Braking slows passive flexion during goal-directed movements of a small limb

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Highlights

- Mantids make targeted forelimb reaches and searches to nearby objects
- Reaches/searches include a large tibial flexion that promotes contact with the object
- Passive forces from the tibial flexor muscle cause large, rapid tibial flexion
- Passive tibial flexions exceed those during reaching necessitating active braking

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In brief

Rossoni and Niven show praying mantids make targeted forelimb reaches/searches incorporating tibial flexion. Passive forces, primarily from the flexor tibiae muscle, produce larger and faster flexion than during reaching. Consequently, targeted reaching requires active braking of passive tibial flexion, a novel control mechanism for a small limb.
Braking slows passive flexion during goal-directed movements of a small limb

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SUMMARY

The movements of animal appendages are determined by extrinsic and intrinsic forces. Extrinsic forces include gravity or friction,1,2 whereas intrinsic forces are generated by active muscle contraction or passive musculoskeletal elements.3,4 For lightweight appendages, such as insect limbs, movements depend more upon intrinsic than extrinsic forces.5,6 Indeed, passive movements of insect limbs can be large and oppose or aid joint flexion, extension, or both.7 Yet, how passive properties contribute to insects’ goal-directed limb movements, such as targeted reaching and searching,7–10 remains unclear. Here, we show that mantids make targeted reaches and searches to objects by using their raptorial forelimbs, employing braking to slow passive flexion of the femoro-tibial (FTi) joint. In most reaches, tibial flexion ensures the forelimb contacts the object. Such tibial flexion is particularly clear when the forelimb misses the object and continues on a downward trajectory or during directed searching movements. We characterize the passive properties of the FTi joint by combining passive movements of excised limbs with apodeme ablations and muscle stimulation. These experiments show that passive properties of the flexor Tibiae muscle-apodeme complex are the primary structural element producing tibial flexion in excised limbs. During reaching and searching, however, tibial flexion is slower and smaller than predicted. This is due to braking, which opposes passive flexion, thereby reducing the magnitude and velocity of tibial flexion. Braking retarding passive movements is a novel behaviorally relevant control strategy for the goal-directed movements of lightweight limbs, such as those of insects.

RESULTS AND DISCUSSION

Many insects7–10 produce goal-directed limb movements to stationary objects within their near environment, detected through visual or tactile stimuli. These movements are distinct from raptorial limb movements to moving prey11,12 or movements targeted to locations on the insects’ body.13–16 The musculoskeletal control of such goal-directed limb movements to external objects is unknown, though musculoskeletal properties have been implicated in limb targeting errors and subsequent correction.1 To determine the contribution of musculoskeletal properties, we used high-speed videography to record the goal-directed limb movements of Madagascan marbled mantids (Polyspilota aeruginosa). When perched at the end of a platform, these mantids perform goal-directed reaching or searching toward nearby objects. Mantids used one or both of their forelimbs during this behavior, producing single or repeated rhythmic movements of their limb segments (Figure 1A), adjusting the joint angles between them (Figure 1B).

Targeted reaches, misses, and searches have similar kinematics

During reaches, mantids raised their forelimb through coxal protraction and femoral levation, coupled with tibial extension. Sometimes, mantids directly contacted target objects with the tarsus as they raised their forelimb (Figures 1C–1E and S1A); more commonly, however, the trajectory of the forelimb was indirect, being raised above the target (Figures 1F–1H and S1B). Subsequent coxal retraction coupled with tibial flexion then lowered the tarsus to contact the object. These reaches resemble those of grasshoppers, which also vary in accuracy when reaching for objects with their forelegs.8 Despite this variability, the individual reaches, misses, and searches of mantids had similar kinematics (Figures 1O and 1P): an initial increase in coxo-femoral, thoraco-coxal, and FTi joint angles was followed by a decrease in thoraco-coxal and femoro-tibial joint angles, while the coxo-femoral joint angle plateaued.

FTi joint movements in goal-directed reaching and searching

To remove variability in the reach motor pattern caused by target distance and the timing of forelimb contact with the target, we...
Figure 1. Praying mantids use similar limb trajectories to reach and search for targets

(A) A diagram of the mantid forelimb with individual segments colored to correspond to the trajectories of the distal ends of the limb segments and positions of the limb segments shown in (C), (F), (I), and (L) and (D), (G), (J), and (M) respectively.

(B) A schematic of the mantid forelimb with angles between limb segments colored to correspond to the angles shown in (E), (H), (K), and (N).

