

Inter-leg Coordination and Static Stability of Walking *Drosophila* in Courtship

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Abstract

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Animals use different gaits (leg coordination patterns) to move at different speeds. Abundant research examines the step characteristics and leg coordination of walking *Drosophila* under controlled conditions, where individual flies exhibit straight forward walking. It remains unclear what walking patterns flies choose under a more complex, naturalistic behavior paradigm, such as courtship. During courtship, male flies exhibit a repertoire of walking behaviors, including following, turning, and circling. These behaviors require precise, flexible temporal and spatial coordination of limb movements. Here I explore how male flies position their legs in courtship context. Using high-speed videography and pose estimation, we tracked male *Drosophila* during engaged (active courtship) and disengaged walking. We found that while stepping kinematics (stance duration and step length) were broadly similar across social contexts, static stability of the leg coordination diverged. Specifically, engaged males exhibited greater use of more stable coordination patterns, particularly at low to intermediate speeds. These findings indicate that while locomotor parameters remain stereotyped, static stability is flexibly modulated during

social interactions. We conclude that social goals, such as tracking or signaling to a mate, shape locomotor strategy. This study highlights how internal and external context shape motor output and raises the question of how neural circuits integrate social cues to influence movement in natural behaviors.

Inter-leg Coordination and Static Stability of Walking *Drosophila* in Courtship

Introduction

Goal-oriented motor behaviors in animals are modulated by context. Context can refer to the internal and ongoing behavioral state of an animal, such as arousal, varying homeostatic needs, locomotor states like running or flying; it can also refer to external (environmental) factors, such as the presence of potential mates or predators (Palmer & William B Kristan, 2011). While the kinematics of walking behavior and general aspects of motor output in *Drosophila* has been extensively studied in a variety of contexts, little is known about how social context (e.g. the presence of a potential mate) modulates walking kinematics and stability in freely moving *Drosophila*. We address this gap by testing how flies change their walking strategies during social interactions. *Drosophila* serves as an ideal system for investigating locomotion during social interactions, such as courtship pursuit. Recent technical advances in animal pose estimation have improved our ability in high-throughput behavioral quantification of multiple, interacting animals (Pereira et al., 2022). Additionally, genetic methods in *Drosophila* allow for cell-type-specific manipulations of sensory receptors that detect self-movement. These advances enable us to track and compare walking kinematics and stability of freely walking and interacting *Drosophila*.

Interlimb coordination plays a crucial role in human gait and facilitates stable and efficient human walking (Varma and Trkov, 2024). This is important for maintaining dynamic stability in individuals with motor disorders, such as Parkinson's disease (PD), since it is expected to be tightly controlled during adaptive walking (Roemmich et al., 2013). *Drosophila*, however, differs from humans and quadrupeds such as horses when it comes to the principles governing the transition between coordination patterns. For humans and quadrupeds, transitions

between interlimb coordination are discontinuous and often occur at a characteristic speed (Alexander, 1989). These walking patterns are also known as “gaits”. For insects such as *Drosophila*, such transitions are probabilistic and continuous (DeAngelis et al., 2019; Wosnitza et al., 2013). The emergence of gaits in humans and quadrupeds is primarily driven by energy optimization (Hoyt & Taylor, 1981), whereas the speed-dependent continuum of leg coordination in *Drosophila* is well captured by a static stability model (Szczecinski et al., 2018). Static stability, in this context, refers to the ability of an animal to maintain its upright posture without falling, quantified by the minimum distance between the center of gravity and the edges of a support polygon with vertices defined by the tip of legs in stance. A larger distance indicates the fly is in a more stable posture. On the other hand, dynamic stability is the ability to control the momentum during gait when the center of gravity is outside of the base of support (Tucker et al., 1998). It is a complex strategy commonly used by large animals, such as horses and humans, whose nervous systems use momentum-based strategies, where the muscle activity only shows a brief action potential burst to initiate the swing phase of a step (Hooper, 2012). In contrast, while dynamic stability is observed in insect interlimb coordination, they primarily rely on static stability for locomotion (Jindrich & Full, 2002). This different approach is reflected in their nervous system; the swing motor neurons of small animals (such as stick insects) fire throughout the swing phase (Hooper, 2012). Therefore, we chose a model based on static stability as our method of analysis.

Motor decisions in everyday life are made during ethologically relevant behaviors that are crucial for survival and reproduction (Flavell et al., 2022). Animals must constantly adapt their movements to a variety of contexts. For example, a foraging animal might adjust its search pattern based on the scarcity or abundance of food, while the same animal will employ a rapid,

high-power escape maneuver when sensing a predator. Similarly, behaviors like nest building or territorial defense require precise, context-specific motor sequence. Courtship is a particularly compelling example of such a behavior, as it involves a complex and dynamic social interaction.

During courtship, male flies display a complex repertoire of behaviors that evolved to achieve reproductive success. This includes following the female, extending and vibrating one wing at a time to produce a species-specific courtship song, tapping her with his forelegs, and bending his abdomen to copulate (Pavlou and Goodwin, 2013). It's assumed that the male fly's behaviors leading up to mating are actively assessed by the female fly by integrating sensory cues of conspecificity and fitness. These can lead to either acceptance or rejection-like behaviors (Connolly and Cook, 1973; Villella and Hall, 2008). In the midst of this complex behavioral sequence, the male fly must carefully orchestrate his steps both spatially and temporally to maintain stability. Misplacing steps or falling can impede his progress through the courtship sequence – hindering his ability to follow the female or produce his songs – and ultimately undermine their mating success, as an unstable display may lead to female rejection and prevent copulation.

To understand how social context shapes locomotor strategy, the current study investigates how walking behavior in male *Drosophila* changes during courtship interactions. Specifically, this study focuses on the male fly to (1) examine how step statistics, such as amplitude and duration, change with body speed during courtship; (2) determine how his leg coordination patterns are affected by different social contexts (engaged vs. disengaged); and (3) investigate how static stability is modulated by walking speed during courtship. These analyses will uncover the structure of complex, courtship-specific leg movements and clarify how flies maintain balance during the critical social behavior.

