \( i = 1, \ldots, 6 \) (see Transparent Methods under Supplemental Information). The empirically observed stability of \( \varphi_{\text{Idl}} \) in vitro suggests that all \( \lambda_{i}^{\text{Idl}} \) satisfy Equation 4. Specifically, we have \( \lambda_{i}^{\text{Idl}} = -2\Gamma H(0) \), prescribing the condition that

\[
\Gamma H(0) > 0.
\]

(Equation 6)

Hence we find that the experimentally observed synchronous rhythms impose constraints on the locust endogenous wiring \( A_{nm} \), \( \Gamma \), expressed explicitly through Equation 6 and implicitly through \( J_{nm}^{\text{Idl}} \)’s remaining eigenvalues, i.e., that \( \lambda_{1}^{\text{Idl}}, \ldots, \lambda_{6}^{\text{Idl}} \) satisfy Equation 4. The challenge is that, as we next show, these conditions exclude the potential stability of other frequently observed gaits. As an example, let us specifically consider the ubiquitous double-tripod gait \( \varphi_{\text{Tri}} = (0, \pi, 0, 0, 0, \pi) \) and examine whether it can coexist with the observed stability of \( \varphi_{\text{Idl}} \). Calculating the Jacobian in Equation 3 around \( \varphi_{\text{Tri}} \), we find

\[
J_{nm}^{\text{Tri}} = \Gamma H(\pi) \left[ A_{nm} - \delta_{nm} \sum_{j=1}^{6} A_{nj} \right] = \left( H(\pi)/H(0) \right) J_{nm}^{\text{Idl}},
\]

(Equation 7)

which provides a direct mapping between \( J_{nm}^{\text{Tri}} \) and \( J_{nm}^{\text{Idl}} \), and in turn between their corresponding eigenvalues: \( \lambda_{i}^{\text{Tri}} = \left( H(\pi)/H(0) \right) \lambda_{i}^{\text{Idl}} \). The crucial point is that because \( H(\pi)/H(0) < 0 \), the condition in Equation 4 cannot be simultaneously satisfied around both gaits, as, indeed

\[
\text{Re} (\lambda_{i}^{\text{Tri}}) \leq 0 \Leftrightarrow \text{Re} (\lambda_{i}^{\text{Tri}}) \geq 0.
\]

(Equation 8)

Hence, in the absence of feedback, i.e., \( k = 0 \), \( \varphi_{\text{Idl}} \) and \( \varphi_{\text{Tri}} \) are mutually exclusive stable states of Equation 1.

This represents our first key conclusion, driven by the empirically observed synchronous rhythms: that the locust endogenous neuronal network, as described by \( A_{nm} \) and \( \Gamma \), naturally drives the insect toward idling, and, as a consequence, cannot support a stable double-tripod gait. Therefore, double-tripod can be ignited by a live insect as an initial condition, but in the presence of even the slightest noise \( \sigma(t) \), it will unconditionally decay back to the naturally stable \( \varphi_{\text{Idl}} \). This conclusion, which at first glance may seem to undermine the premise of insect locomotion, can, in fact, help explain its true nature. Indeed, live locusts do not exhibit stable locomotive gaits, but rather initiate sporadic short bouts of, e.g., double-tripod locomotion, separated by potentially long, stable periods of idling (Ariel et al., 2014; Bazazi et al., 2012; Kramer and McLaughlin, 2001). To observe this, in Figure 3A, we averaged 43 real bouts obtained from the locust, to construct a typical empirical double-tripod bout. Indeed, we find that it is best described by a transient state, sharply transitioning to idling after a limited duration.

To confront this observation with Equation 1 we constructed \( A_{nm} \) as appears in Figure 2C, setting \( \Gamma = 1 \). We then tested the dynamics of the system in Equation 1 under no feedback (\( k = 0 \)), starting at \( t = 0 \) from two initial conditions: \( \varphi(t = 0) = \varphi_{\text{Idl}} \) and \( \varphi(t = 0) = \varphi_{\text{Tri}} \). To evaluate the stability of each of these states we measured the order parameters

\[
\xi_{\text{Idl}}(t) = \frac{1}{6} \sum_{n=1}^{6} e^{\text{Re}(\lambda_{i}^{\text{Idl}}) t}, \quad \xi_{\text{Tri}}(t) = \frac{1}{6} \sum_{n=1}^{6} (-1)^{n} e^{\text{Re}(\lambda_{i}^{\text{Tri}}) t}.
\]

(Equation 9)

which range from \( \xi_{\text{Idl}} = 1 \) for a perfect \( \varphi_{\text{Idl}} \) to \( \xi_{\text{Idl}} = 0 \) in the double-tripod regime; similarly we have \( \xi_{\text{Tri}} = 1 \) for a perfect \( \varphi_{\text{Tri}} \), versus \( \xi_{\text{Tri}} = 0 \) as the double-tripod decays to idling. As expected we find that whereas \( \varphi_{\text{Idl}} \) is stable, the double-tripod gait, \( \varphi_{\text{Tri}} \), is unstable, expressed by the gradual decay of \( \xi_{\text{Tri}} \) to zero (Figure 3B).

The problem is that while the transient nature of \( \varphi_{\text{Tri}} \) is consistent with the empirically observed locomotive bouts, the temporal profile of this decay is highly unrealistic, in some cases exhibiting a long plateau at
0 < \xi_{1i} < 1 instead of the empirically observed sharp transition between walking and idling (Figures 3B and 3C, red). This type of locomotion, a continuous period of mixed gaits, is not only physically prohibitive but also stands in sharp contrast with the empirically observed behavior in Figure 3A, where the insect features a sharp transition from walking to idling. Hence we show below that feedback mechanisms play a crucial role in shaping the actual transient profile of the double-tripod gait, leading to the desired abrupt locomotive instances.

