

The green leafhopper, *Cicadella viridis* (Hemiptera, Auchenorrhyncha, Cicadellidae), jumps with near-constant acceleration

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This Corrigendum relates to *J. Exp. Biol.* **216**, 1270-1279.

There is an error on p.1276, line 15. The value of the force that the two feet exchange with the ground was incorrectly stated as 2.89 N. The prefix 'm' was missing and the correct wording is '2.89 mN'.

In addition, on p.1271, lines 4–7, the sentence 'However, the instantaneous force applied to the ground during the extremely fast thrust phase of the jump has not been characterized in these small animals' was misleading and does not take into account previously published data by other researchers. This sentence should be replaced by the following paragraph and additional references.

'Detailed kinematics, kinetics and the ground reaction forces of jumping have been previously published: for seven species of leafhopper (Brackenbury, 1996; Burrows, 2007b; Burrows, 2008a), including *Cicadella viridis*; for other closely related hemipterans such as froghoppers (Burrows, 2006a; Burrows, 2009a; Sutton and Burrows, 2010), psyllids (Burrows, 2012), planthoppers (Burrows, 2009a; Burrows, 2010) and treehoppers (Burrows, 2013). Detailed kinematics during take-off are also available for several more species, such as: hemipteran shore bugs (Burrows, 2009b) and Peloridiidae (Burrows et al., 2007); stick insects (Burrows, 2008); othopterans such as locusts (Bennet-Clark, 1975; Queathem and Full, 1995; Sutton and Burrows, 2008; Cofer et al., 2010), bush crickets (Burrows and Morris, 2002), Proscopiidae (Burrows and Wolf, 2002) and pygmy mole crickets jumping from both land (Burrows and Picker, 2010) and water (Burrows and Sutton, 2012); and fleas (Siphonaptera) (Bennet-Clark and Lucey, 1967; Rothschild, 1972; Sutton and Burrows, 2011). In these studies, high-speed cameras were used at frame rates of up to 5000 frames s⁻¹ and enabled up to 20 pictures of the insect to be captured during the few milliseconds in which it accelerates. This time resolution is insufficient to allow the statistical analysis of the kinematics we describe and so we filmed the thrust phase of the green leafhopper, *Cicadella viridis*, at 8000 frames s⁻¹. This allowed us to generate up to 45 pictures of this insect as it accelerated during a jump.'

The authors apologize to their colleagues for incompletely crediting their previously published work. They assure readers that the data, results and conclusions of the article are not affected.

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RESEARCH ARTICLE

The green leafhopper, *Cicadella viridis* (Hemiptera, Auchenorrhyncha, Cicadellidae), jumps with near-constant acceleration

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SUMMARY

Jumping insects develop accelerations that can greatly exceed gravitational acceleration. Although several species have been analysed using different tools, ranging from a purely physical to a morpho-physiological approach, instantaneous dynamic and kinematic data concerning the jumping motion are lacking. This is mainly due to the difficulty in observing in detail events that occur in a few milliseconds. In this study, the behaviour of the green leafhopper, *Cicadella viridis*, was investigated during the take-off phase of the jump, through high-speed video recordings (8000frames⁻¹). We demonstrate that *C. viridis* is able to maintain fairly constant acceleration during overall leg elongation. The force exerted at the foot–ground interface is nearly constant and differs from the force expected from other typical motion models. A biomechanical model was used to highlight that this ability relies on the morphology of *C. viridis* hind legs, which act as a motion converter with a variable transmission ratio and use the time-dependent musculo-elastic force to generate a nearly constant thrust at the body–ground interface. This modulation mechanism minimizes the risk of breaking the substrate thanks to the absence of force peaks. The results of this study are of broad relevance in different research fields ranging from biomechanics to robotics.

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INTRODUCTION

Insects are the largest group of arthropods and the most varied class among animals on Earth (Engel and Grimaldi, 2004; Ødegaard, 2000). The evolutionary success of insects is due not only to their high reproductive capacity, but also to their ability to fly, their physiological and morphological adaptations and their small size (Engel and Grimaldi, 2004). Indeed, this latter characteristic has allowed them to colonize virtually all ecosystems (Ritzmann et al., 2004). However, their small scale has made them easy targets for a wide number and variety of larger predators. During evolution they have refined many different escaping strategies (Cain, 1985; Masters and Eisner, 1990). One of the main methods used by insects to escape from predators is to increase the speed of locomotion (Bennet-Clark and Lucey, 1967; Evans, 1972; Christian, 1978; Brackenbury and Hunt, 1993; Maitland, 1992).

Locomotion is generally used by almost all animal species to feed, to avoid predators and for social interaction (Reilly et al., 2007). Therefore, locomotion is considered an important element of survival, as it is able to influence the morphology and physiology of organisms (Dickinson et al., 2000). Among insects, using jumping as a form of locomotion is a good example of how the need to change the speed of locomotion has been accompanied by morphological and physiological changes. Possible reasons why some species of insects have developed jumping locomotion could be to facilitate movement from one place to another during food and mate searching (Mazzoni et al., 2010), as well as to escape from predators (Burrows,

2007b). In many cases insects have developed the ability to easily handle the wide variety of substrates found in nature (Bernays, 1991; Jindrich and Full, 2002). Owing to their small size, jumping locomotion strategies allow them to reach high speed, acceleration and distance in a short time (Chapman, 1998; Ritzmann and Zill, 2009). An insect's leg is generally composed of six segments articulated by monocondylar joints and dicondylar pivots held together by an elastic membrane (Wootton, 1999). During evolution, this basic structure has undergone several morphological adaptations, especially in insects used to jumping, such as orthopterans, fleas, some coleopterans (e.g. Chrysomelidae, Alticinae) and hemipterans (e.g. Cercopidae, Cicadellidae, Membracidae and Psyllidae). In many cases insects have also developed mechanisms to store the energy produced by slow muscle contraction before the jump and to release it quickly, similarly to a loaded spring. To date, jumping locomotion has been studied to understand kinematics, neural mechanisms, energy cost and scale effects (Alexander, 1995; Biewener and Blickhan, 1988; Scholz et al., 2006), but also to extract bio-mimetic principles to develop robotic platforms, which could use these mechanisms to move in unstructured and uneven terrains (Cham et al., 2004; Scarfogliero et al., 2009). The jumping strategy of insects has been studied by means of high-speed video recordings and anatomical or physiological observations (Bennet-Clark and Lucey, 1967; Brackenbury and Wang, 1995; Burrows and Morris, 2003; Burrows, 2006).