Results

We used a high-speed video camera (150 fps) to record wild-type male and female dyads (Canton-S strain) from the top and we used SLEAP (Pereira et al., 2022) to track and extract 2D kinematics of the fly leg tips and body. The smaller yellow circle on the left side of the panel was used to highlight the location of the two flies within the larger arena, whereas the larger yellow circle on the right is a magnified inset to provide a more detailed view and to display the pose-estimation nodes on their bodies (**Figure 1A**). The pose estimation model was trained on a dataset of over 1500 manually labeled frames. To validate the model's performance, we compared the predicted positions of the legs and wing tips against the ground-truth labels, confirming the reliability of the tracking data (**Figure 1B**).

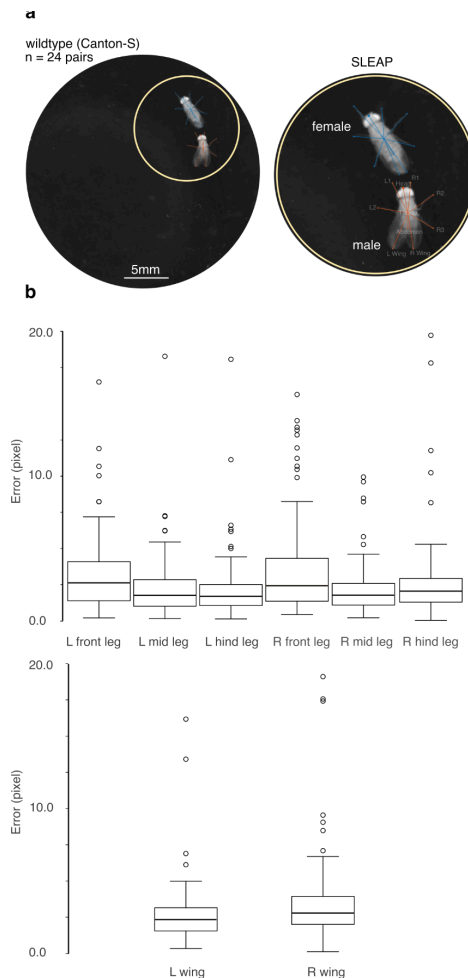


Figure 1 Experimental setup and pose estimation for tracking *Drosophila* kinematics (a) We tested pairs of flies in circular arenas and then annotated the head, thorax, abdomen, and each leg tips. (b) Node distances (ground truth vs. prediction) of leg and wing tips from the centroid and centered instance models in SLEAP. (b) Validation of pose estimation accuracy.

With these accurate kinematics, we focused our kinematic analyses on walking bouts in engaged and disengaged social contexts. The walking bouts were defined by three key social interaction metrics: inter-fly distance, fly heading angle, and fly wing angle (**Figure 2A**). Engaged walking was defined as periods when males were within 5 mm of the female, oriented within 45° of her thorax, and had wing extension angles greater than or equal to 15°—indicative of active courtship. Walking in disengaged contexts were characterized by bouts where males were further away, misaligned, and had closed wings (**Figure 2A**). These specific thresholds were selected based on the distributions of each metric, which are shown with their cut-offs in the histogram (**Figure 2B**). All walking bouts that did not meet the criteria simultaneously were classified as belonging to disengaged contexts (**Figure 2C, 2D**). Flies in the circular arena displayed forward walking bouts, lateral movements, and other rotational movements. A previous study quantifying step kinematics of freely walking flies in isolation has found the average walking speed to be 11–32 mm s⁻¹ (Wosnitza et al., 2013). Engaged males were moving slower than disengaged males, exhibiting forward walking speeds typically below 5 mm s⁻¹, lateral speeds below 3 mm s⁻¹, and rotational speeds below 2.5 deg s⁻¹ (**Figure 3**). These results demonstrate that males modulate their walking speed based on courtship engagement, likely reflecting a shift in behavioral priorities from efficient locomotion to precise, goal-directed tracking.