(C) Forelimb trajectory during a direct reach resulting in the limb contacting the target as it was raised. The trajectories of the distal ends of limb segments are shown.

(D) Forelimb position sequence during a direct reach. The position of each limb segment is indicated every 20 ms.

(E) The angles of the forelimb joints during a direct reach.

(F) Forelimb trajectory during an indirect reach, when the limb was raised above the target. Details as in (C).

(G) Forelimb position sequence during an indirect reach. Details as in (D).

(H) The angles of the prothoracic joints during an indirect reach.

(I) Forelimb trajectory during a missed reach. Details as in (C).

(J) Forelimb position sequence during a missed reach. Details as in (D).

(K) The angles of the prothoracic joints during a missed reach.

(L) Forelimb trajectory during a searching sequence. Details as in (C).

(M) Forelimb position sequence during searching. Details as in (D).

(legend continued on next page)
analyzed missed reaches and searches. We divided movements into three phases based on the FTi joint, which spanned the largest angle and had the most distinct dynamics (Figures 2A and 2B). During the initial draw phase, the tibia attained maximal extension while the forelimb was lifted by femoral levation and coxal protraction. During the subsequent throw phase, the tibia remained extended while the femur was depressed. The sweep phase was initiated by tibial flexion, which, concurrent with coxal retraction and femoral levation, caused the tarsus to sweep downward through an arc in front of the mantid. The duration of reaches correlated with the duration of all individual phases (Figures 2C and Table S1; Pearson’s correlation: draws, $r = 0.79$, $p < 0.001$; throws, $r = 0.79$, $p < 0.001$; sweeps, $r = 0.61$, $p < 0.001$). Thus, the duration of each of the phases (draw, throw, and sweep) of reaches/searches could be adjusted, contrasting with the mantids’ raptorial strike, the duration of which is primarily adjusted through tibial flexion.17

We compared FTi joint movements during the sweep phase of a sample of missed reaches and searches (Figure S2, Table S2). There was no significant difference in the duration of sweeps (Wilcoxon rank-sum test, $W = 230$, $p = 0.342$) or the angular range (Student’s t test, $t(38) = 1.88$, $p = 0.067$) between reaches and searches. We fitted an exponential decay to the sweeps of reaches and searches. Again, there was no significant difference in the time constants of reaches and searches (Wilcoxon rank-sum test, $W = 169$, $p = 0.481$). This shows that the sweep phase of reaches and searches is similar, suggesting similar underlying control mechanisms.

Passive properties return the FTI joint to a narrow range of resting angles

To determine how passive biomechanical properties contribute to mantid goal-directed forelimb movements, we focused on the sweep phase during which the FTI joint flexes (Figures 1–1N, 2A, and 2B). Imposing different angles on the FTI joint of excised forelimbs and releasing the tibia produced a passive movement returning the tibia to a resting angle. This angle arises from the counterbalance of intrinsic passive forces produced by muscular and skeletal elements acting at the hinge joint to promote or retard rotation.18 Following imposed flexion, the hinge joint attains a more flexed resting angle, whereas following imposed extension, it attains a more extended resting angle.4,5,18 This difference was evident at the mantid FTI joint, where the resting angle differed significantly depending on the angle from which the tibia was released (Friedman’s ANOVA, $\chi^2 (4) = 25$, $p < 0.001$; $n = 72$). An imposed full flexion caused the tibia to passively extend to a resting angle of 27.7° [24.6°–28.6°] [median [interquartile range] here and throughout], significantly smaller (pairwise Wilcoxon rank-sum test [PWR-S hereafter] post-hoc, $p = 0.018$) than the resting angle of 32.6° [28.0°–34.3°] following imposed joint angles of 180°, 135°, 90°, and 45°, which did not differ significantly (PWR-S post-hoc, $p = 0.969$ for each). Thus, when the FTI joint is extended beyond the resting angle, intrinsic passive properties produce tibial flexion, whereas intrinsic passive properties produce extension following flexion from its resting angle. Although the FTI joint resting angle is smaller in mantid forelimbs than the limbs of other polynopteran insects,5 it likewise differs between passive flexions and extensions.