Nowadays, a great number of features have been identified, such as average take-off velocity, average thrust, leg morphology and kinematics, and the mechanisms for storing and releasing muscular energy (Gronenberg, 1996; Burrows, 2003). However, the instantaneous force applied to the ground during the extremely fast thrust phase of the jump has not been characterized in these small animals. The Auchenorrhyncha (suborder of Hemiptera) includes some of the most accomplished jumpers. The cercopid *Philaenus spumarius* (4.0–9.8 mm body length) takes off in 1.0–1.5 ms with a take-off velocity of 2.5–4.2 m s⁻¹ (Burrows, 2003). Some species of cicadellids such as *Empoasca vitis*, *Aphrodes makarovi*, *Cicadella viridis* and *Graphocephala fennahi* (3.5–9.2 mm body length) take off in 4.4–6.4 ms, with a speed of approximately 1.1–2.5 m s⁻¹ (Burrows, 2007b). Both *P. spumarius* and the abovementioned cicadellids have jumping muscles (i.e. trochanteral levator and depressor muscles) housed in the metathorax (Burrows, 2003; Burrows, 2007b). In this way, the hind legs used to propel the jump are lightweight and can be quickly accelerated. Moreover, these two antagonist muscles have a co-contraction period just before the jump is initiated (Burrows, 2007a). This co-contraction period, which anticipates the take-off (i.e. cocked phase), is longer in Cercopidae (~2 s) than in Cicadellidae (80 ms) (Burrows, 2007a; Burrows, 2007c). Furthermore, there is also a difference in the duration of the acceleration period: 1 ms in cercopids *versus* 4–6 ms in cicadellids (Burrows, 2007a; Burrows, 2007b); the latter makes Cicadellidae the best candidates for experimental observations.

Individuals of the green leafhopper, *C. viridis* (Linnaeus 1758) (Fig. 1), can be easily observed and collected; they have good jumping performance (Burrows, 2007b) and can easily be reared in laboratory conditions. Data extracted from videos of *C. viridis* jumps, taken at 1000–5000 frames s⁻¹, already exist and provide measures of average speed and acceleration (Burrows, 2007b). Even if average values provide useful information for making comparisons among different animals, they are partial because they do not provide instantaneous figures on the interaction between the ground and the legs. Furthermore, the instantaneous force applied to the ground during the thrust phase of the jump has not been characterized in *C. viridis*. There is a need for tailored observations in order to allow

instantaneous investigation of the abovementioned parameters and to properly address the optimization mechanisms of the jumping motion.

Our work aimed to investigate the mechanism followed by insects for jumping and to obtain information on which optimization mechanisms are at work during the jumping process. From a biomechanical point of view, it is very important to know and be able to analyse in detail the instantaneous development of powerful forces that occur in extremely fast time periods. To address this goal, this research analyses the jumping take-off in *C. viridis*, through high-speed recordings, in order to determine the trajectory, instantaneous velocity and instantaneous acceleration. The most relevant result is that *C. viridis* individuals accelerate their body at a constant acceleration (152 m s⁻² on average), exerting a constant force throughout the leg elongation phase of the take-off. On average, the take-off velocity is 0.88 m s⁻¹, the mean take-off angle is 57.55 deg and the acceleration period is 5.6 ms. A curve was finally derived through inverse kinematic analysis that represents the force exerted by *C. viridis* musculo-elastic structures *versus* leg elongation.

As a final introductory remark we would like to comment on the main rationale motivating this research. As roboticists, we started speculating on the fact that for a jumping system the force exerted by body structures has to be optimized in order to avoid structural damages while guaranteeing minimal weight and long jumping distance. We observed that the work exerted on a jumping body to acquire a given kinetic energy is equal to the force applied on that body multiplied by the relative displacement between the body and the soil. This work is equivalent to the kinetic energy and, together with the jumping angle, it produces a take-off speed and allows a distance to be covered. This work may result either from a variable force multiplied by leg elongation or from a constant force multiplied by the same displacement. It is evident that, for equal work, the force in the second case has a lower value than the peak force in the first case (as a consequence of the mean integral value theorem). This consequently minimizes the risk of substrate failure and damage to the parts of the legs in contact with the ground. We then verified whether this also occurs in animals, validating our hypothesis for artificial systems. Therefore, the results of our study

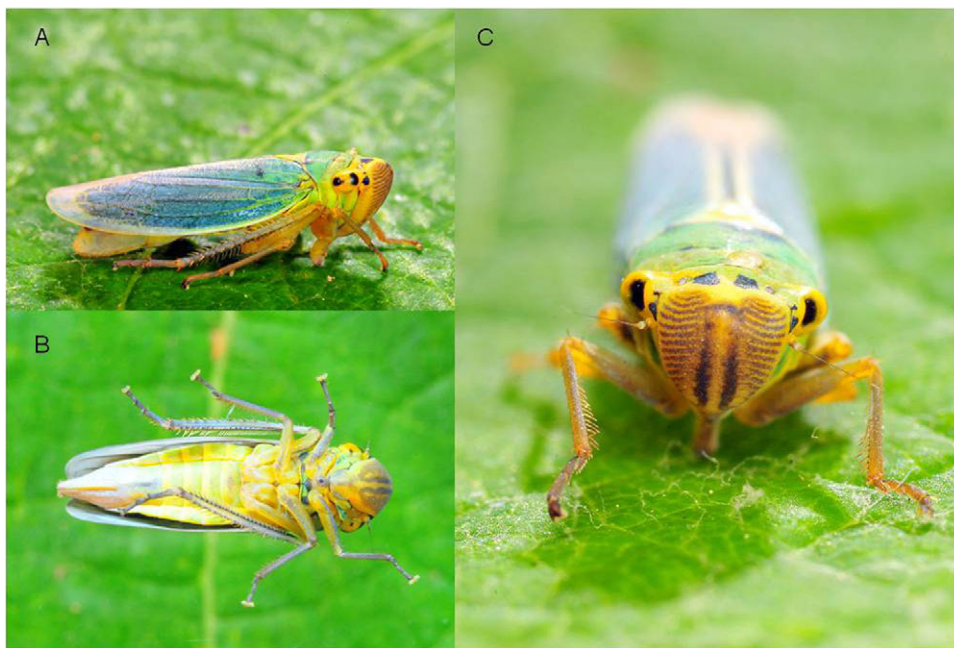


Fig. 1. The green leafhopper, *Cicadella viridis*. Lateral view (A), ventral view (B) and frontal view (C) of a *C. viridis* female.