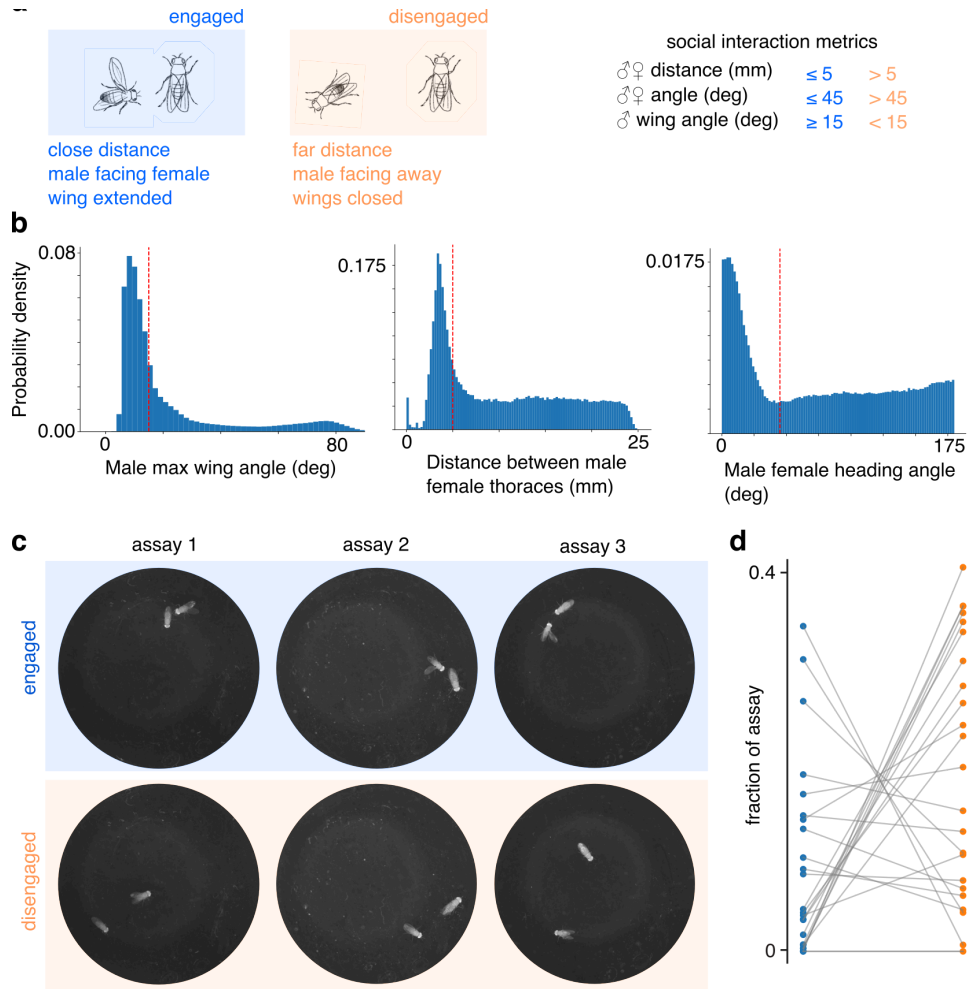


Figure 2 Classification of engaged and disengaged social contexts based on behavioral metrics
(a) We defined two social contexts, “engaged” and “disengaged”, based on three metrics.
(b) Histograms of social interaction metrics across all assays with the red dashed lines indicating cut-offs used for context classifications. **(c)** Example frames for each social context from 3 assays. **(d)** Fraction of the assay (n=22) that was classified as engaged or disengaged.

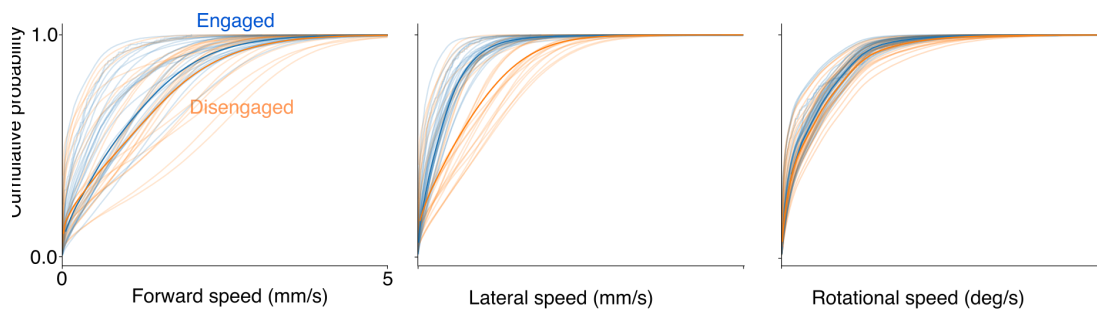


Figure 3 Engaged males exhibit slower walking speeds during courtship Cumulative probability of forward (left), lateral (middle), and rotational (right) speeds of male flies. Bold lines are averages.

To compare engaged and disengaged walking kinematics, we analyzed two stepping parameters of all pairs of legs: stance duration and step length. Stance duration is the amount of time one of the feet is in contact with the ground during a single step. Step length is the distance from the point of initial liftoff of one foot to the point of second liftoff of the same foot (Branch et al., 2008). We found that the key relationships between stepping kinematics and average body speed were similar between flies in different contexts. Stance duration remained fairly constant across speeds. The cumulative probability plots for the front, middle, and hind legs show that the curves for engaged and disengaged flies largely overlap (**Figure 4A**). The lack of correlation between stance duration and average body speed is shown by the nearly flat population fit lines and R^2 values close to zero for all leg pairs in both contexts (**Figure 4B**). Step length also remained fairly constant across speeds.

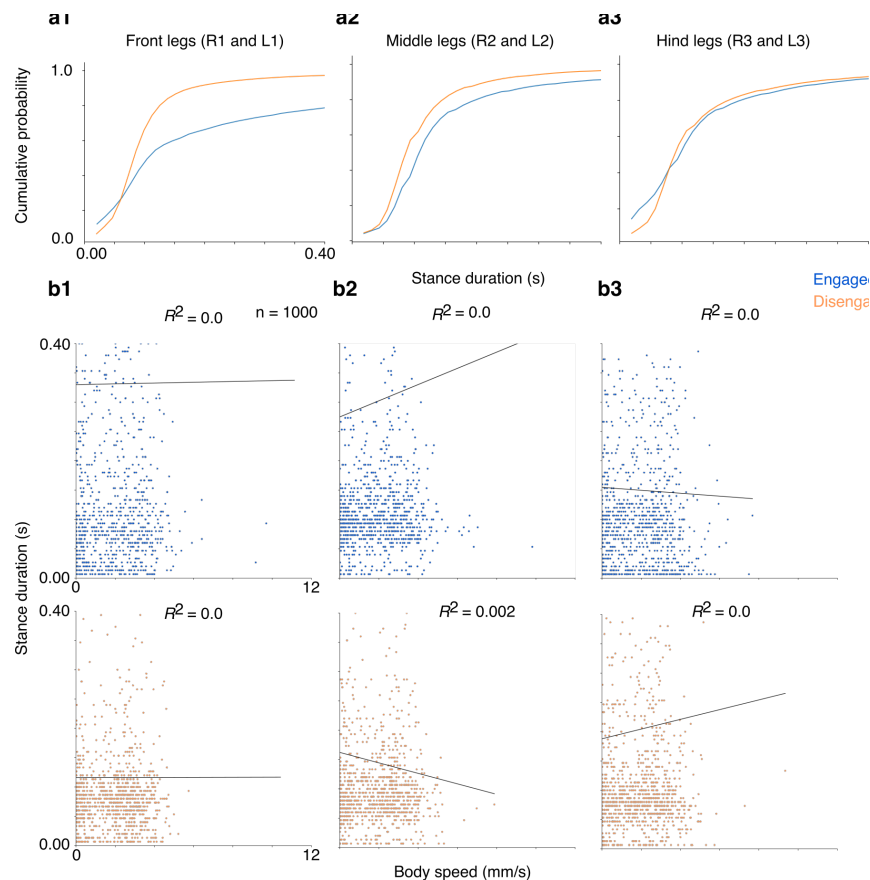


Figure 4 Stance duration remains constant across speeds and social contexts (a) Cumulative probability of stance duration of the front, middle, and hind legs for male flies in each context **(b)** Stance duration as a function of average body speed: n , number of steps. Gray line, population fit. R^2 was computed from the population fit.