The flexor tibiae muscle-apodeme complex is necessary to produce the FTI joint resting angle

The tibia is controlled by two opposing muscles, the extensor tibiae and the larger flexor tibiae.19 To test the contribution of these muscles to FTI joint passive movements, we cut the apodeme of the flexor, the extensor, or both, and compared the resting angle attained by passive flexion or extension in each case to those of intact limbs (Figures 3A and 3B). Cutting either or both apodemes significantly altered the resting angle (Kruskal-Wallis test, $\chi^2 (7) = 63.14$, $p < 0.001$; Table S3). Extensor apodeme ablation did not significantly alter the FTI joint resting angle following passive flexion compared to intact limbs (PWR-S post-hoc, $p = 0.061$) but did produce a significant difference following passive extension (PWR-S post-hoc, $p = 0.020$). Conversely, flexor apodeme ablation significantly altered the resting angle following passive flexion (PWR-S post-hoc, $p = 0.022$) but not passive extension (PWR-S post-hoc, $p = 0.898$). The resting angle following passive extensions of limbs in which both apodemes were cut did not differ significantly in comparison to intact limbs (PWR-S post-hoc, $p = 0.898$), whereas passive flexions produced significantly larger resting angles (PWR-S post-hoc, $p = 0.001$). Thus, the flexor tibiae muscle-apodeme complex is necessary for attaining the resting angle following passive flexion, whereas the extensor tibiae muscle-apodeme complex is needed to achieve the resting angle following passive extension. When both apodemes are cut, non-muscular passive components intrinsic to the joint itself4 are sufficient to achieve the resting angle following imposed flexion and passive extension.

The flexor tibiae muscle-apodeme complex determines the time constant of passive flexions

To understand the contribution of passive properties to the timing of tibial movements, we quantified the time course by which the FTI joint attains the resting angle after imposed displacement by tracking passive tibial movements. We approximated the time courses of the tibial movement with an exponential decay to provide a single time constant, permitting comparison among conditions and experimental treatments (Figure S3; for discussion, see STAR Methods). These exponential decays closely fitted the time course tibial movements ($R^2 = 0.977$ [0.963–0.985]). Ablation of either or both apodemes significantly altered the time constant with which the resting angle was attained (Kruskal-Wallis test, $\chi^2 (7) = 63.5$, $p < 0.001$; Table S4, Figures 3C and 3D). Passive flexions had significantly different time constants to passive extensions, which were slower

(0) The angles of the prothoracic joints during searching.
(O) The prothoracic thoraco–coxal, coxo–femoral, and femoro–tibial angles of the movements shown in (C)–(N).
(P) Changes in prothoracic joint angles, normalized by initial angle, of the movements shown in (C)–(N). Arrows in (O) and (P) indicate the time progression from initial positions.
See also Figure S1.
Extensor apodeme ablation did not significantly affect time constants of either passive extensions or flexions (PWR-S post-hoc, \( p = 0.279 \) and \( p = 0.934 \), respectively). However, flexor apodeme ablation significantly affected the passive flexions’ time constant (PWR-S post-hoc, \( p = 0.005 \)), producing slower movements, though it did not significantly affect passive extensions (PWR-S post-hoc, \( p = 0.786 \)). The time constants of both passive flexions and extensions significantly differed from limbs in which both apodemes were ablated (PWR-S post-hoc, \( p < 0.001 \) and \( p < 0.001 \), respectively), producing slower movements compared to intact limbs. Thus, muscle-apodeme complexes influence the time constants of tibial passive flexions and extensions in mantids. The extensor tibiae muscle-apodeme complex has a limited effect on the time constant of passive extensions, influencing them only when the flexor apodeme was also ablated. By contrast, the flexor tibiae muscle-apodeme complex is a major determinant of the fast time constant of passive flexions.

**Passive properties of the FTi joint are unaffected by preceding muscular activity**

The passive properties of the FTi joint may be influenced by transient forces produced by muscle stretch and by the amplitude and velocity of movements. To address this possibility, we recorded the tibial movements of excised forelimbs during and after stimulating the extensor tibiae muscle (see STAR Methods). By stimulating the extensor tibiae at different frequencies, we extended the FTi joint to different angles, which was followed by passive flexions returning the tibia to the resting angle (Figure S4). We compared the time constants of tibial flexion following electrical stimulation of the extensor tibia muscle with those of passive flexions following imposed tibial extensions to a range of angles. There was no significant difference between the time constants of passive...
Tibial flexions during sweeps have slower time constants than passive flexions.