have a broad relevance in the design of jumping systems. Finally, a by-product of our research has been to demonstrate that kinematics in *C. viridis* plays an important role in optimizing the dynamics of the jump, intrinsically providing constant acceleration without instantaneous modulation of muscle force by the nervous system.

MATERIALS AND METHODS

Experimental setup

Cicadella viridis adults (Fig. 1) of both sexes were collected between April and September 2009 and April and June 2011 in Pontedera, Pisa, Italy (43°41'19.62"N, 10°45'13.91"E and 43°36'18.88"N, 10°35'05.96"E), in grasses behind cane thickets. Specimens were reared in the laboratory within four polycarbonate terrariums (250×250×250 mm) filled with potting soil and wild grasses (genera *Juncus*, *Carex* and *Holcus*) collected in the same habitat of the insects. These plants served also as food for *C. viridis*. A total of 67 insects were used for the observations and video-recordings. They were placed, one at a time, in a polycarbonate chamber (80×75×18 mm, length × height × width, S. B. di Bertoldo Giorgio, Treviso, Veneto, Italy) with a roof made of a thin elastic net. Temperature was maintained at 26±2°C and relative humidity at 40±5% during all experiments. The thrust phase that anticipates take-off was analysed using a HotShot 512 SC high-speed video camera (NAC Image Technology, Simi Valley, CA, USA), following a method recently used for analytical characterisations of different insect behaviours (Benelli et al., 2012a; Benelli et al., 2012b; Benelli et al., 2013). Sequential images from each jump were captured at a rate of 8000 frames s⁻¹ with an exposure time of 0.125 ms. The HotShot 512 SC video camera stores images with a resolution of 512×256 pixels directly to its internal memory. These images were downloaded into a dedicated computer for data analysis. The area in which the insects were expected to jump was lit with four LED illuminators (RODER SRL, Oglanico, Torino, Italy) that emit light (420 lm each) at $\lambda=628$ nm. The red light was chosen because it matches the maximum absorption frequency of the camera and does not damage the visual apparatus of the insects because they do not possess receptors for that wavelength (Briscoe and Chittka, 2001).

Video-tracking methodology

Selected videos were edited with NAC HSSC Link software (NAC Image Technology) in order to isolate the take-off portion from the whole video. Some videos were analysed in advance with the native NAC software of the high-speed camera, which requires manual tracking of an area at a time. We developed an original image-processing algorithm, to reduce possible errors and automate the tracking in some cases. Moreover, because a wide range of software is commercially available, a metal sphere (diameter: 5 mm) freely falling under gravity was used as benchmark to compare the tracking results from different software, the manual tracking method and our algorithm. These tests were used to assess whether ProAnalyst suite (Xcitex, Cambridge, MA, USA) software was able to provide reliable tracking of moving objects and show negligible errors in the trajectories of tracked areas.

Definitive video tracks were analysed, using automatic tracking with ProAnalyst suite, to mark out the motion of the *C. viridis* centre of mass (G_c , hereafter) situated between the metacoxae (Burrows, 2007c). The tracking methodology was based on the selection of a distinct feature and the determination of its frame-by-frame motion characteristics (i.e. position, velocity and acceleration) over time, with respect to the image plane. During automatic tracking, the user selects the feature location in a single initial frame. This feature is

defined as a rectangular region of pixels in the initial frame. The software then examines subsequent frames and automatically finds and tracks the feature. In order to avoid bias, each characteristic feature parameter was configured as follows. With the search radius multiplier, we configured how large of an area to search for template matches, i.e. a percentage of the initial region size defined for that feature. A value of 100% indicates that the algorithm should search in a region as large as the initial region size. Because larger values result in larger search areas and thus in an increased probability of false matches, although a typical value for this parameter is 300% we used a value of 150% in all analysed videos. The sensitivity of the matching algorithm was configured using threshold tolerance. The tracking algorithm assigned a value between 0 and 1 to all points within the search region, indicating how well they match the template region. All values below a set threshold were discarded. A typical threshold value of 0.85 was used for this parameter. With the sub-pixel accuracy algorithm, the best-fit match to the template at a sub-pixel level was estimated. A two-pass dual matching algorithm was also used to avoid false matches. Indeed, this technique was more able to distinguish features with both dark and light features. Finally, we made sure that trajectory prediction algorithms both in the horizontal and vertical directions were disabled. Each automatic tracking process made by the software was carefully followed and checked by eye to assure that the resultant auto-tracked paths corresponded to the actual raw image sequence.