The scatter plots for the front, middle, and hind legs in both engaged and disengaged contexts show nearly flat population fit lines, with R^2 values ranging from 0.0 to 0.006 (**Figure 5**). In addition, stance duration and step length were of similar magnitude for engaged and disengaged walking flies (**Figure 4, 5**). The relationships between stepping kinematics and walking speeds of flies in our courtship dataset were not consistent with prior work on freely walking, isolated flies (Szczecinski et al., 2018). Stance duration is strongly anticorrelated to walking speed in the prior work.

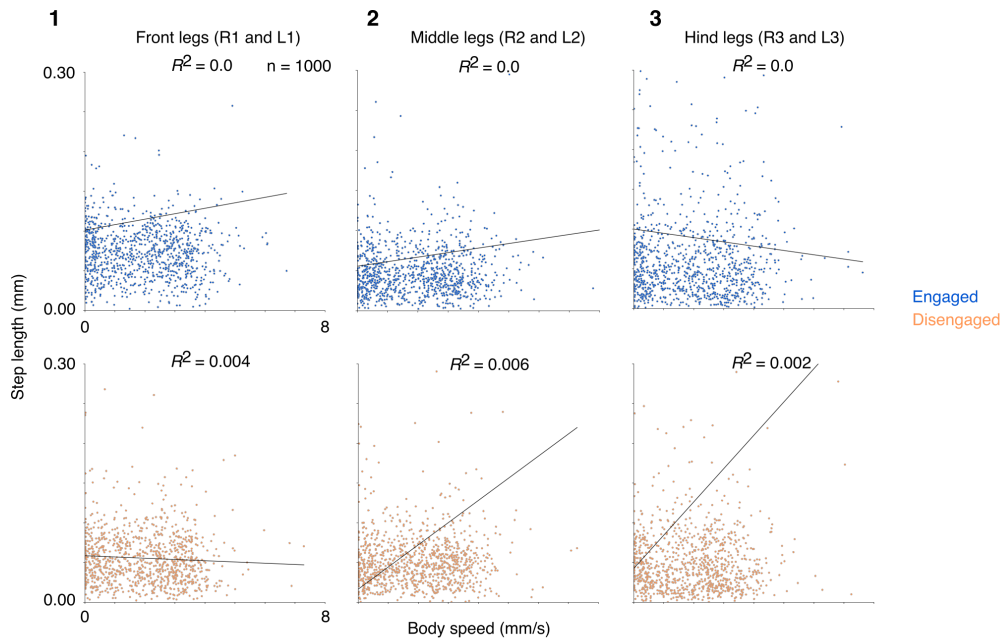


Figure 5 Step length remains constant across speeds and social contexts

Step length as a function of average body speed: n , number of frames. Gray line, population fit. R^2 was computed from the population fit.

We next compared inter-leg coordination across contexts. Our analysis focused on walking bouts that lasted for a minimum of two seconds (**Figure 6A**). We quantified the number of legs that were in the stance phase of the step cycle at each frame in time, which remains constant for idealized coordination patterns, such as the tetrapod coordination pattern where 4 legs are in stance (DeAngelis et al., 2019). We found that the probability of having a specific number of legs on the ground was highly dependent on walking speed, but these patterns were similar for both engaged and disengaged flies. At the slowest speeds, flies in both contexts were most likely to have 5 or 6 legs on the ground. As speed increased, they transitioned to having 4 legs on the ground most often at intermediate speeds. Finally, as body speed increased further, flies in both contexts showed an increased probability of having only 3 legs in stance (**Figure 6B**). This is consistent with prior work showing that freely walking, isolated flies are more likely to use a canonical wave coordination pattern at lower speeds, tetrapod coordination pattern at intermediate speeds, and tripod coordination pattern at higher speeds (Mendes et al., 2013).