**In Vivo Locomotive Bouts (k > 0)**

To model locomotion in live locust, we enable feedback by setting \( k > 0 \) on the right-hand side of Equation 1. To sustain a double-tripod gait, the sensory input must mirror to, e.g., node 1 the current phases of nodes 3 and 5, with whom it is supposed to synchronize. This can be achieved through a feedback function of the form

\[
 f_t(\varphi) = \sum_{m=1}^{6} C_{mn} \varphi_m, \tag{Equation 10}
\]

where \( \sum_{m=1}^{6} C_{mn} = 1 \) and \( C_{mn} = 0 \) if \( n \) and \( m \) are not in the same tripod-trio (see Transparent Methods under Supplemental Information). Using Equation 10 in Equation 1 introduces feedback that reflects to each node the state of its double-tripod counterparts. For instance, node 1 receives feedback on the states of nodes 1, 3, and 5, in the form of a weighted average, with the weights determined by the arbitrary coefficients \( C_{mn} \) (Figure 2F). If 1 diverts from its coordinated motion with 3 and 5, due to internal noise, the information in \( f_t(\varphi) \) will steer it back toward its desired phase \( \varphi_1 = \varphi_3 = \varphi_5 \). Such averaging represents an internal noise correction mechanism, allowing to reinforce the double-tripod gait in the face of naturally occurring disturbances (e.g., \( n(t) \)). In a sense, it serves to re-stabilize the double-tripod gait, leading to the desired abrupt locomotive instances.

**Adding such feedback, the Jacobian in Equation 3 becomes**

\[
 J_{nm}^{id} = \Gamma H'(0) \left[ A_{nn} - \delta_{nm} \sum_{j=1}^{6} A_{nj} \right] + k H'(0)(C_{nm} - \delta_{nm}). \tag{Equation 11}
\]
simplicity, we consider below the system’s response to a single (small) perturbation \(d_4\).

Hence their sixth eigenvalue \(\lambda_6\) is the one that determines the stability of the two states: for \(J_{\text{Tri}}^{\text{nm}}\) it equals \(\lambda_6^{\text{Tri}} = -2I(H(0))\), which, following Equation 6 is, indeed, negative. For \(J_{\text{Tri}}^{\text{nm}}\) on the other hand, we have \(\lambda_6^{\text{Tri}} = -2I(H(\pi))\). Recalling that \(H(\pi)\) is opposite in sign to \(H(0)\), we conclude that \(\lambda_6^{\text{Tri}}\) is inevitably positive, and hence regardless of the strength of the feedback \(k\), \(\varphi_{\text{Tri}}\) continues to be unstable.

We have now reached our second key conclusion, that despite feedback, which we explicitly designed to reinforce \(\varphi_{\text{Tri}}\), the double-tripod gait remains unstable. In a sense, we have assumed the ideal conditions for double-tripod stability, encoding through Equation 10 an intrinsic hard-wired mechanism to correct discrepancies from double-tripod motion, and yet, as long as \(\varphi_{\text{Idl}}\) is stable, double-tripod remains an unstable transient state, independent of the feedback strength \(k\). The crucial point is, however, that while in the absence of feedback \((k \to 0)\) the double-tripod bouts exhibit an irregular transient behavior (Figure 3C), the presence of feedback in the form of Equation 10 helps shape them in the desired form of time-limited sharp bursts, as observed in real insect locomotion (Figure 3A).

To demonstrate this we repeated in Figure 4 the simulation of Equation 1, this time with varying levels of feedback \(k\). Indeed, in the limit of weak feedback, i.e., \(k \to 0\), we continue to observe the non-realistic transitions to idling, a discrepancy occurring in approximately one of every two realizations (Figure 4A). As \(k\) is increased, however, the frequency of bad transitions decreases (Figure 4B), until at \(k \geq \Gamma\) we observe perfect metastable double-tripod bouts, all of which have roughly equal duration (Figure 4C, green).

Each realization features a clean and stable double-tripod instance, \(\xi_{\text{Tri}}(t) = 1\), terminated by a sudden sharp transition to stable idling, \(\xi_{\text{Tri}}(t) = 0\). The resulting bouts, indeed, successfully recover the observed structure of the real in vivo locomotive bout (blue).

To systematically assess the performance of our model we measured the probability density \(P(T)\) for a tripod bout to have duration \(T + \Delta T\). For \(k = 0\) we obtain a multi-modal distribution (Figure 4D), with a bounded density of good bouts (green) versus separated peaks of bad irregular bouts (red). As \(k\) is increased the density of irregular bouts decreases (Figure 4E), until at \(k = \Gamma\) it vanishes completely, as predicted (Figure 4F). Under these conditions we find that \(P(T)\) is well fit by an exponential distribution (solid line), indicating that most locomotive bouts are of similar duration. We also extracted \(P(T)\) from our empirically measured sample of locust bouts, finding that it, indeed, features the predicted exponential form (blue squares), an additional independent corroboration for our proposed model.

In Figure 4H we show the resulting locomotive bouts (solid line), in which at random instances the locust initiates a double-tripod gait, which then relaxes to idling via Equation 1, exhibiting realistic locomotive patterns.