Data analysis

In the fully levated position (i.e. the configuration just before the jump), the first movement of the hind legs was referred to as $t_0=0$ ms, so as to align and compare various jumps. The instant when the hind legs lost contact with the ground was considered as the end of the acceleration period, t_{fin} (Fig. 2). The polynomial regression method (Chambers, 1992) was used to analyse data sets of trajectories and instantaneous velocities. The curve that best fit the observed data was obtained by estimating polynomial coefficients with a tentative degree, testing their significance and analysing the differences between calculated and observed values (i.e. residual analysis). If residuals were normally distributed, homoscedastic and not autocorrelated, the analysis was interrupted and the regression model was considered acceptable. For each jump's trajectory and instantaneous velocity, polynomial regressions from the 1st to the 12th degree were calculated, so as to include a wide range of possible functions and not restrict the analysis to less general models (e.g. linear, exponential or logarithmic regression). In order to verify a more specific motion model associated with accelerating bodies, the constant-power model (Stephenson, 1982) was also tested, analysing a 0.5 degree regression model for velocity over time. Among the regression models obtained, those with a low significance of the coefficient of the highest-degree monomial ($P<0.05$) or a low value of the coefficient of determination R^2 were discarded. To evaluate the effectiveness of the accepted regression models, a standardized residual analysis was conducted using the Shapiro–Wilk test for normality (Royston, 1995), the Breusch–Pagan test for heteroscedasticity (Breusch and Pagan, 1979) and the Durbin–Watson test for autocorrelation (Durbin and Watson, 1971). When the diagnostic analysis of the residuals from the above regression models revealed heterogeneous or non-Gaussian errors, a Box–Cox power transformation (Box and Cox, 1964) was used on the dependent variable. The transformation involves a λ parameter that can be estimated from the data using the method of maximum likelihood. This is a useful method to smooth heteroscedasticity when the distribution of the dependent

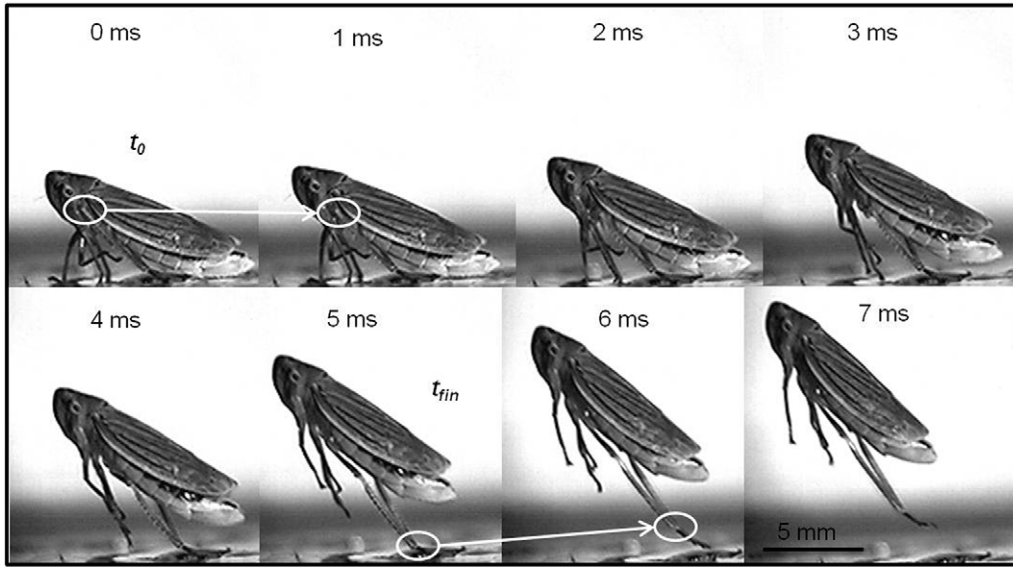


Fig. 2. Sequential images of a typical *Cicadella viridis* jump were used to illustrate the methodology for determining the set of experimental data to be analysed. The initial time (t_0) is set at the beginning of the thrust, intended as the start of body movement simultaneously with the synchronous movement of the hind legs; the final time (t_{fin}) is the occurrence of the legs' detachment from the ground.

variable, despite being positive, is unknown. Data analysis and tests were performed with R software (version 2.6.2, R Foundation for Statistical Computing, Vienna, Austria).

Model description

A mathematical model of *C. viridis* legs was built in order to clarify and identify the underlying mechanism determining the kinematics and dynamics of the take-off phase. The position (x and y coordinates) of the leg joints was obtained from videos showing the ventral, frontal and lateral views of the take-off phase of the jump (Fig. 3). Average data for the limb size and mass measured on the individuals that performed the experiments were used to programme the model ($l_a=4.21$ mm, $l_b=2.45$ mm, $d=0.82$ mm, $m=19$ mg, where l_a is the tibial length, l_b is the femur length, d is the distance between the two coxo-trochanteral joints and m is mass).

RESULTS

General description of experimental data

The results are based on an analysis of 67 individuals of *C. viridis*. All 67 jumps were studied in order to extract the three-dimensional kinematics and spatial configuration of the legs, while a subset of 46 jumps (32 females and 14 males), characterized by a trajectory parallel to the camera observation plane, was used for analysing the position of the centre of mass over time. A total of 217 ± 45 frames were analysed from each video. Measurements are given as means

\pm s.e.m. The movies of two selected *C. viridis* jumps are included as supplementary material (supplementary material Movies 1, 2).

Morphological measurements and take-off characterisation

The hind leg length of tested *C. viridis* specimens is 98% of total body length, while the ratio between the hind tibia and the hind femur is 1.7 (Table 1). Starting from the assumption that each jump begins when both hind legs are simultaneously depressed at the coxo-trochanteral joint with the extension of the femoro-tibial joint, the mean take-off time measured in the experiments is 5.6 ms and the body is accelerated to a mean take-off velocity of 0.9 m s^{-1} , with a mean take-off angle of 57.5 deg (Table 2).

Take-off trajectory

The displacement coordinates were extracted from *C. viridis* jumps ($N=46$) whose trajectory lay in a plane very close to perpendicular with respect to the longitudinal axis of the video camera. The beginning of the thrust phase was characterized by the motion of the trochanter, clearly manifested by the movement of the femur to the back of the body ($t=0$). This occurs while the tarsi remain anchored to the ground in the same position. The *C. viridis* centre of mass (G_c , hereafter) was tracked in each frame starting at $t=0$ until detachment from the ground at t_{fin} (Fig. 2). The displacement of each *C. viridis* G_c was determined by analysing the sequential images taken from the side (Fig. 4). To extract the trajectories from the videos, at least four areas containing the G_c were identified in order to eliminate bias related to the choice of the feature's shape. ProAnalyst software, after setting the parameters as explained in

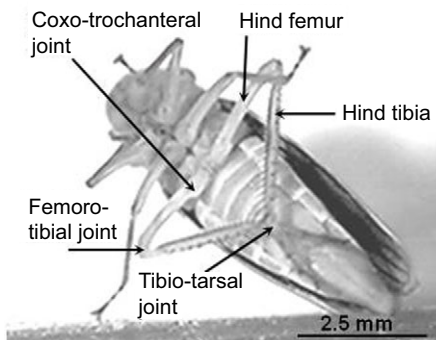


Fig. 3. Ventral view of *Cicadella viridis* with leg joint description.