To determine the contribution of passive movements to goal-directed behavior, we compared the FTi joint angle between sample sweeps and passive flexions (Figures 4A and 4B). The time constants of tibial flexions during sweeps and passive movements differed significantly (Wilcoxon rank-sum test, W = 1850, p < 0.001), as did the variance in the angle at which tibial flexion began (Levene’s test, F(1) = 34.2, p < 0.001). During sweeps, tibial flexions were slower (0.083 [0.048–0.162]) and initiated from a more restricted range of angles (142°–148°) than passive flexions (time constants: 0.047 [0.039–0.064], initial angles: 105°–141°). The slower tibial flexion during sweeps suggests that there is braking of the tibia when reaching.

We compared the angular range spanned during sweeps with that produced through passive flexion from the same initial angle and in the same time interval of the behavioral sequence. The angular range spanned by the tibia during sweeps and passive flexions significantly differed (Student’s paired t test, t(39) = 7.30, p < 0.001), with sweeps spanning a smaller angular range.
Indeed, most sweeps (n = 35, 87.5%) spanned a smaller angle than that of matched passive flexions, which exceeded the angle spanned by 157% [126%–268%]. The angular difference between sweeps and matched passive flexions (Figure 4C) suggests that braking of the passive movement of the tibia during sweeps accounts for a reduction of 22.7% [9.2%–44.9%].
Tibial flexion during sweeps involves active braking of passively driven flexion

Goal-directed limb movements require accurate control of the displacement and timing of limb segments. In mantids, reaching and searching incorporate tibial flexion during the sweep phase that brings the forelimb into contact with the target. Passive flexion, primarily due to the flexor tibiae muscle-apodeme complex, is faster and larger than the tibial flexion observed during sweeps. Thus, the FTi joint trajectory during sweeps is produced by braking that opposes the passive flexion. The experimental evidence presented here shows such braking cannot be explained by changes in the passive properties of the flexor or extensor tibiae muscle-apodeme complex following active tibial extension. Consequently, braking of tibial flexions during sweeps must be active, the most likely source of which is the extensor tibiae muscle, though we cannot exclude a role for inhibitory or modulatory motor neurons that can modify muscle properties.

Intrinsic passive forces acting at joints are known to contribute to the active movements of lightweight limbs. After the limb achieves the desired amplitude, it can be passively driven by such elastic forces. Such passive forces can be non-linear; transient passive forces following transient stretch may exceed steady-state passive forces, thereby aiding control. Previous studies of polynoepiteran insects have shown that during passively driven flexion, the tibia may be allowed to move freely or else be accelerated via muscular contractions. Here, we show that the reverse is also true; braking can also slow the velocity of passively driven movements. This is more similar to the movement of heavier vertebrate limbs, during which antagonist muscles activate to slow the inertia-driven momentum of the limb. While heavyweight limbs are more subject to inertia and lightweight limbs more subject to viscoelastic forces, our results suggest that the mechanisms via which they control targeted movements are more similar than previously considered. Passive properties intrinsic to lightweight limbs can influence and indeed drive movement but, like heavyweight limbs, control over motion can be achieved through acceleration or braking.

The control of goal-directed movements is evident when considering reaching in mantids. The total duration of the reach is achieved by adjusting the durations of distinct movement phases. This contrasts with raptorial strikes produced by the forelimbs, the duration of which is primarily adjusted through tibial extension, and walking movements of other insects, where the step duration is adjusted by regulating only one of two behavioral phases while the duration of the other stays largely constant. The difference between reaching and raptorial strikes or walking suggests that reaches are not merely modified steps or strikes but require a higher degree of flexibility. Moreover, the sequence of behavioral phases in the reach could be repeated to produce searching. This suggests that a smooth transition exists between reaching and searching—similar motor patterns can produce different behaviors, depending on the context. Reaches and searches have been documented in several different orders of insects, though whether there is any true homology between these movements remains unclear.

The mantid forelimb exhibits several morphological features consistent with its raptorial function. Mantid reaches span a similar angular range to those of the raptorial strike, and the flexion of the FTi joint is a key component of prey capture and restraint. Thus, it is possible that the small resting angle of the FTi joint and the fast passive flexion produced by the flexor tibiae muscle-apodeme complex is primarily an adaptation for the strike. Many insect limbs are versatile, and perform a range of different behaviours, but how they adapt fixed passive properties to behaviors requiring high accuracy is largely unknown. The active braking of the mantid’s passively driven tibial flexion during reaches slows the tarsus prior to contact. This reduces the force generated upon impact, possibly allowing the tarsus to grip the surface of the object it contacts and/or reducing the likelihood of damaging the thin tarsus, which is extended throughout the reach but is retracted during the raptorial strike presumably also to prevent damage.

STAR METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.08.052.