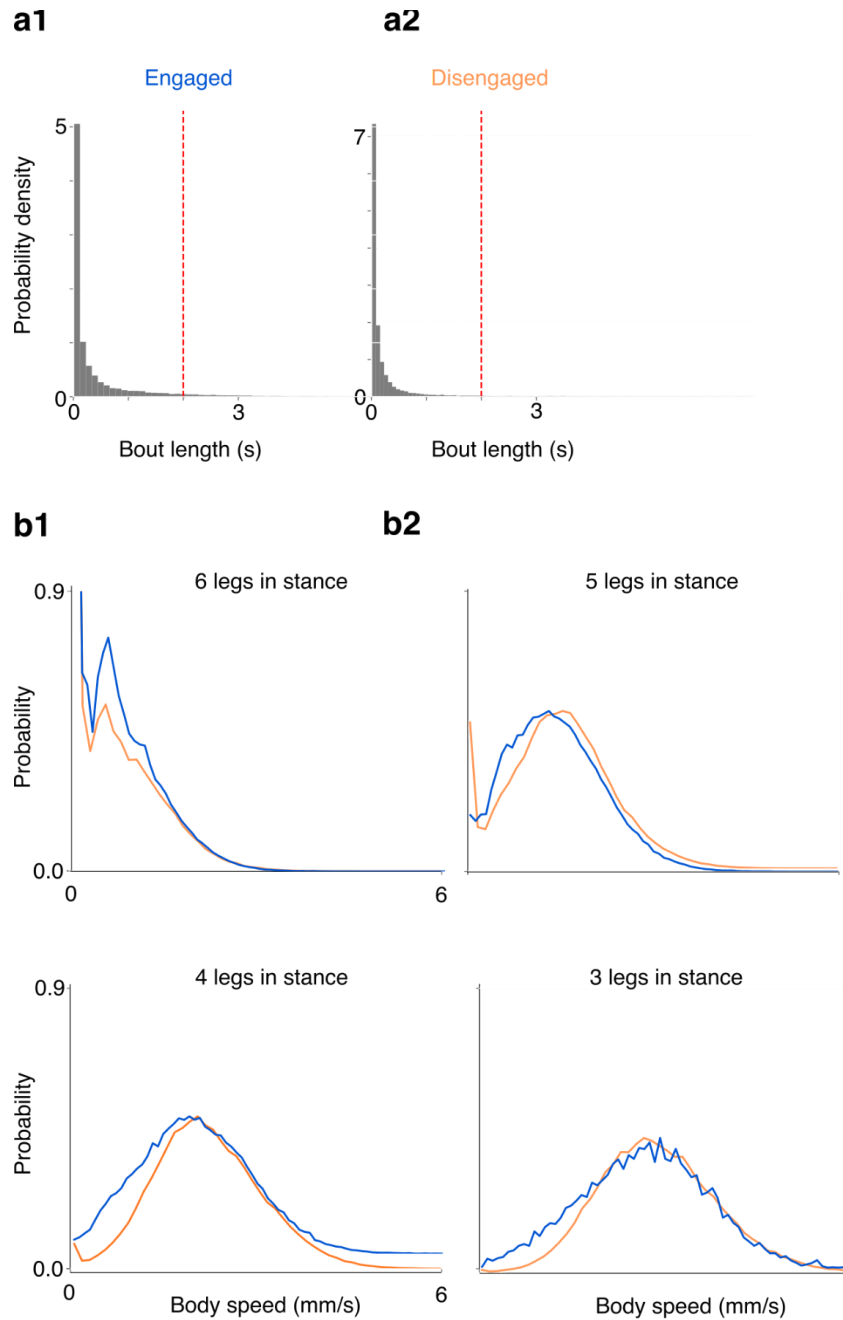


Figure 6 Footfall pattern changes with walking speed regardless of social context (a) Histograms of bout length in the different contexts. Vertical lines indicate a cut-off of two seconds. **(b)** Probability of male flies exhibiting 3, 4, 5, or 6 legs in stance during minimum 2-second bouts across body speed. Lines are speed-binned averages of the probability.

Finally, we looked at the static stability. We focused on flies having 3 legs in stance across speeds in engaged and disengaged context because a minimum of three points of contact is required to form a support polygon to calculate static stability. We found differences in the key relationship between static stability of the flies and their body speeds across contexts. For example, flies in an engaged context had more instances where a more stable inter-leg coordination pattern was used between low to intermediate body speeds (0 to 4 mm/s). We defined and visualized static stability as the minimum distance from the fly's center of mass (thorax) to the edge of the support polygon formed by three legs in stance; a larger distance corresponds to a high stability score and a more stable posture (**Figure 7A**). A comparison of the overall distribution of these scores reveals a clear divergence between social contexts. The histogram for engaged males shows a distribution shifted towards higher stability values, while the distribution for disengaged males is concentrated at lower stability scores, indicating they more frequently adopt less stable postures (**Figure 7C**). When examining this relationship as a function of walking speed, the scatter plots show that engaged males consistently achieved more stable postures, particularly at low to intermediate body speeds (0 to 4 mm/s), compared to disengaged males (**Figure 7B**). In summary, we found that although static stability was different between engaged and disengaged flies (**Figure 7**), step kinematics were broadly similar (**Figure 4, 5**).