Table 1. Measured values of *Cicadella viridis* body length and hind leg length

Body part	Length (mm)
Whole body	8.46 ± 0.07
Hind leg	8.31 ± 0.07
Hind leg, femur	2.45 ± 0.02
Hind leg, tibia	4.21 ± 0.03
Ratio	
Tibia/Femur	1.72 ± 0.01
Hind leg/Body	0.98 ± 0.00

Values are means \pm s.e.m. ($N=46$).

Table 2. *Cicadella viridis* jump characteristics, extracted from experimental data analysis

Jump characteristic	Mean \pm s.e.m. (N=46)
Take-off angle (deg)	57.55 \pm 1.62
Take-off velocity (m s ⁻¹)	0.88 \pm 0.03
Take-off acceleration (m s ⁻²)	151.96 \pm 8.55
Time to take-off ($\times 10^{-3}$ s)	5.64 \pm 0.17

the Materials and methods section, tracked these areas automatically. The series of coordinates obtained were averaged so as to have a single mean trajectory (x_c, y_c) for the G_c . The displacement of the G_c coordinates (x_c, y_c) in the plane was analysed using the polynomial regression method. In all cases, G_c trajectories were also analysed using the Box–Cox transformation. This analysis showed that individual G_c trajectories are not significantly different from linear trajectories (Box–Cox transformation: $\lambda=1$, 95% confidence interval, $N=46$) during take-off in all jumps analysed (Fig. 5).

The mean take-off angle calculated from the regression line slope was 57.55 \pm 1.62 deg (Fig. 6). Because the *C. viridis* trajectory was not always perfectly orthogonal to the camera, and because the y_c displacement plotted against time [$y_c(t)$] was larger than the x_c displacement (due to the fact that the take-off angle is greater than 45 deg), the y displacement was analysed first. The reason for this is mainly because the vertical displacement was not affected by the trajectory angle with respect to the axes of the camera, and also because it offered a greater pixel range that, in turn, guaranteed a lower incidence of intrinsic software errors. However, taking into account that errors in x_c displacement (which are not quantitatively perceptible by the eye) only result in an under-calculation of the mean velocity and acceleration and do not change the outcome of this research – i.e. the analysis of the instantaneous development of these two physical quantities – we used displacement *versus* time curves (Fig. 7) for instantaneous velocity analysis.

Instantaneous velocity

Cicadella viridis displacement in each jump was used to calculate instantaneous velocity ($\Delta y/\Delta t$). The values obtained were analysed using the polynomial regression method testing models from the 1st to the 12th degree (fitting linear model in R) and comparing these results with those from the constant-power model. The models giving the best results were verified afterwards *via* residual analysis using the Shapiro–Wilk test for normality, the Breusch–Pagan test for heteroscedasticity and the Durbin–Watson test for

autocorrelation. The choice of the model that best fitted *C. viridis* data was based on the evaluation of the R^2 value of the same model and on the significance of the coefficient of the highest-degree monomial. When this coefficient was significant with a probability equal or higher than 95%, the model was also verified using the abovementioned tests. It was rejected if its significance was lower than 95%. When more than one regression model met the verification criteria, we used a one-way ANOVA to verify whether there was a significant diversity among them. As a result, we showed that the velocity $v(t)$ can be approximated with a linear function of time (mean \pm s.d. $R^2=0.9201\pm 0.0469$, $N=46$). Only in a few cases did the constant-power model fit the data, but the fit was more negative (mean \pm s.d. $R^2=0.7745\pm 0.1315$, $N=4$) than constant force. The straight line is the best model that fits data with statistical significance in all the jumps analysed (Fig. 8). Thus, we can conclude that the speed of the *C. viridis* G_c increases with a near-constant acceleration during the whole take-off phase.

Model of hind-leg kinematics and dynamics

Because of the short take-off time, the capability to convert musculo-elastic force into constant force at the foot–ground interface cannot be based on the modulation of neuro-muscular activity. It must depend on the inherent characteristics of the legs. In fact, neuronal activities have typical response times in the range of 10 to 100 ms, while the whole jump takes just a few milliseconds. In order to clarify this intriguing issue and see whether there is a mechanism that allows this peculiar behaviour, a model of the insect legs was built to determine the kinematics and dynamics of the take-off phase.

The free body diagram of the insect during the jump is based on a series of kinematic and biomechanical observations and hypotheses. By analysing motion kinematics, it can be seen that the insects rotate the coxae before starting the jump until the two legs are aligned on the same plane. Then, during elongation, the legs move, remaining on this plane while in contact with the ground; leg movement, therefore, can be analysed with a two-dimensional model. The legs are modelled as rigid bodies and the flexural joints (femoro-tibial joint E and coxo-trochanteral joint F) are approximated to rotational hinges because their dimension can be neglected if compared with the length of the legs. The stiffness of the flexural joint is also negligible because the work needed to bend the joint is significantly smaller than that stored in the muscle during jumping. Contact between the ground and the feet can be modelled as a rotational hinge (O) with the assumption of no slipping. The