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AUTHOR CONTRIBUTIONS

S.R. and J.E.N. designed the experiments/analysis. S.R. performed the experiments/analysis. S.R. drafted the manuscript with input from J.E.N., and both authors contributed to it thereafter. Both authors approve the final version of the manuscript and are accountable for all aspects of the work.

DECLARATION OF INTERESTS

The authors declare no competing interests.
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STAR METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---------------------|--------|------------|
| Deposited data      |        |            |
| Resting FTi angles after surgery | This study | https://doi.org/10.25377/sussex.20606427 |
| Resting FTi angles following imposed extension/flexion | This study | https://doi.org/10.25377/sussex.20606427 |
| Time constants of sweeps | This study | https://doi.org/10.25377/sussex.20606427 |
| Time constant of FTi angles after surgery | This study | https://doi.org/10.25377/sussex.20606427 |
| Reach phase duration | This study | https://doi.org/10.25377/sussex.20606427 |

Experimental models: Organisms/strains

| Polyspilota aeruginosa | BugzUK | N/A |

Software and algorithms

| ImageJ, version 2.1.0 | National Institutes of Health | ImageJ, RRID:SCR_003070 |
| MATLAB, version 9.2 | MathWorks | MATLAB, RRID:SCR_001622 |
| RStudio, version 1.0.136 | R Core Team | RStudio, RRID:SCR_000432 |
| Spike2, version 8.05 | Cambridge Electronic Design | Spike2 Software, RRID:SCR_000903 |

Other

| A-M systems differential amplifier, model 1700 | A-M systems | https://www.a-msystems.com/p-202-model-1700-differential-ac-amplifier.aspx |
| Canon EOS 7D camera | Canon | https://www.canon.co.uk/for_home/product_finder/cameras/digital_slr/ eos_7d_mark_ii/ |
| GC-PX100 JVC camera | JVC | https://uk.jvc.com/microsite/eu/gc-px100/index.html |
| Micro 1401-3 digital-to-analog converter | Cambridge Electronic Design | https://ced.co.uk/products/microhistory#mic3 |

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources can be directed and will be fulfilled by the lead contact, Jeremy Niven (j.e.niven@sussex.ac.uk).

Materials availability
This study did not generate new materials.

Data and code availability

- Data will be deposited in the University of Sussex Research Data Repository and will be made publicly available here: https://doi.org/10.25377/sussex.20606427.
- This paper does not report original code.
- Any additional information required to reanalyse the data reported in this paper is available from either lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Male and female Madagascan marbled praying mantids (*Polyspilota aeruginosa*) were purchased from a local supplier (BugzUK, Norwich, Norfolk, U.K.) and maintained in individual cages at the School of Life Sciences, University of Sussex, U.K. They were fed with live crickets and maintained in a 12/12 hour light/dark cycle at room temperature (21–23°C) until they reached adulthood. Experiments were performed on adults only.

METHOD DETAILS

Animal preparation, stimulus presentation and videography
To record reaching behaviour, we positioned a 10.2 x 2 cm² walkway, with a 5.2 x 5.2 cm² platform at one end, in the centre of a 75 x 60 x 60 cm³ white arena illuminated from overhead. A hole in the arena wall allowed a high-speed camcorder (GC-PX100 JVC Ltd,
Yokohama, Japan) to be positioned perpendicular to length of the walkway for filming. Mantids placed on the walkway were allowed to walk to either end of the walkway and perform reaches to targets. Reaches were filmed at either 50 frames per second (fps) or 200 fps as required, and the camcorder was manually adjusted immediately prior to reach initiation, to ensure that the filming angle was orthogonal to the trajectory of the forelimb. On the few occasions that the filming plane and limb movements did not align satisfactorily such movements were discarded from analysis.

**Passive tibial movements in excised forelimbs**

Resting angles of the femoro-tibial (FTi) joint were measured as in previous studies of the locust and stick insect limbs.[4,35] Forelimbs were excised at the thoraco-coxal joint and embedded in modelling clay (Plasticine®, U.K.), proximal side uppermost. Tarsi were removed from the limbs, ensuring that the tibiae were free to move on the horizontal plane.

Angles were imposed upon the FTi joint of excised limbs for approximately 1 s and the passive movement after release was filmed at 50 fps (Canon EOS 7D, Tokyo, Japan). Resting joint angles were photographed (Canon EOS 7D, Tokyo, Japan) 10 s after release from the imposed position. In some instances, further passive movement was seen after this initial 10 s; in these situations, the resting angle was photographed again 20 s after release. To investigate the mechanisms of the FTi joint in intact limbs, we imposed an initial full extension. Then, we imposed a descending series of release angles of approximately 180° (full extension), 135°, 90°, 45° and 0° (full flexion). We then compared resting angles following each step of the descending series of release angles.