**Origins of the Metastable Locomotive Bouts**

To understand the roots of the observed locomotion patterns, consider the behavior of Equation 1, under the initial condition \(\varphi(t = 0) = \varphi_{\text{Tri}}\), i.e., double-tripod. Being an unstable state, even the slightest perturbation \(\delta\varphi(t)\), an inevitable consequence of the noise \(\kappa(t)\), will cause the system to divert to the stable \(\varphi_{\text{Idl}}\), hence leading from \(\xi_{\text{Tri}}(t = 0) = 1\) to \(\xi_{\text{Tri}}(t \to \infty) = 0\). The important point, however, is not the transition itself, which is unavoidable, but rather the form of this transition, sharp or irregular. In reality, such perturbations are continuously affecting the system because of the stochastic term \(\kappa(t)\); however, for simplicity, we consider below the system’s response to a single (small) perturbation \(\delta\varphi(0)\) introduced at \(t = 0\). This allows us to track the evolution of \(\delta\varphi(t)\) through the linearized Equation 1, which takes the form

\[
\frac{d\delta\varphi}{dt} = \sum_{m=1}^{6} J_{\text{Tri}}^{\text{nm}} \delta\varphi_m(t),
\]

(Equation 13)

where \(J_{\text{Tri}}^{\text{nm}}\) is the system’s Jacobian taken from Equation 12. Its solution is

\[
\delta\varphi(t) = \sum_{j=1}^{6} B_j \varphi_j \exp(\lambda_j^\text{Tri} t),
\]

(Equation 14)
Figure 4. Sharp Locomotive Bouts Shaped by Feedback

We tested the patterns of double-tripod locomotive bouts under different levels of sensory feedback $k$. For small $k$, $k=0$ (A), and $k=0.5$ (B) we continue to observe irregular transitions (red) from double tripod to idling. The number of bad transitions decreases as $k$ is increased. The duration of each bout is defined at the point at which $\xi_{\text{Tri}}(t) = 0.15$ for the last time, namely, when it crosses the black dashed lines.

(C) For $k=1 = \Gamma$ we obtain perfect bouts (green), featuring a metastable double-tripod gait that terminates with a sudden transition to idling, as observed in empirical patterns of locomotion. Here the duration of each bout is defined as the half-life, marked by the dashed line at $\xi_{\text{Tri}}(t) = 0.5$. For comparison, we also show the average empirical bout $v$ versus $t$ (also shown in Figure 3A), where we normalized $v(t=0) = 1$ (blue). We find that our simulated bouts successfully retrieve the empirically observed locomotion.

(D) The probability density $P(T)$ versus $T$ for a bout of duration $\tau \in (T, T + dT)$ as extracted from $10^5$ realizations for $k = 0$. A significant fraction of bad transitions (red peaks) is observed, corresponding to the long irregular gaits (red) featured in (A).

(E) $P(T)$ versus $T$ for $k=0.5$. Irregular gaits (red peak) continue to be observed.

(F) For $k=1 = \Gamma$ the density $P(T)$ (green circles) no longer exhibits the bad peaks, instead featuring an exponential tail (solid line). This indicates that now all bouts follow a regular bounded form, as observed in (C). We also measured $P(T)$ from our empirical bouts (blue squares), finding that real locomotion is indeed, characterized by an exponential distribution, as predicted by our model. Note that in our simulations $T$ has arbitrary units (bottom horizontal axis), whereas in the empirical measurements $T$ is measured in seconds (top horizontal axis). Therefore, we do not expect the two distributions (green, blue) to fully coincide, only to layout on the same linear slope.

(G) The resulting locomotive bouts for $k = 1 = \Gamma$, featuring regular bounded double-tripod instances separated by varying periods of idling. In our simulations we used $\Gamma = 1$, $k$ as it appears in each panel, $\sigma = 0.01$, and $A_{\text{emp}}$ as described in Transparent Methods, under Supplemental Information.
where \( \overrightarrow{\varphi}(0) = \sum_{i=1}^{6} B_i \overrightarrow{\nu}_i \) is the eigenvector decomposition of the perturbation at \( t = 0 \) in the base \( \overrightarrow{\nu}_i \), spanned by \( J_n \) ’s eigenvectors (see Transparent Methods under Supplemental Information). To assess the magnitude of the coefficients \( B_i \), we consider the size of the perturbation \( \delta \overrightarrow{\varphi}(0) \), which, driven by the system’s intrinsic noise levels, \( \nu(t) \), has each of its components extracted from \( \delta \theta_n(0) \sim \cdot \cdot \cdot (0, \nu^2) \). This provides, on average, \( \delta \theta_n(0) \sim \pm \sigma \), and hence \( |\delta \theta_n(0)| \sim \sigma^2 \). Using our eigenvector decomposition, this translates to

\[
\sum_{i=1}^{6} B_i^2 \sim 6\sigma^2 \Rightarrow B_i \sim \sigma. \tag{Equation 15}
\]

linking \( B_i \) to the system’s intrinsic levels of noise. The only exception is \( B_6 \), which precedes the eigenvector \( \overrightarrow{\nu}_6 = (1/\sqrt{6})(1.1.1.1.1.1)^T \), associated with the vanishing \( \lambda_6^{(n)} = 0 \). This vector represents a uniform shift in all phases, having no impact on the gait, which is only characterized by the relative terms \( \sigma ^{\overrightarrow{\nu}_6} \). Therefore, we only focus on perturbations orthogonal to \( \overrightarrow{\nu}_6 \), ignoring this trivial uniform phase shift, namely, we set \( B_6 = 0 \) in Equation 14. We are thus left with only five terms on the right-hand side of Equation 14, \( i = 1, \ldots, 4 \) and \( i = 6 \) (see Transparent Methods under Supplemental Information).