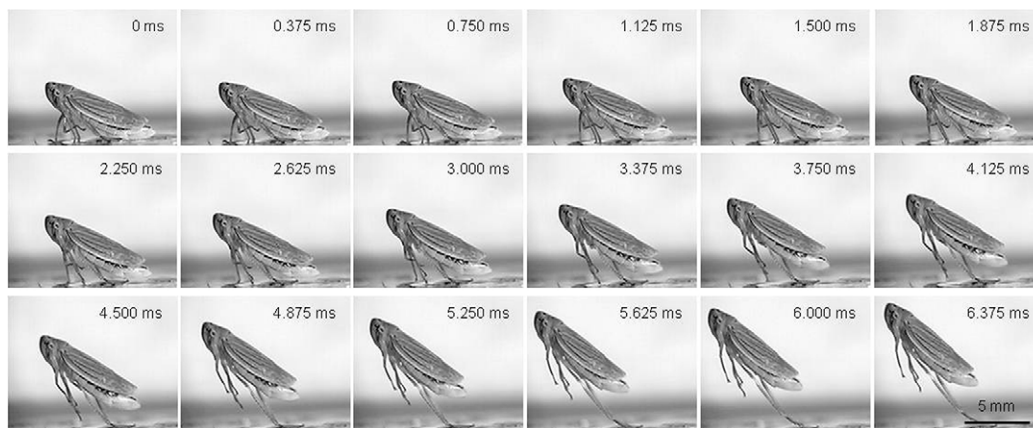


Fig. 4. Sequential images of a typical *Cicadella viridis* jump, lateral view. The images were recorded at 8000 frames s⁻¹. In this selected jump, take-off is 0.375 ms after the initial movement of the femoro-tibial joint of the hind legs. The images are arranged in rows from left to right.

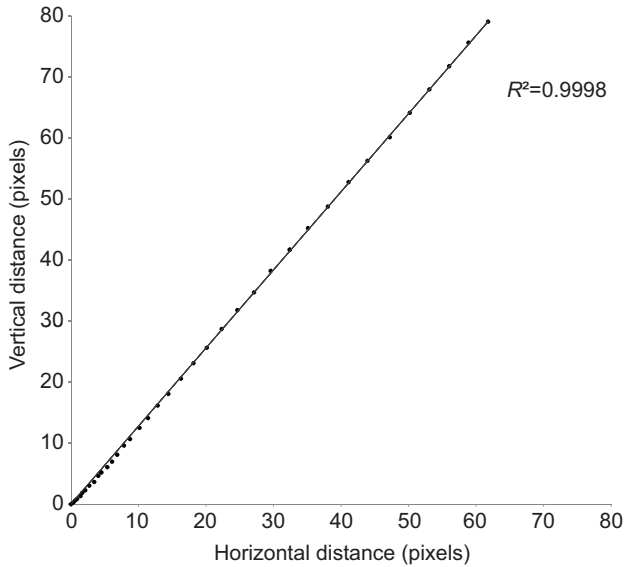


Fig. 5. *Cicadella viridis*. Centre of mass (G_c ; measured in pixels) displacement of a selected jump. The straight line is generated by the linear regression model applied to rough data ($R^2=0.9998$) and confirmed by the Box–Cox transformation ($\lambda=1$, 95% confidence interval). Normality was tested with the Shapiro–Wilk test.

free body diagram of the insect is shown in Figs 9 and 10. G_i is the centre of mass of the generic i th body, \vec{R} is the reaction force of one leg on the ground and $\vec{F}_{i \rightarrow j}$ is the force generated by the i th body on the j th body.

Three kinematic variables (the angles between the tibia and the ground and between the femur and the longitudinal axis of the *C. viridis* body, γ and θ , respectively, and the position of G_c along the y -axis, y_c) are introduced to describe the movement of the insect

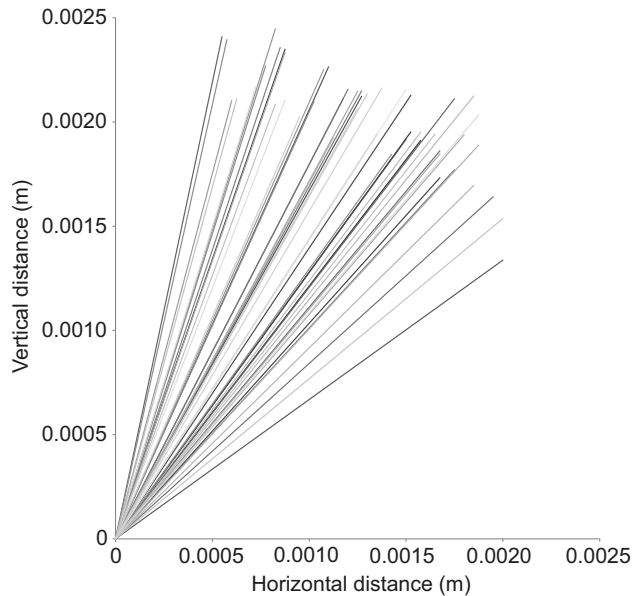


Fig. 6. Centre of mass trajectories during take-off in 46 jumps of *Cicadella viridis*. The results were obtained by displaying the regression straight lines of rough trajectories (vertical distance over horizontal distance). These data were used to calculate the mean (\pm s.e.m.) angle taken (57.55 ± 2.29 deg).

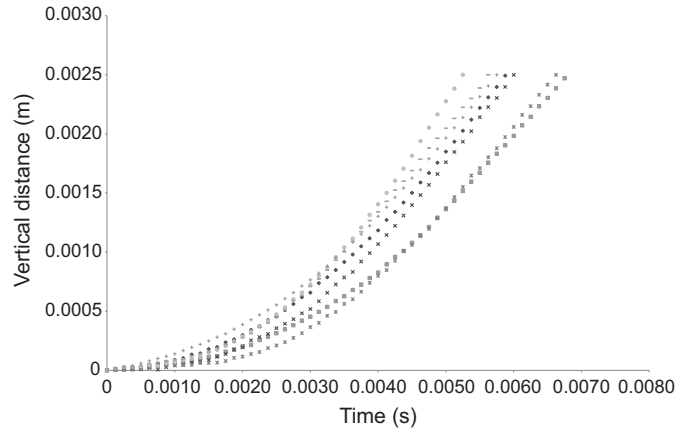


Fig. 7. *Cicadella viridis*. Displacement over time during the take-off phase of seven selected jumps. These curves are an example of the results obtained for the distance (m) versus time (s) curves in 46 jumps. Instantaneous velocity was calculated from these rough data and was then statistically analysed and averaged.

during the jump. Those variables respect the geometrical constraints described by the following equations:

$$y_c = l_a \sin \gamma - l_b \cos \theta, \quad (1)$$

$$d/2 = l_a \cos \gamma - l_b \sin \theta, \quad (2)$$

where l_a and l_b are the lengths of the tibia and the femur, respectively, and d is the distance between the two coxo-trochanteral joints.