After measurements in excised but intact legs, a small rectangular flap was cut in the cuticle at the level of the femoral brushes.[36] Saline® was applied to this rectangular window. In the right limb of each mantid, the flexor tibiae apodeme was cut, whereas in the left limb of each mantid, the extensor tibiae apodeme was cut. Once an apodeme was cut, the angles in the sequence described above were imposed again and, following release, the passive movements and resting angles of the joint were recorded. The limbs were once again immersed in saline and the other apodeme was cut. The imposed angle sequence was then repeated, and the passive limb movements and resting angles recorded.

To elicit passive flexions following muscular extension of the tibia, we inserted coated silver wires 120 μm diameter medially into the extensor tibiae muscle of intact excised limbs.[19] Stimuli were designed using the graphical editor in-built in Spike2 software (version 8.05, CED, Cambridge, U.K.). Stimuli were delivered using a Micro 1401 digital-to-analog converter (CED, Cambridge, U.K.) linked to an extracellular amplifier and stimulus generator (differential amplifier model 1700, A-M systems, Sequim, WA, U.S.A.). Stimuli were delivered to the extensor tibiae as a single pulse, five pulses at 7.5 Hz, five pulses at 20 Hz, or ten pulses at 50 Hz, the latter of which produced a complete extension. Tibial movements were recorded at 200 fps (GC-PX100 JVC Ltd, Yokohama, Japan).

**QUANTIFICATION AND STATISTICAL ANALYSIS**

Video analysis of behavioural sequences and passive movements were performed offline using ImageJ (National Institutes of Health, Bethesda, MD, U.S.A.). The duration of each phase of the reaches was manually recorded. Joint angles were measured either directly with the inbuilt angle tool, or calculated using relative joint positions, tracked using the MTrackJ plugin.[37] To extract time constants of tibial movements, angle traces were trimmed so that they started at the point of maximal angular velocity of the joint. A single-exponential function was then fitted to FTi angles (Figure S3) using Matlab R2017a (version 9.2, MathWorks Inc, Natick, MA, U.S.A.). The time constant, \( \tau \), was extracted from the fitted function for statistical analysis. The exponential decay closely approximated the trajectories of the passive movements of the tibia (Figure S3A, \( R^2 = 0.977[0.963-0.985] \)). This provided a single metric by which trial movements could be compared under different condition and treatments. However, such exponential decays are only approximations to the dynamics, which are more accurately described by a power function (Figure S3B). To compare tibial flexion in reaches and passive movements, the passive flexions were averaged and an exponential function fitted. This function was then solved numerically for the initial FTi angle of the sweep. The angular range spanned in passive flexions from this point in the same time interval as the sweep was then calculated. Angular ranges were compared statistically between actual sweeps and passive flexions.

Statistical tests were implemented using R studio software, version 1.0.136, and R software, version 3.3.2 (R Core Team, 2013). The median and interquartile range were used as descriptive statistics. Normality was tested using the Shapiro-Wilk test in the "pastrocs" package. Equality of variance was tested using the Levene’s test in the "car" package. Significance p values of 0.05 were used for all tests, except for multiple tests, where p values were adjusted using Hommel’s method. Correlations were tested using Pearson’s \( r \)-test, implemented in the "Hmisc" package. All remaining statistical tests were part of the "stats" package. For comparisons of data with normal distributions and homogeneous variance between two independent groups, we used Student’s \( t \) tests. For comparisons of data with non-normal distributions or heterogeneous variance between two independent groups, we used Wilcoxon rank sum tests. For comparisons of data with non-normal distributions or heterogeneous variance amongst multiple independent groups, we used Kruskall-Wallis tests. For comparisons of non-normally distributed data with heterogeneous variance amongst paired groups, we used a Friedman rank sum test. Post-hoc comparisons were made using pairwise two-tailed Wilcoxon signed-rank tests.
Braking slows passive flexion during goal-directed movements of a small limb