Let us first analyze the first terms \( i = 1, \ldots, 4 \). For sufficiently strong feedback \( k \geq \Gamma \), we have, for these four terms \( \lambda_6^{(n)} < 0 \), leading to a rapid exponential decay with a typical timescale of \( \tau_0 \sim k^{-1} \), small in the limit of large \( k \) (see Transparent Methods under Supplemental Information). This represents a rapid convergence to zero, which leaves Equation 14, after a brief transient time, dominated by the single positive eigenvalue \( \lambda_6^{(n)} = -2\Gamma \theta^2(\pi) > 0 \), whose associated eigenvector is \( \overrightarrow{\nu}_6 = (1/\sqrt{6})(1,-1,-1,-1,1,1)^T \). As a result, Equation 14 converges to

\[
\delta \overrightarrow{\varphi}(t) \sim \sigma \overrightarrow{\nu}_6 e^{\nu_6 t}, \tag{Equation 16}
\]

where

\[
\tau_6 = \frac{1}{\lambda_6} = \frac{-1}{2\Gamma \theta^2(\pi)}, \tag{Equation 17}
\]

and where we used Equation 15 to replace \( B_i \) with \( \sigma \). The timescale \( \tau_6 \), associated with \( \overrightarrow{\nu}_6 \), controls the rate of the exponential divergence that drives the system away from the perturbative regime, and toward the stable \( \overrightarrow{\varphi}_{id} \). We, therefore, find that the unstable \( \overrightarrow{\varphi}_{un} \), exhibits, in response to noise, two separate timescales \( \tau_6 < \tau_0 \). The first, \( \tau_0 \), represents the rapidly decaying components of \( \delta \overrightarrow{\varphi}(t) \), driving the system back toward \( \overrightarrow{\varphi}_{un} \). Once these short-lived components decay, the system is driven by the remaining component \( \overrightarrow{\nu}_6 \), diverging away from double-tripod at a rate \( \tau_6 \).

**Metastability**

Equation 16 describes the temporal behavior of the perturbation \( \delta \overrightarrow{\varphi}(t) \), however the true transient profile of the double-tripod bout, and its decay to idling, are captured by \( \tilde{\tilde{\xi}}_{un}(t) \) and \( \tilde{\tilde{\xi}}_{id}(t) \) of Equation 9. Taking the state of system to be \( \overrightarrow{\varphi}_{un} + \delta \overrightarrow{\varphi}(t) \) and extracting \( \delta \overrightarrow{\varphi}(t) \) from Equation 16, we can write these two order parameters as (see Transparent Methods under Supplemental Information)

\[
\tilde{\tilde{\xi}}_{un}(t) = \frac{1}{6} \left| \sum_{n=1}^{6} \exp \left( -i \frac{-1}{\sqrt{6}} \sigma e^{\nu_6 t} \right) \right| = \frac{1}{6} \left| \sum_{n=1}^{6} \left( 1 - i \frac{-1}{\sqrt{6}} \sigma e^{\nu_6 t} \right) \right| = 1, \tag{Equation 18}\]

and

\[
\tilde{\tilde{\xi}}_{id}(t) = \frac{1}{6} \left| \sum_{n=1}^{6} \left( -1 \right)^n \exp \left( -i \frac{-1}{\sqrt{6}} \sigma e^{\nu_6 t} \right) \right| = \frac{1}{6} \left| \sum_{n=1}^{6} \left( 1 - i \frac{1}{\sqrt{6}} \sigma e^{\nu_6 t} \right) \right| = \frac{\sigma e^{\nu_6 t}}{\sqrt{6}}, \tag{Equation 19}\]

where we have used the linear approximation \( e^{-it} \approx 1 - it \) to obtain the estimates on the right-hand side of both expressions. These estimates are valid as long as \( \sigma e^{\nu_6 t} \ll 1 \), or equivalently, as long as \( t < \tau \), where

\[
\tau = -\tau_6 \ln \sigma = \frac{1}{2\Gamma \theta^2(\pi)} \ln \sigma, \tag{Equation 20}\]

and where we have used Equation 17 to express \( \tau_6 \).

Equations 18, 19, and 20, our final prediction, represent the temporal profile of the transition from an initial double-tripod gait to idling, as predicted by Equation 1. They emerge from the negotiation between the
Figure 5. The Lifetime of a Double-Tripod Bout
We measured the average duration ($\tau$) (half-life, as in Figure 4C) as obtained from Equation 1 under different coupling strengths $\Gamma$ and noise levels $\sigma$. (A) $\tau$ versus $\Gamma$ (circles) features the scaling $\tau \sim \Gamma^{-1}$ (solid line), as predicted by Equation 20. (B) $\tau$ versus $\sigma$ (circles) shows a logarithmic decline, once again in agreement with Equation 20. In our simulations we used $k = 1$, $\Gamma$ and $\sigma$ as they appear in each panel, and $A_{in}$ as described in Transparent Methods, under Supplemental Information; each data point (circle) represents an average over 100 realizations. For each data point we calculated the error as the 95% confidence interval, namely, $\text{Err} = 2 \text{STD}/\sqrt{n}$, where STD is the standard deviation extracted from the 100 realizations and $n = 100$. The resulting errors are not shown, as they were found to be negligibly small, fitting within the green circles.

DISCUSSION
Modeling insect locomotion often relies on stable gaits, seeking the parameters in Equation 1 that can offer, e.g., a stable double-tripod state. Here, we have shown, based on empirical observations, that this description must be refined: on the one hand $A_{in}$, the insect’s internal wiring, is tuned toward idling, ensuring that all instances of locomotive bouts converge to the rest state $\varphi_{id}$. On the other hand, once $\varphi_{Tri}$ is initiated, the insect’s encoded feedback mechanisms, Equation 10, correct for noise, and help sustain a temporarily stable locomotive bout. The relative strengths of these two competing forces is captured by the parameters $k$ and $\Gamma$ in Equation 1, whose magnitude determines the role of descending inputs versus that of the internal CPG network. This suggests a spectrum of potential behaviors, from animals whose locomotion is internally wired, i.e., CPG driven, to ones that are controlled by environmental feedback. Our model predicts that the latter will feature extremely weak fictive rhythms in vitro, absent sensory feedback, whereas the former will exhibit internally wired gaits, such as $\varphi_{Tri}$, even in vitro. Encouraging indications in this direction have been recently observed on the stick insect (Ayali et al., 2015a; Mantziaris et al., 2017), which seems to be environment driven, versus the cockroach, which is likely CPG driven (Ayali et al., 2015a; David et al., 2016; Fuchs et al., 2011). Our experiment-based analysis here places the locust between these two extremes with $k$ of comparable magnitude to $\Gamma$.

