Shared signatures of foot placement control for stable locomotion in humans, mice, and flies

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Summary

Foot placement control, i.e. placement of the swinging leg in a manner that corrects recent errors, is crucial for stability in humans, yet it is unknown whether other species use this control mechanism. In humans, foot placement variability is explained by past errors in the upper body state, while in smaller animals, foot placement patterns are thought to be dominated by the walking speed as opposed to errors. This lack of shared control signatures hinders a cross-species understanding of locomotor stability. Here, using large scale locomotion data, we discover signatures of body state error-based foot placement in mice and flies, previously only shown to exist in humans.

Introduction

Stable locomotion is a fundamental motor skill for many legged animals as it allows them to move from place to place without time-consuming course corrections. Two different theoretical models explain how animals control their foot placement for locomotion. Model 1, a feedforward-only controller, is thought to dominate in smaller animal and assumes forward velocity-dependent foot placement patterns (Figure 1, red). Model 2, a feedforward-feedback controller, assumes a combination of velocity-dependent feedforward and body state error-dependent feedback control, (Figure 1, red+blue). Here, we test empirical support for these control models in overground locomotion in flies, mice, and humans.

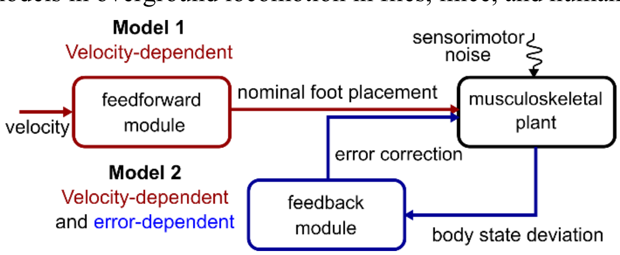

Figure 1: Two alternative control models for foot placement

Methods

We evaluated the two alternative hypothesized control models (Figure 1) using large scale locomotion data in humans [1], mice [2] and flies [3]. The phase-locked positions of the limbs as well as the positions of the body were analyzed while the individuals were freely moving. The location and timing of individual contacts were extracted. The contact location was regressed against the movement velocity to extract the signatures of velocity-dependent foot placement. The deviations in foot placement relative the nominal was regressed against the body deviations relative to the nominal to identify signatures of the body state error-dependent foot placement.

Results and Discussion

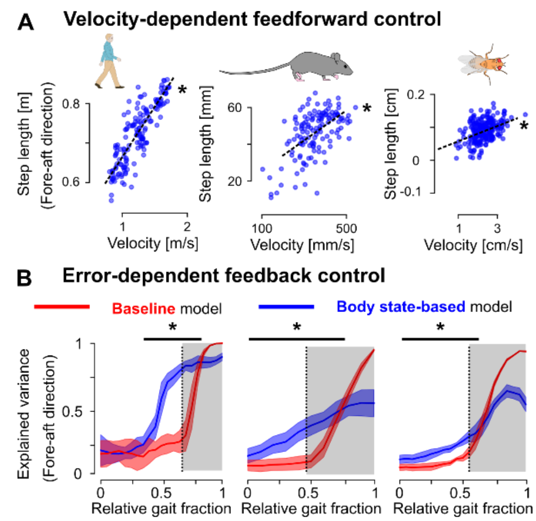

Figure 2: The fore-aft foot placement (A) is explained by velocity whereas the lateral foot placement (B) is explained by body state errors in humans, mice, and flies.

The fore-aft foot placement was correlated with velocity (Figure 2A), but the lateral foot placement was not in humans, mice, and flies. The variability in lateral foot placement was better predicted by the body deviations than by a baseline model based on the variability in foot kinematics during the previous gait cycle (blue and red in Figure 2B, respectively), even before the initiation of leg swing (gray rectangles in Figure 2B). These results provide empirical support for the hypothesized feedforward-feedback control model 2, demonstrating the existence of both velocity-dependent and body state error-dependent control signatures across species. We also observed a decoupling between control of the fore-aft and lateral foot placement across species.

Conclusions

We show that humans, mice, and flies exhibit velocity- and error-dependent foot placement control, which highlights a shared stabilizing locomotor control strategy across species that could help understand the comparative neural basis of stable locomotion.

Acknowledgments

ADC is supported by a fellowship of the K. Lisa Yang ICoN Center at MIT.

References

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