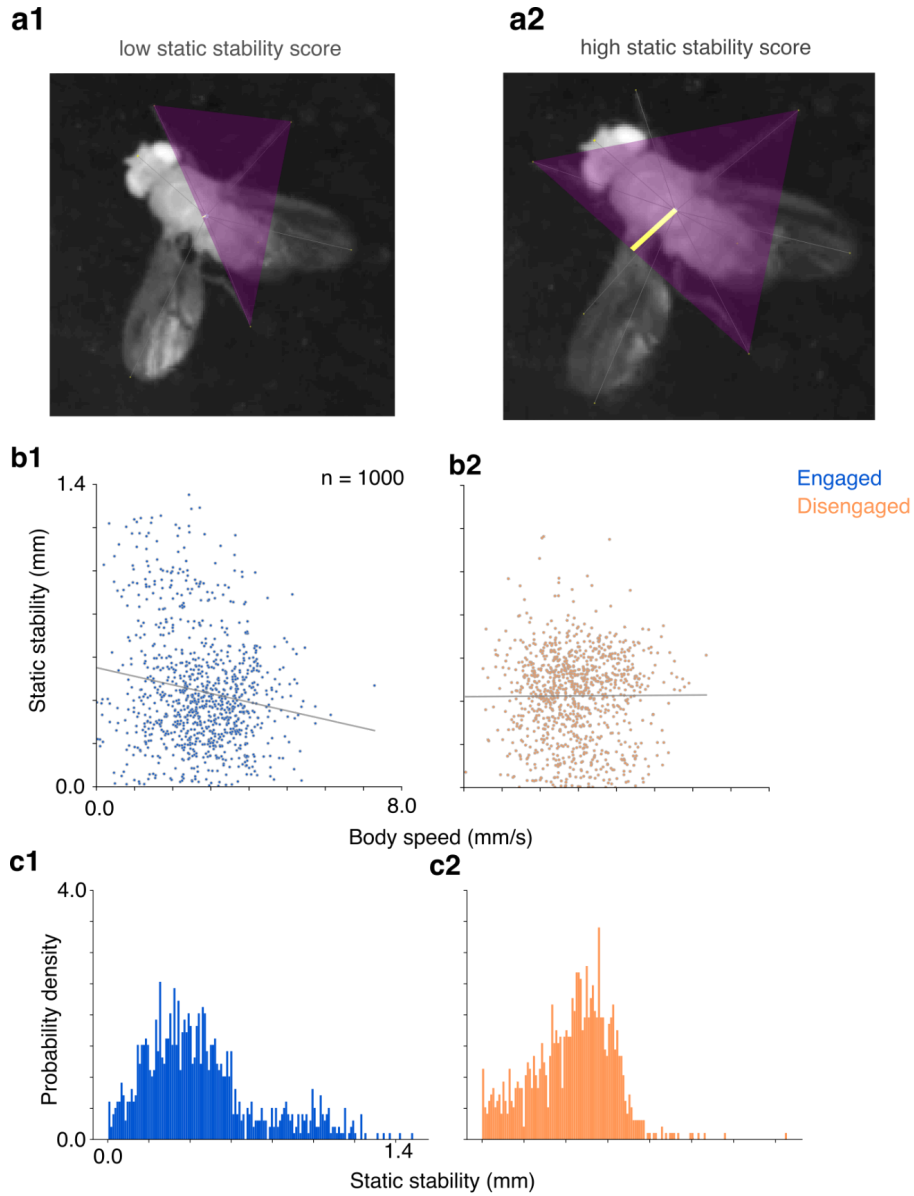


Figure 7 Engaged males exhibit greater static stability at low to intermediate speeds (a) We formed a triangle (purple) from any three legs currently in stance in a video frame and defined the center of mass as the thorax position. The minimal distance between the thorax and the edge of the triangle defines a value for static stability (yellow) **(b)** Static stability as a function of body speed: n , number of frames. Gray line, population fit. R^2 was computed from the population fit. **(c)** Histograms of static stability of the 1000 randomly selected frames from each social context.

Discussion

In this study, we conducted freely walking experiments involving a male and a female wild-type flies in a circular arena (**Figure 1, 2**). Male flies in engaged context exhibited similar walking behavior and step kinematics to male flies in disengaged context (**Figure 3, 4, 5, 6**). However, we later showed that flies used more stable inter-leg coordination patterns at slow and intermediate speeds in engaged context (**Figure 7**). On a high level, we investigated how the complex social context of courtship influences the walking behavior of male *Drosophila*. Our analysis revealed a nuanced interplay between locomotor control and behavioral goals. The surprising finding was that fundamental stepping parameters—stance duration and step length—remained largely constant across different walking speeds in both engaged and disengaged contexts. This was unexpected because it directly contradicts established literature on isolated flies, where stance duration is strongly anticorrelated with walking speed. In contrast, our finding that static stability is actively modulated was less surprising, yet profoundly significant. Our main contribution is the discovery that engaged males flexibly adjust their static stability, particularly at the low to intermediate speeds characteristic of courtship tracking. This implies that an animal's internal state and external social cues can fundamentally reshape motor strategies, prioritizing behavioral success over simple locomotor economy.

During courtship, a male perceives his potential mates through visual, olfactory, and gustatory senses that direct him to initiate courtship (Krstic et al., 2009). These sensory streams are then integrated with mechanosensory and proprioceptive signals of body positions to then guide his actions, which unfold through a series of coordinated courtship behaviors (Krstic et al., 2009). Prior work has suggested that proprioception is most important at slower walking speeds and that flies use a more feedforward motor program when walking faster (Bidaye et al., 2018).

While some studies have manipulated mechanosensory neurons in other behavioral contexts, their specific role during courtship has not been systematically examined (Mamiya et al., 2018; Hampel et al., 2015). It would be valuable to investigate the kinematic deficits resulting from chordotonal neuron manipulation in courtship assays, specifically to ascertain if such deficits are mediated by the social interaction between the male and female flies.

This discrepancy might be explained by males prioritizing courtship-related goals (like orientation or tracking) over other locomotion goals, leading to more stereotyped stepping regardless of speed. In addition, the neural circuits activated during courtship may favor fixed motor output patterns that support courtship success, rather than continuously adjusting to speed.

Methods

Freely walking experiments

Wild-type flies (Canton S) were raised in bottles using an incubator at 25 degrees Celsius with a 12:12 Light:Dark regime. Experimental males and females are collected between 0-10 hours post-eclosion and kept individually in cotton-plugged polystyrene vials for 3-10 days before testing. Experiments are performed at 25 °C and the humidity of the test room is maintained between 30%–50%. No anesthesia (CO₂ or ice cold) was used before recording sessions. At the start of the recording session, we introduced one male and one female fly at zeitgeber time 0-4 hours with an aspirator. The fly chamber was illuminated with infrared strips and a bright white LED strip. Videos were recorded with a Basler aca1300-200um camera at 150 fps and 1280x1024 pixels from a top down view. The workflow of the recording was programmed in Bonsai Rx and a 30-minute video was obtained for each session. The recording begins within 2 minutes after introducing flies to the chamber.

Animal pose estimation was performed with SLEAP v1.3.3 (Pereira et al., 2022). We trained a model based on 1507 frames from 15 random videos (321 labeled frames from male-female assays, 629 from same-sex paired-animal assays, and 557 from single-animal assays) using the multi-animal top-down model. The following 11 points were tracked for all animals: head, thorax, abdomen, left and right wings, front, middle, and hind legs (**Figure 1A**). Inference and identity-tracking on all videos in the dataset were performed on the high-performance computing cluster at the University of Washington via an unattended batch job. A simple tracker was used for the general tracking option with 'iou' as the similarity matching method and number 5 as the track window length. The body parts' X-Y positions were extracted, missing values were interpolated from adjacent frames, and time series were smoothed with a Savitzky-Golay filter before further analysis. Male-female distance was calculated as the frame by frame Euclidean distance between the male and female thorax positions. Male-female angle was the angle (in degrees) between the male's facing direction and the direction to the female's thorax. Male wing angle was the maximum of the left and right wing opening angles relative to head direction (**Figure 2A**).