This point brings us back to the biology of insect locomotion, and specifically the double-tripod gait. This unique gait is prevalent among all insect models studied thus far: from the slow walking stick
insect, where it is mostly observed in young immature animals, to the fast cockroach, where the double-tripod gait is the principal gait used in practically all walking speeds and environmental contexts (Ayali et al., 2015a). Similarly, it was found in moth (Johnston and Levine, 1996), as well as in the fly (Wosnitza et al., 2012). All these different insects likely share basic features of their locomotion wiring diagram (Ayali et al., 2015a), yet they may differ significantly in other attributes, e.g., their intrinsic noise level, or their internal balance between CPGs and sensory feedback. Hence, our modeling approach can provide insight beyond the locust, exposing principles that are generally applicable to insect locomotion. In a broader perspective, metastable states play an important role in many neuronal tasks, which assume a temporary excitation, later relaxing to the globally stable state (Fukai, 1990; Haldeman and Beggs, 2005; Kelso and Tognoli, 2007). Such processes allow organisms to transition to a desired state, e.g., walking, but at the same time avoid fixating at that state for longer than desirable.

Going beyond insects, intermittent motion is a common feature of animal locomotion in general (Kramer and McLaughlin, 2001). Although this intriguing phenomenon has attracted much attention in the behavioral and behavioral ecology fields, this present work is a first attempt to provide a rigorous dynamic model to account for this unique behavior. Last, to the best of our knowledge, intermittent motion as a dominant feature has thus far not been incorporated in bio-inspired technology, and specifically in the growing field of insect-inspired robotics (Aoi et al., 2017; Delcomyn, 2004; Minati et al., 2018; Ritzmann et al., 2000; Schmitt and Holmes, 2001). The current work may provide the means to embark on this and other such interdisciplinary endeavors.

Limitations of the Study
The experimental data that served as the basis of the current work were obtained from experiments conducted in vitro. As previously discussed in much detail (Knebel et al., 2017, 2019), although this reductionist approach is common and has been very advantageous in the study of neuronal oscillators, there are also some clear limitations to this approach, namely, that cautiousness is advised when directly applying the conclusions to the intact behaving animal. Similarly, this study was based on data extracted exclusively from the locust. Analogous results have been observed using other insect preparations, and, as discussed above, present a case for generalization. Still, as with any such case, oversimplification of the biological complexity should be avoided. Our mathematical analysis condenses the multiple microscopic details of locomotion into a reduced description of phase-coupled oscillators. Although this provides insight into the high-level characteristics of locomotion, e.g., the trade-off between internal and external driving mechanisms, it overlooks the complexity of the microscopic interacting components. Therefore, our modeling framework may provide limited insight on the specific biological mechanisms underlying locomotion.

DATA AVAILABILITY
All codes to reproduce the results presented here are freely accessible at https://github.com/eranreches/The-metastability-of-the-double-tripod-gait-in-locust-locomotion. Experimental data are available upon reasonable request.

METHODS
All methods can be found in the accompanying Transparent Methods supplemental file.

SUPPLEMENTAL INFORMATION
Supplemental Information includes Transparent Methods and two figures and can be found with this article online at https://doi.org/10.1016/j.isci.2019.01.002.

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AUTHOR CONTRIBUTIONS
All authors designed and conducted the research; E.R. performed the analytical and numerical work under the supervision of B.B.; D.K. and J.R. conducted the experiments under the supervision of A.A.

DECLARATION OF INTERESTS
The authors declare no competing interests.

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Supplemental Information

The Metastability of the Double-Tripod Gait in Locust Locomotion

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Figure S1. Related to Figure 3b. Reduction to two phase-oscillators. (a) Collapsing the double-tripod gait into two effective oscillators $\varphi_L$ (blue) and $\varphi_R$ (orange). The relative phase $\Delta \varphi = \varphi_{LR} = 0$ in idling and $\pi$ in double-tripod. (b) – (c) The coupling $-\Gamma H_\Delta$ vs. $\Delta \varphi = \varphi_{LR}$ under positive (green) and negative (red) coupling. The dynamically stable gaits appear as solid circles; the unstable ones appear as empty circles. Double-tripod ($\pi$) and idling ($0, 2\pi$) are mutually exclusive stable gaits, the former stable under $\Gamma < 0$, whereas the latter under $\Gamma > 0$. 
Figure S2. Related to Figure 3b. Stability analysis in gait-space. (a) We selected 100 random initial conditions and mapped their trajectories in the three dimensional gait-space. We find that all initial states are drawn to the single basin of attraction, centered around (1,0,0), i.e. idling. To help follow the paths we use a color code, where \((\xi_{\text{Idl}}, \xi_{\text{Tri}}, \xi_{\text{Pace}})\) are represented by (red, green, blue). (b) – (c) Projections of all trajectories to the two dimensional sub-spaces \((\xi_{\text{Idl}}, \xi_{\text{Tri}})\) and \((\xi_{\text{Idl}}, \xi_{\text{Pace}})\).
Transparent Methods

