Analyzing the Interplay Between Local CPG Activity and Sensory Signals for Inter-leg Coordination in *Drosophila*

William Nourse[1(✉)], Nicholas Szczecinski[1,2], Moritz Haustein[2], Till Bockemühl[2], Ansgar Büschges[2], and Roger Quinn[1]

[1] Case Western Reserve Universtiy, Cleveland, OH 44106, USA
`nourse@case.edu`
[2] Zoological Institute, University of Cologne, Cologne 50674, Germany

Abstract. Leg coordination is important for walking robots. Insects are able to effectively walk despite having small metabolisms and size, and understanding the neural mechanisms which govern their walking could prove useful for improving legged robots. In order to explore the possible neural systems responsible for inter-leg coordination, leg positional data for walking fruit flies of the species Drosophila melanogaster was recorded, where one individual leg was amputated at the base of the tibia. These experiments have shown that when amputated, the remaining stump oscillates in a speed-dependent manner. At low walking speeds there is a wide range of possible stump periods, and this variance collapses down to a minimum as walking speed increases. We believe this behavior can be explained by noisy pattern generation networks (CPGs) within the legs, with intra-leg load feedback and inter-leg global signals stabilizing the network. In this paper, this biological data will be analyzed so that a simplified neuromechanical model can be designed in order to explain this behavior.

Keywords: Drosophila · Sensory feedback · Inter-leg coordination

1 Introduction

A robot with the neuromechanical design of an insect could be successful in walking, and accordingly many robots have been designed to mimic the behavior seen in insects and arthropods, including the praying mantis [4] and lobster [1]. One area of active study within insect locomotion is inter-leg coordination, where behavioral studies on stick insects [3] and fruit flies [5] have been performed. Previous work has studied the behavior of walking flies where various legs were amputated [2]. We aim to further analyze this behavior observed in *Drosophila* so that we may design better walking controllers for legged robots.

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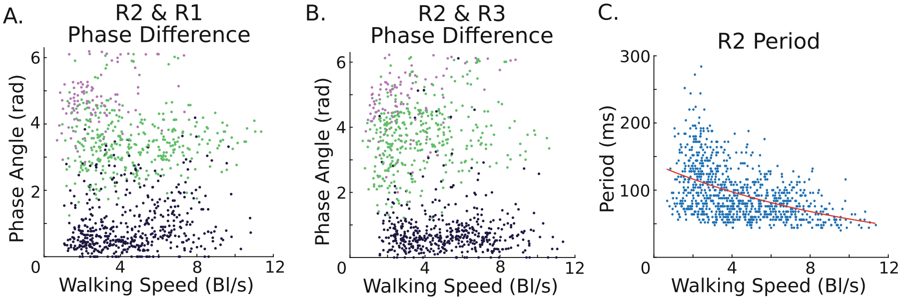

Fig. 1. R2 phase and period with respect to walking speed in body-lengths per second. Each data point corresponds to a single DEP event of R2. Shown in (A) and (B) are the phase locations of the specific DEP between the previous and next AEP in R1 or R3, respectively. Color refers to the DEP timing, with black corresponding to the first DEP after the reference AEP, green to the second, and purple to the third and beyond (color figure available online). Shown in (C) are the periods between R2 DEPs, and their corresponding walking speeds. An exponential regression curve for (C) is shown in red.

2 Methods

All analysis was performed on data collected following the methods presented in [2]. 12 males of *Drosophila melanogaster* had their right middle leg (R2) amputated distal to the femur, were tethered and placed on an air-supported polypropylene sphere, and were recorded by a high-speed video camera as they walked. Eighty-three trials of data were collected, with the data consisting of recorded timestamps corresponding to the anterior and posterior extreme positions (AEP and PEP) of the intact right front and hind legs (R1 and R3), as well as dorsal and ventral extreme positions (DEP and VEP) of R2.

The behavior of R2 was characterized through analysis of the oscillation period and the phase relationships between R2 and the intact legs (R1 and R3). Phase differences between the legs were computed using

$$\Phi_{R2} = \frac{t^{DEP} - t_{-}^{AEP}}{t_{+}^{AEP} - t_{-}^{AEP}} \tag{1}$$

where Φ_{R2} is the phase offset of R2, t^{DEP} is the timestamp where R2 reaches a DEP, t_{-}^{AEP} is the timestamp of the reference leg AEP immediately preceding t^{DEP}, and t_{+}^{AEP} is the following reference leg AEP. This calculates where the given R2 DEP falls within the AEP period of a reference leg, with the resulting data shown in Fig. 1. The data presented here appears different than shown in [2], as more data is present at slower walking speeds. At these slow walking speeds, it is possible for R2 to exhibit several consecutive DEPs between each reference AEP. Due to this and the varied scattering of the phase and period information across a range of walking speeds, it was necessary to characterize this variable behavior. The data was sorted into bins based on the fly's average walking speed between each pair of reference AEPs, then each bin was described using a probability density function to compare the relative likelihood of different states within a given speed. Polar histograms of the phase information are presented in Fig. 2, and the period information in Fig. 3. The experimental data rarely had long durations at one speed, so phase drift could not be quantified. However, the data analyzed in [2] showed preferential inter-leg latencies, suggesting that phase drift is not present.