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Figure S1. Mantids *Polyspilota aeruginosa* use similar motor patterns for reaching and searching. Related to FIGURE 1. (A) Sequential images of a mantid performing a direct reach. (B) Sequential images of a mantid performing an indirect reach. (C) Sequential images of a mantid performing a missed reach. (D) Sequential images of a mantid performing a searching sequence.
Figure S2. The sweep phase of a reach can be fitted by an exponential decay function. Related to FIGURE 4. (A) FTi angles during a reach (pale green), with an exponential decay function (dark green) fitted to the tibial flexion. (B) Angular speed of the tibia, the peak of which was used to delimit the portion of tibial flexion to fit with an exponential decay function.
Figure S3. Passive FTi movements are fitted by power functions and closely approximated by exponential decay functions. Related to FIGURE 3 and STAR methods. (A) Exponential decays (solid lines) fitted to passive tibial flexions and extensions (dots) following imposed extension or flexion, respectively. (B) Power functions (solid lines) fitted to passive tibial flexions and extensions (dots) following imposed extension or flexion, respectively. The raw data is for the intact limb or following extensor and/or flexor muscle ablations.
Figure S4. Electrical stimulation of the extensor muscle at different frequencies produces extensions followed by passive flexions in isolated, intact limbs. Related to FIGURE 4. (A) The response of the FTi joint to single pulse stimulation of the extensor tibiae (n=5). Mean FTi joint angles (dashed lines) and entire range of data (shaded areas) are shown here and in panels A-D. (B) The response of the FTi joint to a train of 5 pulse stimuli delivered at 7.5 Hz to the extensor tibiae (n=5). (C) The response to a train of 5 pulse stimuli at 20 Hz delivered to the extensor tibiae (n=5). (D) The response to a train of 10 pulse stimuli at 50 Hz to the extensor tibiae (n=3), which can produce full extension of the tibia. (E) Exponential decay functions (solid lines) fitted to FTi angles (shaded areas show the standard error around the mean) of passive flexions following electrical stimulations of the extensor tibiae muscle. The time constants (τ) of the passive flexion after stimulation of the extensor tibiae are indicated in the legend.
| Behaviour  | Median [interquartile range] |
|-----------|-----------------------------|
| Total reach | 245 [185-533] ms |
| Draw       | 62.5 [45.0-137.5] ms       |
| Throw      | 153 [103-240] ms           |
| Sweep      | 42.5 [12.5-80.0] ms        |

**Table S1.** The durations of behavioural phases of mantid reaches. Related to **FIGURE 2.** Medians and interquartile ranges of the durations of reaches and reach phases (n = 77).
| Parameter        | Sweeps during missed reaches | Sweeps during searches |
|------------------|------------------------------|------------------------|
| Duration         | 80 [80-120] ms               | 80 [60-100] ms         |
| Angular range    | 28.2 [16.5-34.0] °           | 35.8 [22.8-46.6] °     |
| Time constants   | 0.074 [0.060-0.109]          | 0.120 [0.047-0.202]    |

Table S2. Parameters of mantid reaches and searches. Related to FIGURE 4. Medians and interquartile ranges of sweep measurements during reaching (n = 17) and searches (n = 23).
Table S3. The effect of surgical ablations on resting angles of the mantid tibia following imposed flexion and extension. Related to FIGURE 3. Post-hoc pairwise comparisons of resting angles in different surgical conditions from either passive extension or flexion. Numbers in row/column headers indicate median, interquartile range, and sample size.

Significance values: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. 