The insect's dynamic behaviour during jumping is analysed with the following assumptions: (1) both hind legs of the insect move symmetrically with respect to the y -axis; (2) gravitational acceleration is neglected because its value is smaller compared with the insect's acceleration during the jump ($152 \text{ m s}^{-2} = 15.5 \text{ g}$); and (3) in accordance with the experimental observations, the insect jumps following a straight trajectory with a constant acceleration. This result leads to the following kinematic equation:

$$\ddot{y}_c = a = 152 \text{ m s}^{-2}. \quad (3)$$

Considering the previous assumption, the dynamics of the system can be written as:

$$\begin{aligned} \text{Body a} & \begin{cases} m_a \ddot{a}_a - \vec{R} + \vec{F}_{b \rightarrow a} \\ I_a \ddot{\gamma} = (\overline{G_a O} \times \vec{R} + \overline{G_a E} \times \vec{F}_{b \rightarrow a}) \cdot \hat{k} \end{cases} \\ \text{Body b} & \begin{cases} m_b \ddot{a}_b = \vec{F}_{a \rightarrow b} + \vec{F}_{c \rightarrow b} \\ I_b \ddot{\theta} = (\overline{G_b E} \times \vec{F}_{a \rightarrow b} + \overline{G_b F} \times \vec{F}_{c \rightarrow b} + \tau \hat{k}) \cdot \hat{k} \end{cases} \\ \text{Body c} & m_c \ddot{y}_c = 2F_{y_{b \rightarrow c}}, \end{aligned} \quad (4)$$

where I is the moment of inertia and \hat{k} is a unit vector perpendicular to the plane where the leg lies during jumping (see Fig. 10).

The dynamic behaviour of *C. viridis* is described by two vector equations (that can be decomposed into two scalar equations each) and three scalar equations where \vec{R} , $\vec{F}_{a \rightarrow b}$, $\vec{F}_{a \rightarrow c}$ and τ are the unknowns. These quantities can be evaluated by combining the insect's dynamic model (Eqn 4) with the geometrical constraints (Eqns 1, 2) and with the kinematic equation describing the constant accelerated movement of the insect (Eqn 3). The previous equations were numerically solved in order to evaluate the torque acting at the

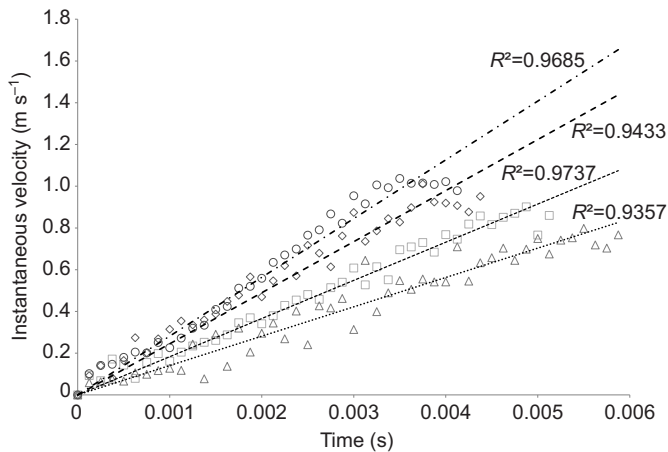


Fig. 8. Example of instantaneous calculated velocity in four typical jumps of *Cicadella viridis*. The linear model analysis of the calculated instantaneous velocity and residual analysis confirm with statistical significance that the constant force model best fits the data (mean $R^2=0.9201$) while the constant-power model and other polynomial models do not satisfy the criterion of acceptability. Four representative jumps are shown in the plot, as well as their regression straight line, which is the representation of the model that best fits the data.

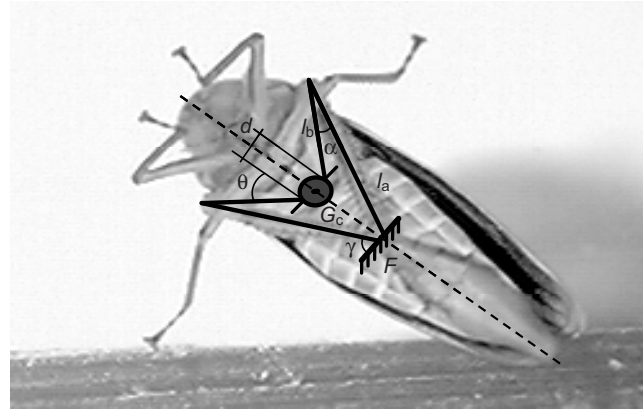


Fig. 9. Schematic representation of the parameters used for analysing *Cicadella viridis* leg kinematics. In the initial configuration, *C. viridis* stands still and the angle between the femur and the longitudinal axis of the body is $\theta=35$ deg. l_b , femur length; l_a , tibial length; d , distance between the coxo-trochanteral joints; G_c , external representation of the centre of mass position; F , thrust on the soil; γ , rotation angle at the tibio-tarsal joint with respect to the soil.

coxo-trochanteral joint (τ) and the force produced by the leg on the ground (\vec{R}). The initial configuration corresponds to the legs standing in the levated position (Fig. 9), and their movement was determined according to a value of constant acceleration of the insect's body of 152 m s^{-2} . At the beginning of the *C. viridis* jump, the angle between the femur and the longitudinal axis of the body is $\theta=35$ deg; the model runs for 7 ms until a complete leg elongation is reached.

By setting a constant acceleration to the insect's body, the results of the depicted dynamic model are: a constant force applied by the two feet on the ground and a variable torque acting at the coxo-trochanteral joint. Hence, during the jump, the legs act as a mechanism with a variable transmission ratio that maps a non-constant musculo-elastic input torque into a constant force at the ground. The force that the two feet exchange with the ground is $F_{\text{out}}=2R_y$, which is equal to 2.89 N, and the value of the ratio between the torque τ and F_{out} is shown in Fig. 11A,B.