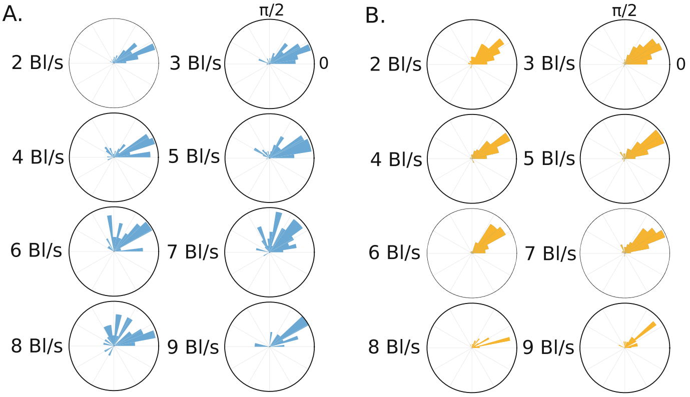

Fig. 2. Probability density functions of R2 phase information. (A) and (B) are the density functions of the first DEP points seen in Fig. 1 (A) and (B) with respect to R1 and R3. Data was sorted into bins by average walking speed (body-lengths/second) between reference AEPs, with each bin represented by a different polar histogram.

3 Results and Discussion

In order to construct a model of the behavior exhibited by *Drosophila* in [2], we needed to further quantify the relationship between the intact legs and stump. As shown in Fig. 2, it appears that the phase relationship between the amputated R2 and the intact R3 is nearly identical across all walking speeds. This suggests that there is some mechanism of direct phase influence between the intact R3 and the stump, which induces a DEP in the R2 stump at a constant point within the period of R3. The phase relationship between the amputated R2 and the intact R1 also appears to be similar across all walking speeds, although the range of possible phase offsets is more varied. This suggests that the phase coupling between R2 and R3 is stronger than between R2 and R1.

Figure 3 suggests that there is a speed-dependent factor affecting the stump's oscillation period. At low walking speeds there appears to be a wide range of possible oscillation periods centered at a slow period, then as walking speed increases the range of possible periods narrows and the average period decreases. This also suggests that the stump's period is not affected by the phase resetting shown in Fig. 2, and could be induced by a separate neural mechanism.

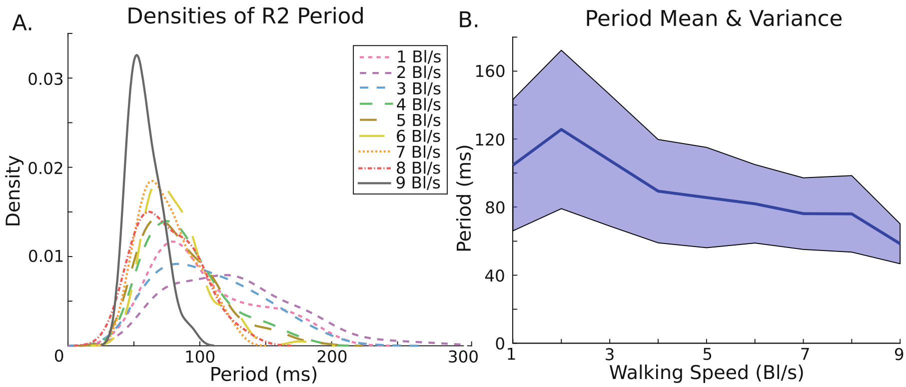

Fig. 3. Probability density functions of R2 period. Shown in (A) are the density functions of the R2 DEP periods, as seen in Fig. 1(C). Points were sorted into bins based on average walking speed, where each bin has a separate density function. Average periods and variances per walking speed are given in (B).

We believe that these results provide particular insights into a potential source for the behavior observed in [2]. Based on our results, we argue that the period of the central pattern generator (CPG) for the R2 stump is naturally noisy, but would be stabilized and regulated by proprioceptive and load feedback if the leg were intact. Without load feedback the stump's period fluctuates until the walking speed increases, increasing the amplitude of velocity feedback and stabilizing the CPG's period. We intend to modify our previously described neuromechanical insect leg model [4] by incorporating these noisy CPG networks and load feedback pathways hypothesized in this work, as well as incorporating multiple legs.

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