Network construction. To construct $A_{nm}$ we used the wiring diagram of Fig. 2c, in which there are a total of 14 directed links, allowing us broad degrees of freedom to select all link weights. We then incorporate several constraints that limit these degrees of freedom: (i) Left right symmetry, reduces the independent parameters to seven; (ii) We take the front and middle contralateral links to be identical, i.e. $l_1 = l_2$, distinguishing only the back contralateral link. This reduction was indicated by recent experimental observations (Knebel et al. 2017); (iii) As explained below, we normalize the sum of incoming rates to each oscillator (in-degree) to unity (Ghigliazza and Holmes 2004). Together, we remain with three independent parameters in $A_{nm}$, $l_1$, $l_3$ and $b_1$, providing

$$A_{nm} = \begin{pmatrix} 0 & f_1 & 0 & l_1 & 0 & 0 \\ b_1 & 0 & f_2 & 0 & l_1 & 0 \\ 0 & b_2 & 0 & 0 & 0 & l_3 \\ l_1 & 0 & 0 & 0 & f_1 & 0 \\ 0 & l_1 & 0 & b_1 & 0 & f_2 \\ 0 & 0 & l_3 & 0 & b_2 & 0 \end{pmatrix}, \quad (S1)$$

where $f_1 = 1 - l_1$, $f_2 = 1 - b_1 - l_1$ and $b_2 = 1 - l_3$. In our simulations we set $l_1 = 0.2$, $l_3 = -0.2$ and $b_1 = 0.1$, reflecting the experimental observation that the CPGs controlling the left and right legs in the two rostral ganglia (i.e. the pro- and mesothoracic ganglia) have an inherent bi-lateral synchrony, whereas the caudal ones (i.e. the metathoracic ganglion) exhibit anti-phase bi-lateral preference (Knebel et al. 2017).

Coupling function and feedback. In our simulations we selected $H(x) = \sin x$, trivially satisfying the required conditions: $H(x)$ is $2\pi$ periodic, $H(0) = H(\pi) = 0$ and $H'(\pi) < 0 < H'(0)$. The feedback in Eq. (10) is set to

$$f_{i=1,3,5} (\varphi_1, \ldots, \varphi_6) = \frac{\varphi_1 + \varphi_3 + \varphi_5}{3} \quad (S2)$$

$$f_{i=2,4,6} (\varphi_1, \ldots, \varphi_6) = \frac{\varphi_2 + \varphi_4 + \varphi_6}{3}, \quad (S3)$$

reflecting to each node the average phase over its double-tripod counterparts, in effect driving the node towards its desired phase, helping sustain the double-tripod gait in the face of noise.
Spectrum analysis. Under these conditions, the eigenvalues of the Jacobian matrix in Eq. (3) are: around $\varphi_{\text{Idl}}$

$$
\lambda_1^{\text{Idl}} = -kH'(0) + \Gamma H'(0) \left[ l_1 + \frac{l_3}{2} - \frac{3}{2} + \sqrt{\frac{4b_1(l_3 - l_1) + (l_3 - 1)^2}{2}} \right]
$$

$$
\lambda_2^{\text{Idl}} = -kH'(0) + \Gamma H'(0) \left[ l_1 + \frac{l_3}{2} - \frac{3}{2} - \sqrt{\frac{4b_1(l_3 - l_1) + (l_3 - 1)^2}{2}} \right]
$$

$$
\lambda_3^{\text{Idl}} = -kH'(0) + \Gamma H'(0) \left[ -l_1 - \frac{l_3}{2} - \frac{1}{2} + \sqrt{\frac{4b_1(l_3 - l_1) + (l_3 - 1)^2}{2}} \right]
$$

$$
\lambda_4^{\text{Idl}} = -kH'(0) + \Gamma H'(0) \left[ -l_1 - \frac{l_3}{2} - \frac{1}{2} - \sqrt{\frac{4b_1(l_3 - l_1) + (l_3 - 1)^2}{2}} \right]
$$

$$
\lambda_5^{\text{Idl}} = 0
$$

$$
\lambda_6^{\text{Idl}} = -2\Gamma H'(0),
$$

and around $\varphi_{\text{Tri}}$

$$
\lambda_1^{\text{Tri}} = -kH'(0) + \Gamma H'(\pi) \left[ l_1 + \frac{l_3}{2} - \frac{3}{2} + \sqrt{\frac{4b_1(l_3 - l_1) + (l_3 - 1)^2}{2}} \right]
$$

$$
\lambda_2^{\text{Tri}} = -kH'(0) + \Gamma H'(\pi) \left[ l_1 + \frac{l_3}{2} - \frac{3}{2} - \sqrt{\frac{4b_1(l_3 - l_1) + (l_3 - 1)^2}{2}} \right]
$$

$$
\lambda_3^{\text{Tri}} = -kH'(0) + \Gamma H'(\pi) \left[ -l_1 - \frac{l_3}{2} - \frac{1}{2} + \sqrt{\frac{4b_1(l_3 - l_1) + (l_3 - 1)^2}{2}} \right]
$$

$$
\lambda_4^{\text{Tri}} = -kH'(0) + \Gamma H'(\pi) \left[ -l_1 - \frac{l_3}{2} - \frac{1}{2} - \sqrt{\frac{4b_1(l_3 - l_1) + (l_3 - 1)^2}{2}} \right]
$$

$$
\lambda_5^{\text{Tri}} = 0
$$

$$
\lambda_6^{\text{Tri}} = -2\Gamma H'(\pi).
$$

• Eigenvalues $\lambda_1^{\text{Tri}}, \ldots, \lambda_4^{\text{Tri}}$. The first four eigenvalues around $\varphi_{\text{Tri}}$ have the following structure: $k$ is multiplied by the negative $-H'(0)$ and $\Gamma$ is multiplied by a product of two terms, the negative $H'(\pi)$ and the function $Z_i(b_1, l_1, l_3)$ ($i, 1, \ldots, 4$) comprising the elements of $A_{nm}$. For example, in $\lambda_1^{\text{Tri}}$ we have $Z_i(b_1, l_1, l_3) = l_1 + l_3/2 - 3/2 + \sqrt{4b_1(l_3 - l_1) + (l_3 - 1)^2}/2$. With this structure it is guaranteed that if $Z_i \geq 0$ then $\lambda_i^{\text{Tri}} < 0$. Under these conditions $\varphi_{\text{Tri}}$ is stable with respect to perturbations in the $\vec{v}_i$ direction. If however $Z_i < 0$, the corresponding
The eigenvalue is still negative if
\[ k > \Gamma \frac{H'(\pi)}{H'(0)} Z_i(b_1, l_1, l_3). \] (S4)

The fraction on the right hand side is of order unity, being exactly one in case \( H(x) = \sin x \).