Swing and stance classification

Leg swing and stance phases were classified based on leg tip speed. Leg positions were smoothed with a Kalman filter. We then calculated instantaneous leg tip speed as the Euclidean norm of the inter-frame position differences. Swing was classified as periods where the smoothed leg tip speeds were above the chosen threshold (20 mm/s). Stance was classified as periods where the leg tip speeds were below or equal to the threshold. The leg tip speed threshold

was empirically determined and based on previously published results of leg instantaneous speed (DeAngelis et al., 2019).

Social context classification

The contexts were classified based on these three behavior metrics: male-female distance, male-female angle, and male wing angle. Engaged context was defined as the periods where male-female distances were below or equal to 5 mm, male-female angles were below or equal to 45°, and male wing angles were greater than or equal to 15°. These thresholds were selected empirically based on the distribution of their values (**Figure 2B**). The opposites were true for classifying disengaged context.

Static stability calculation

Static stability was calculated as the minimum distance between the fly's thorax and the support polygon formed by legs in stance phase at each frame. If three or more legs were in stance phase, the COM-to-hull distance was defined as the minimum Euclidean distance from the thorax to the edges of the support polygon. If fewer than three legs were in stance or the thorax was outside of the support polygon, the frame was excluded from further analysis.

References

- Alexander, R. M. (1989). Optimization and gaits in the locomotion of vertebrates. *Physiological Reviews*, 69(4), 1199–1227.
<https://doi.org/10.1152/physrev.1989.69.4.1199>
- Basu, J., & Nagel, K. (2024). Neural circuits for goal-directed navigation across species. *Trends in neurosciences*, 47(11), 904–917. <https://doi.org/10.1016/j.tins.2024.09.005>
- Bidaye, S. S., Bockemühl, T., & Büschges, A. (2018). Six-legged walking in insects: How CPGs, peripheral feedback, and descending signals generate coordinated and adaptive motor rhythms. *Journal of Neurophysiology*, 119(2), 459–475.
<https://doi.org/10.1152/jn.00658.2017>
- Brach, J. S., Studenski, S., Perera, S., VanSwearingen, J. M., & Newman, A. B. (2008). Stance time and step width variability have unique contributing impairments in older persons. *Gait & posture*, 27(3), 431–439. <https://doi.org/10.1016/j.gaitpost.2007.05.016>
- Büschges, A., & Ache, J. M. (2025). Motor control on the move: From insights in insects to general mechanisms. *Physiological Reviews*, 105(3), 975–1031.
<https://doi.org/10.1152/physrev.00009.2024>
- Connolly, K., & Cook, R. (1973). Rejection Responses by Female *Drosophila melanogaster*: Their Ontogeny, Causality and Effects upon the Behaviour of the Courting Male. *Behaviour*, 44(1/2), 142–166.

Currier, T. A., & Nagel, K. I. (2018). Multisensory Control of Orientation in Tethered Flying *Drosophila*. *Current biology : CB*, 28(22), 3533–3546.e6.

<https://doi.org/10.1016/j.cub.2018.09.020>

DeAngelis, B. D., Zavatone-Veth, J. A., & Clark, D. A. (2019). The manifold structure of limb coordination in walking *Drosophila*. *eLife*, 8, e46409.

<https://doi.org/10.7554/eLife.46409>

Flavell, S. W., Gogolla, N., Lovett-Barron, M., & Zelikowsky, M. (2022). The emergence and influence of internal states. *Neuron*, 110(16), 2545–2570.

<https://doi.org/10.1016/j.neuron.2022.04.030>

Gattuso, H. C., van Hassel, K. A., Freed, J. D., Nuñez, K. M., de la Rea, B., May, C. E., Ermentrout, B., Victor, J. D., & Nagel, K. I. (2025). Inhibitory control explains locomotor statistics in walking *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America*, 122(16), e2407626122.

<https://doi.org/10.1073/pnas.2407626122>

Goulding, M., Bollu, T., & Büschges, A. (2025). Sensory Feedback and the Dynamic Control of Movement. *Annual review of neuroscience*, 48(1), 405–423.

<https://doi.org/10.1146/annurev-neuro-112723-042229>

Hampel, S., Franconville, R., Simpson, J. H., & Seeds, A. M. (2015). A neural command circuit for grooming movement control. *eLife*, 4, e08758.

<https://doi.org/10.7554/eLife.08758>

Hooper, S. L. (2012). Body size and the neural control of movement. *Current Biology*,

22(9), R318–R322. <https://doi.org/10.1016/j.cub.2012.02.048>

- Hooper, S. L., Guschlbauer, C., Wieters, F., Aswendt, M., & Büschges, A. (2025). Passive responses in mouse hind leg locomotion. *Current Biology*, 35(7), 1459-1469.e4.
<https://doi.org/10.1016/j.cub.2024.12.048>
- Hoyt, D. F., & Taylor, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature*, 292(5820), 239–240. <https://doi.org/10.1038/292239a0>
- Jindrich, D. L., & Full, R. J. (2002). Dynamic stabilization of rapid hexapedal locomotion. *Journal of Experimental Biology*, 205(18), 2803–2823.
<https://doi.org/10.1242/jeb.205.18.2803>
- Krstic, D., Boll, W., & Noll, M. (2009). Sensory Integration Regulating Male Courtship Behavior in *Drosophila*. *PLOS ONE*, 4(2), e4457.
<https://doi.org/10.1371/journal.pone.0004457>
- Mamiya, A., Gurung, P., & Tuthill, J. C. (2018). Neural Coding of Leg Proprioception in *Drosophila*. *Neuron*, 100(3), 636–650.e6. <https://doi.org/10.1016/j.neuron.2018.09.009>
- Mendes, C. S., Bartos, I., Akay, T., Márka, S., & Mann, R. S. (2013). Quantification of gait parameters in freely walking wild type and sensory deprived *Drosophila melanogaster*. *eLife*, 2, e00231. <https://doi.org/10.7554/eLife.00231>
- Palmer, C. R., & Kristan, W. B. (2011). Contextual modulation of behavioral choice. *Current Opinion in Neurobiology*, 21(4), 520–526.
<https://doi.org/10.1016/j.conb.2011.05.003>

Pavlou, H. J., & Goodwin, S. F. (2013). Courtship behavior in *Drosophila melanogaster*: Towards a “courtship connectome.” *Current Opinion in Neurobiology*, 23(1), 76–83.