|                  | Intact flexion 33.1° [30.5-36.0, n=19] | Intact extension 28.0° [26.7-29.9, n=18] | Flexor cut flexion 46.7° [44.8-50.6, n=11] | Flexor cut extension 28.0° [23.9-35.1, n=9] | Extensor cut flexion 25.3° [21.7-29.3, n=9] | Extensor cut extension 18.7° [14.4-20.8, n=9] | Both muscles cut flexion 52.6° [46.1-58.9, n=18] | Both muscles cut extension 24.8° [20.5-32.7, n=18] |
|------------------|----------------------------------------|----------------------------------------|-------------------------------------------|-------------------------------------------|-------------------------------------------|-------------------------------------------|-----------------------------------------------|-----------------------------------------------|
| Intact extension | 0.102                                  | -                                      | -                                         | -                                         | -                                         | -                                         | -                                             | -                                             |
| Flexor cut       | 0.022 *                                | <0.001 ***                             | -                                         | -                                         | -                                         | -                                         | -                                             | -                                             |
| Flexor cut       | 0.012 *                                | 0.898                                  | 0.898                                     | -                                         | -                                         | -                                         | -                                             | -                                             |
| Flexor cut       | 0.760                                  | 0.898                                  | 0.005 **                                 | 0.898                                     | -                                         | -                                         | -                                             | -                                             |
| Extensor cut     | 0.061                                  | 0.898                                  | 0.004 **                                 | 0.074                                     | 0.380                                     | -                                         | -                                             | -                                             |
| Extensor cut     | 0.002 **                               | 0.020                                  | 0.004 **                                 | 0.801                                     | 0.008 **                                 | 0.002                                    | <0.001 ***                                   | -                                             |
| Both muscles     | 0.001 ***                              | <0.001 ***                             | 0.008 **                                 | 0.008 **                                 | 0.801                                     | 0.002                                    | <0.001 ***                                   | 0.001 ***                                   |
| Both muscles     | 0.171                                  | 0.898                                  | 0.003 **                                 | 0.898                                     | 0.898                                     | 0.259                                     | -                                             | -                                             |
| condition                                | intact flexion | intact extension | flexor cut flexion | flexor cut extension | extensor cut flexion | extensor cut extension | both muscles cut flexion | both muscles cut extension |
|------------------------------------------|----------------|------------------|--------------------|---------------------|----------------------|------------------------|--------------------------|---------------------------|
| intact extension                         | 0.100          | 0.100            | 0.254              | 0.136               | 0.054                | 0.159                  | 0.272                    | 0.272                     |
|                                          | [0.079-0.133,  | n=22             | [0.0205-0.319,     | [0.094-0.172,       | [0.039-0.096,         | [0.108-0.205,           | [0.168-0.332,             | [0.168-0.332,             |
|                                          | n=17]          |                  | n=8]               | n=9]                | n=9]                | n=13]                  | n=18]                    | n=18]                     |
| flexor cut flexion                       | 0.047          |                  |                    |                     |                      |                        |                          |                           |
|                                          | [0.036-0.066,  |                  |                    |                     |                      |                        |                          |                           |
|                                          | n=17]          |                  |                    |                     |                      |                        |                          |                           |
| flexor cut extension                     | 0.005          | 0.098            |                    |                     |                      |                        |                          |                           |
|                                          | [0.0254-0.319, |                  |                    |                     |                      |                        |                          |                           |
|                                          | n=8]           |                  |                    |                     |                      |                        |                          |                           |
| extensor cut flexion                     | 0.009          | 0.786            | 0.545              | 0.786               | 0.545                |                        |                          |                           |
|                                          | [0.094-0.172,  |                  |                    | [0.094-0.172,       | [0.094-0.172,        |                        |                          |                           |
|                                          | n=9]           |                  |                    | n=9]                | n=9]                |                        |                          |                           |
| extensor cut extension                   | 0.934          | 0.189            | 0.041              | 0.161               | 0.056                |                        |                          |                           |
|                                          | [0.039-0.096,  |                  | [0.041-0.161       | [0.056-0.161        | [0.056-0.161         |                        |                          |                           |
|                                          | n=9]           |                  |                    |                     |                     |                        |                          |                           |
| extensor cut extension                   | 0.002          | 0.279            | 0.892              | 0.934               | 0.056                |                        |                          |                           |
|                                          | [0.108-0.205,  |                  |                    | [0.108-0.205,       | [0.108-0.205,        |                        |                          |                           |
|                                          | n=13]          |                  |                    | n=13]               | n=13]               |                        |                          |                           |
| both muscles cut flexion                 | <0.001         | 0.005            | 0.934              | 0.333               | 0.003                | 0.892                  |                          |                           |
|                                          | [0.168-0.332,  |                  |                    | [0.003-0.333       | [0.003-0.333        | [0.003-0.333           |                          |                           |
|                                          | n=18]          |                  |                    |                     |                     |                        |                          |                           |
| both muscles cut extension               | <0.001         | <0.001           | 0.934              | 0.212               | 0.001                | 0.776                  | 0.934                    |                           |
|                                          | [0.168-0.308,  |                  |                    | [0.001-0.212       | [0.001-0.212        | [0.001-0.212           | [0.001-0.212            |                           |
|                                          | n=18]          |                  |                    |                     |                     |                        |                          |                           |

**Table S4. The effect of surgical ablations on passive movement time constants of the mantid tibia following imposed flexion and extension.** Related to FIGURE 3. Post-hoc pairwise comparison of time constants (τ) of either passive extension or flexion in different surgical conditions. Numbers in row and column headers indicate median, interquartile range, and sample size for each condition. Significance values: * = p < 0.05, ** = p < 0.01, *** = p < 0.001.