The last term \( Z_i \) is also typically of order unity, since all its components \( b_1, l_1, l_3 \), are extracted from \( A_{nm} \), which is normalized such than \( \sum_{m=1}^{6} A_{nm} = 1 \). Hence, excluding extreme cases, most of \( A_{nm} \)’s entries, and therefore also \( Z_i(b_1, l_1, l_3) \), are of the order one. It thus follows that \( \lambda_i^{\text{Tri}} < 0 \) for \( i = 1, \ldots, 4 \) as long as \( k \gtrsim \Gamma \), as appears in the main text.

Eigenvalue \( \lambda_5^{\text{Tri}} \). This eigenvalue corresponds to the constant eigenvector \( \vec{v}_5 = (1, 1, 1, 1, 1) / \sqrt{6} \). A perturbation in the direction of \( \vec{v}_5 \) represents a uniform shift in all phases, having no effect on the relative phases, and hence has no bearing on state of the system. Such perturbation, which does not affect the insect’s gait, should not grow or decay in time, but remain constant, as indeed ensured by the fact that \( \lambda_5^{\text{Tri}} = \lambda_5^{\text{Idl}} = 0 \).

Normalization of \( C_{nm} \) in \( f_n(\vec{\varphi}) \). As explained above, the dynamics Eq. (1), must be invariant under a uniform phase shift \( \delta \vec{\varphi} \propto (1, 1, 1, 1, 1) ^T \), as such shift conserves all relative phases between the oscillators. This is only ensured if \( \lambda_5^{\text{Tri}} = \lambda_5^{\text{Idl}} = 0 \). Therefore, both Jacobian matrices in Eqs. (11) and (12) must satisfy \( J \cdot \vec{v}_5 = 0 \), mapping to \( \sum_{m=1}^{6} J_{nm} = 0 \) (where we use \( J \) to denote \( J^{\text{Idl}} \) or \( J^{\text{Tri}} \), respectively). This, in turn, leads to \( \sum_{m=1}^{6} (C_{nm} - \delta_{nm}) = 0 \), and hence to the normalization condition \( \sum_{m=1}^{6} C_{nm} = 1 \).

Dimension reduction (Fig. S1). To specifically analyze the behavior of Eq. (1) around \( \vec{\varphi}_{\text{Idl}} \) and \( \vec{\varphi}_{\text{Tri}} \) we use the unique symmetries of these gaits to reduce the six-dimensional description to a single equation. Consider \( \Delta \varphi = f_1(\vec{\varphi}) - f_2(\vec{\varphi}) \), where \( f_i(\vec{\varphi}) \) are taken from Eqs. (S2) and (S3). This parameter captures the relative phases between the two tripod-trios, being \( \Delta \varphi = 0, 2\pi \) for idling and \( \Delta \varphi = \pi \) for double-tripod. Summing over the relevant equations, we use Eq. (1) to construct a direct equation for \( \Delta \varphi \) (under \( k = 0 \), obtaining
\[
\frac{d\Delta \varphi}{dt} = -\Gamma H_{\Delta}(\Delta \varphi),
\] (S5)
where $H_{\Delta}(\Delta \phi) = H(\Delta \phi) - H(-\Delta \phi)$. The stable fixed points satisfy $H_{\Delta}(\Delta \phi) = 0$ and $-\Gamma H'_{\Delta}(\Delta \phi) < 0$. Since $H(x)$ and $H'(x)$ are both $2\pi$ periodic we have $H(j \pi) = H(-j \pi)$ for all $j = 0, 1, \ldots$, providing $H'_{\Delta}(0) = 2H'(0)$ and $H'_{\Delta}(\pi) = 2H'(\pi)$. We, therefore, recover the stability criteria: for idling we have $-2\Gamma H'(0) < 0$ and for double-tripod we require $-2\Gamma H'(\pi) < 0$. As explained in the main text, these represent two mutually exclusive conditions.

The basin of attraction of the idling gait (Fig. S2). The two competing states we consider - $\vec{\phi}_{\text{idl}}$ vs. $\vec{\phi}_{\text{Tri}}$ – are characterized by unique symmetries that allow rigorous analytical treatment, either as we do in the paper, or through the reduction to a two-phase system. Most generally, however, it is difficult to analyze the complete six-phase system, and the reduction to two phases is not necessarily relevant, absent the special symmetries of $\vec{\phi}_{\text{idl}}$ and $\vec{\phi}_{\text{Tri}}$. Hence, in principle, there might be an additional stable fixed-point $\vec{\phi}$ besides $\vec{\phi}_{\text{idl}}$, that our analysis overlooks. To examine this, as a first step, we tested stability, specifically for unique gaits, such as pace or gallop, finding that they, too are unstable. This, of course, cannot exclude the potential stability of any arbitrary state $\vec{\phi}$. On the other hand, most arbitrary phase vectors $\vec{\phi}$ do not constitute a meaningful gait anyhow, and hence even if they are stable, it seems that they are likely not featured by real insects. Still, for completeness, we used numerical simulations to examine the phase-space, and test for the existence of additional stable fixed-points. To reduce the six-dimensional space to a presentable two or three-dimensions, we consider three gaits: $\vec{\phi}_{\text{idl}} = (0, 0, 0, 0, 0, 0)^T$, $\vec{\phi}_{\text{Tri}} = (0, \pi, 0, \pi, 0, \pi)^T$ and $\vec{\phi}_{\text{Pace}} = (0, 0, 0, \pi, \pi, \pi)^T$, which we characterize by