<https://doi.org/10.1016/j.conb.2012.09.002>

Pereira, T. D., Tabris, N., Matsliah, A., Turner, D. M., Li, J., Ravindranath, S., Papadoyannis, E. S., Normand, E., Deutsch, D. S., Wang, Z. Y., McKenzie-Smith, G. C., Mitelut, C. C., Castro, M. D., D’Uva, J., Kislin, M., Sanes, D. H., Kocher, S. D., Wang, S. S.-H., Falkner, A. L., ... Murthy, M. (2022). SLEAP: A deep learning system for multi-animal pose tracking. *Nature Methods*, 19(4), 486–495.

<https://doi.org/10.1038/s41592-022-01426-1>

Pratt, B. G., Lee, S.-Y. J., Chou, G. M., & Tuthill, J. C. (2024). Miniature linear and split-belt treadmills reveal mechanisms of adaptive motor control in walking *Drosophila*. *Current Biology*, 34(19), 4368-4381.e5.

<https://doi.org/10.1016/j.cub.2024.08.006>

Ramdyia, P., Lichocki, P., Cruchet, S., Frisch, L., Tse, W., Floreano, D., & Benton, R. (2015). Mechanosensory interactions drive collective behaviour in *Drosophila*. *Nature*, 519(7542), 233–236. <https://doi.org/10.1038/nature14024>

Roemmich, R. T., Field, A. M., Elrod, J. M., Stegemöller, E. L., Okun, M. S., & Hass, C. J. (2013a). Interlimb coordination is impaired during walking in persons with Parkinson’s disease. *Clinical Biomechanics*, 28(1), 93–97.

<https://doi.org/10.1016/j.clinbiomech.2012.09.005>

Roemmich, R. T., Field, A. M., Elrod, J. M., Stegemöller, E. L., Okun, M. S., & Hass, C. J. (2013b). Interlimb coordination is impaired during walking in persons with Parkinson’s

disease. *Clinical Biomechanics (Bristol, Avon)*, 28(1), 93–97.

<https://doi.org/10.1016/j.clinbiomech.2012.09.005>

Safa, A. T., Biswas, T., Ramakrishnan, A., & Bhandawat, V. (2025). Leg compliance is required to explain the ground reaction force patterns and speed ranges in different gaits. *bioRxiv : the preprint server for biology*, 2024.09.23.612940.

<https://doi.org/10.1101/2024.09.23.612940>

Saltin, B. D., Goldsmith, C., Haustein, M., Büschges, A., Szczecinski, N. S., & Blanke, A. (2025). A parametric finite element model of leg campaniform sensilla in *Drosophila* to study campaniform sensilla location and arrangement. *Journal of the Royal Society, Interface*, 22(226), 20240559. <https://doi.org/10.1098/rsif.2024.0559>

Szczecinski, N. S., Bockemühl, T., Chockley, A. S., & Büschges, A. (2018). Static stability predicts the continuum of interleg coordination patterns in *Drosophila*. *Journal of Experimental Biology*, 221(22), jeb189142. <https://doi.org/10.1242/jeb.189142>

Tao, L., Wechsler, S. P., & Bhandawat, V. (2023). Sensorimotor transformation underlying odor-modulated locomotion in walking *Drosophila*. *Nature communications*, 14(1), 6818. <https://doi.org/10.1038/s41467-023-42613-8>

Tucker, C. A., Ramirez, J., Krebs, D. E., & Riley, P. O. (1998). Center of gravity dynamic stability in normal and vestibulopathic gait. *Gait & Posture*, 8(2), 117–123. [https://doi.org/10.1016/S0966-6362\(98\)00030-7](https://doi.org/10.1016/S0966-6362(98)00030-7)

Varma, V., & Trkov, M. (2024). Investigation of intersegmental coordination patterns in human walking. *Gait and Posture*, 112, 88–94. <https://doi.org/10.1016/j.gaitpost.2024.05.010>

Villella, A., & Hall, J. C. (2008). Neurogenetics of courtship and mating in *Drosophila*.

Advances in Genetics, 62, 67–184. [https://doi.org/10.1016/S0065-2660\(08\)00603-2](https://doi.org/10.1016/S0065-2660(08)00603-2)

Wechsler, S. P., & Bhandawat, V. (2023). Behavioral algorithms and neural mechanisms underlying odor-modulated locomotion in insects. *The Journal of experimental biology*, 226(1), jeb200261. <https://doi.org/10.1242/jeb.200261>

Wosnitza, A., Bockemühl, T., Dübber, M., Scholz, H., & Büschges, A. (2013). Inter-leg coordination in the control of walking speed in *Drosophila*. *Journal of Experimental Biology*, 216(3), 480–491. <https://doi.org/10.1242/jeb.078139>

Yang, H. H., Brezovec, L. E., Capdevila, L. S., Vanderbeck, Q. X., Adachi, A., Mann, R. S., & Wilson, R. I. (2023). Fine-grained descending control of steering in walking *Drosophila*. *bioRxiv : the preprint server for biology*, 2023.10.15.562426. <https://doi.org/10.1101/2023.10.15.562426>