$$
\xi_{\text{idl}}(t) = \frac{1}{6} \left| \sum_{n=1}^{6} e^{i\phi_n(t)} \right|, \quad \xi_{\text{Tri}}(t) = \frac{1}{6} \left| \sum_{n=1}^{6} (-1)^n e^{i\phi_n(t)} \right|,
$$

$$
\xi_{\text{Pace}}(t) = \frac{1}{6} \left| \sum_{n=1}^{3} e^{i\phi_n(t)} + \sum_{n=4}^{6} (-1)^n e^{i\phi_n(t)} \right|,
$$

all ranging from zero, when the gait is absent, to unity for a perfect idling/double-tripod/pace gait. Starting from an arbitrary (six-dimensional) state $\vec{\phi}$ we track the trajectory of the system in the reduced three-dimensional gait-space $(\xi_{\text{idl}}, \xi_{\text{Tri}}, \xi_{\text{Pace}})$. We find in Fig. S2 that all such trajectories lead to $(1, 0, 0)$, i.e. a perfect idling state. Had there been another basin of attraction $\vec{\phi}$, one would expect that some of the initial conditions
would lead to it, which in gait-space would be expressed by an arbitrary mixture \((a, b, c)\). Here we studied 100 random initial conditions, including also the specific initial conditions of a perfect double-tripod, given by \((ξ_{\text{Idl}}, ξ_{\text{Tri}}, ξ_{\text{Pace}}) = (0, 1, 1/3)\) and a perfect pace, \(i.e.\) \((ξ_{\text{Idl}}, ξ_{\text{Tri}}, ξ_{\text{Pace}}) = (0, 1/3, 1)\). As the figure indicates, we find no other attractor than \(\bar{ϕ}_{\text{Idl}}\), namely \((1, 0, 0)\) in gait-space. Note that while our initial conditions span the entire six-dimensional phase-space, in this reduced gait-space some areas are avoided. For instance, one cannot have, for any arbitrary selection of \(ϕ\), the points \((1, 1, 1)\) or \((0, 0, 0)\) in this gait-space, therefore our initial conditions and their ensuing trajectories systematically avoid the corners of this space. Also, while in the complete six dimensional space trajectories cannot intersect, in the projection to gait-space, such intersections are possible. Together, this analysis indicates that idling is indeed the unique steady state of the system. We emphasize again that, while excluding any other gait is not possible analytically, and hence our reliance on numerical analysis, the specific exclusion of the double-tripod stability is, in fact, an analytical result, independent of the specific choice of parameters.

**Numerical simulations.** To simulate the behavior of Eq. (1) we used an Euler stepper. The stochastic term was treated using the Euler-Maruyama scheme, in which \(ν(t)\) is generated via \(dν = Xσ\sqrt{dt}\), where \(X ∼ N(0, 1)\) is a Normally distributed random variable, and \(dt\) is the differential time-step of the Euler algorithm.

**The order parameters \(ξ_{\text{Idl}}\) and \(ξ_{\text{Tri}}\).** To derive \(ξ_{\text{Idl}}\) and \(ξ_{\text{Tri}}\) in Eqs. (18) and (19) we introduce the perturbed state \(\bar{ϕ}_{\text{Tri}} + δϕ(t)\) into Eq. (9). For \(ξ_{\text{Tri}}\) we have

\[
ξ_{\text{Tri}} = \frac{1}{6} \left| \sum_{n=1}^{6} (-1)^n e^{iϕ_n} e^{iδϕ_n(t)} \right|.
\]

Using \(\bar{ϕ}_{\text{Tri}} = (\pi, 0, \pi, 0, \pi, 0)^T\), we have \(e^{iϕ_n} = (-1)^n\), which together with the existing factor of \((-1)^n\) in Eq. (S7) leads to \(ξ_{\text{Tri}} = 1/6|\sum_{n=1}^{6} e^{iδϕ_n(t)}|\). Next we use Eq. (16), with \(\tilde{v}_6 = (1/\sqrt{6})(1, -1, 1, -1, 1, -1)^T\), to arrive at the result of Eq. (18). A similar derivation leads to \(ξ_{\text{Idl}}\) in Eq. (19).

**Empirical bouts.** To quantitatively measure walking bouts in living locusts, 50 animals were placed in a round arena (diameter of 60 cm). A video camera monitored their activity from above. Subsequently, manual tracking of the locusts was conducted for ~ 6 minutes
of the movie. The distance moved between subsequent frames was used for estimating the locusts’ instantaneous speed, allowing, at 29 frames-per-second, a temporal resolution of \( \sim 3 \times 10^{-2} \) seconds. Walking termination profile was calculated as follows. Walking was defined as a movement exceeding 0.5 cm/s. Only walking bouts longer than 5 seconds followed by a pause of at least 2 seconds were analyzed, providing a total of 43 individual bouts. The speed profiles of all selected bouts were calculated and overlaid by fixing their pause onsets across each other (first frame in which the speed crossed 0.5 cm/s at the end of the bout). In this alignment all bouts terminate concurrently, allowing us to meaningfully capture the (average) profile of the termination. To obtain the plot of Fig. 3a the profiles were averaged at each time point \( t \). To estimate the error at \( t \) we used 95% confidence intervals, \( \text{Err} \approx 2\sigma(t)/\sqrt{n(t)} \), where \( \sigma(t) \) is the standard deviation of the sample at time \( t \) and \( n(t) \) is the size of each sample, here being \( n(t) = 43 \) for all \( t \). To measure \( P(T) \) in Fig. 4f (blue), we used a more comprehensive set of empirical bouts, to accumulate a sufficient statistical sample. Hence, we collected all walking bouts for which \( \tau \geq 1 \text{sec} \), separated by a pause of similar duration. This results in a sample of 307 bouts, ranging from \( \sim 1 \) to 35 seconds.
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