This peculiar behaviour is related to the geometry of the legs. In fact, when they are fully levated or fully extended, each leg is close to a point of singularity (close to $\alpha=0$ and 180 deg; Fig. 9, Fig. 11B). In these positions, a small variation of θ does not correspond to a G_c motion; therefore, even a small torque applied at the coxo-trochanteral joint is converted into a much higher thrust action at the foot-ground interface. Because the leg moves between these two extreme positions during extension, a variable transmission ratio is obtained. This ratio, defined as input torque τ versus output force F_{out} , varies during *C. viridis* leg extension from a value close to zero, to a maximum and then back to zero. This bell shape inherently compensates the typical musculo-elastic pattern, converting the variable musculo-elastic force at input into an almost constant force at output. Considering the experimental evidence that this force is constant (discussed above), the pattern of the torque at the coxo-trochanteral joint follows the path of the variable transmission ratio shown in Fig. 11A.

DISCUSSION

Morphology and take-off characterisation

Among insects, in terrestrial locomotion legs must counterbalance body weight, but also provide active elongation and propulsive thrust

in movements such as escaping a predator or catching prey (Wootton, 1999). As a response to these movements, the ground reaction force has to counteract the exerted thrust in both the normal and the tangential direction, avoiding subsidence or slippage in order to seek effective motion. During the jump, the ground reaction force is much higher than the whole body weight, and high stresses are exerted on both the substrate and the legs (Burrows and Sutton, 2008). The segments (i.e. podomeres) of *C. viridis* hind legs should be stiff and lightweight. Indeed, both the femur and the tibia are tubular. The tibia is longer than the femur and it is also straight. These characteristics are very close to the theoretical optimum needed to resist multidirectional forces, to reduce the risk of damaging the exoskeleton during compression (Currey, 1967) and to minimize torsional shear stress that might displace the joints or damage the podomeres (Wootton, 1999). Another particular characteristic of the *C. viridis* hind leg is that its size is 82 to 98% of body length and 1.9 times the foreleg length. In jumping insects, it has been observed that the length of the hind leg is strictly correlated to the time needed to take-off, but not to the take-off velocity (Burrows and Sutton, 2008).

Instantaneous take-off velocity

For a given take-off speed, a longer acceleration time generates a lower ground reaction force, which helps minimize the risk of structure rupture in slender limbs. From a morphological viewpoint, the hind legs are very light compared with the whole body weight, suggesting that the force generated by the small tibial extensor muscle could be neglected, and that the key movement for the jump depends on the rapid depression of the trochanter by means of the large trochanteral depressor muscles located in the thorax (Burrows, 2007c). The *C. viridis* antagonist muscles acting on the coxo-trochanteral joint, which have a similar size and weight, have the same lever arm when the leg is completely retracted close to the body before the jump. In this phase, it was found that the motor activity pattern consists of a co-activation of both antagonistic muscles. This condition, while not generating any movement, causes a slight forward displacement of the *C. viridis* metacoxa and metathorax, which could provide energy storage in skeletal structures

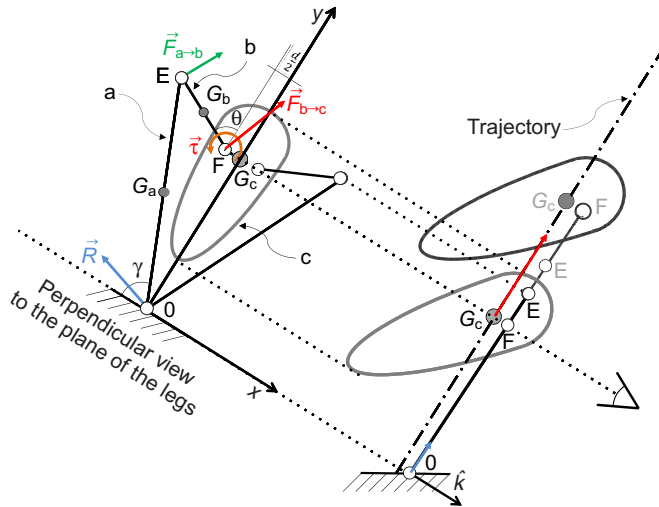


Fig. 10. Formal free body diagram of *Cicadella viridis* during the jump. The right part of the figure shows the insect moving along a straight trajectory with a slope of 58 deg. The left part of the diagram is a view of the insect perpendicular to the plane that contains the legs. See the List of symbols for definitions of the symbols displayed here.

(Burrows, 2007c). The peak extensor's activity, together with the decreased retractor's activity just before take-off, is enough to trigger the rapid extension of the coxo-trochanteral joint, releasing any stored energy in tendon and skeletal structures. During such elongation, the lever arm of the extensor muscle increases up to a maximum when the leg is fully extended, while the retractor's lever arm remains mostly unchanged. Considering these characteristics, the jumping force generated by *C. viridis* should have a typical spring-like pattern. It should soon reach a maximum value and it should decrease down to zero at complete leg elongation. Overall, our findings clearly demonstrated that *C. viridis* instantaneous velocity increases with a near-constant acceleration during the whole take-off acceleration period (that is, the time used by *C. viridis* to take off from the ground). This means that the legs in contact with the ground exert a nearly constant force at the body-ground interface. This is a relevant and interesting result if one takes into account that the thrust for jumping is generated by a musculo-elastic system that, due to its nature, does not provide a constant force.

Model of hind-leg kinematics

In order to understand how force transformation during *C. viridis* jumping is accomplished, hind-leg kinematics was analysed. It was highlighted that a motion – such as that of *C. viridis* during the take-off phase of the jump – with a constant force at the foot-ground interface minimizes stresses both in the legs and the substrate for a given take-off speed, representing a behaviour close to the theoretical optimum (Scarfogliero et al., 2009). This suggests that the morphology of *C. viridis* legs, and their displacement with respect to G_c , is responsible for the conversion of a musculo-elastic action into a constant force at the feet. The capability to convert a musculo-elastic force into constant force can be seen as a further specialization developed by *C. viridis*, minimizing the risk of subsidence or ruptures, and preserving the readiness for the jump. When analysing these findings in a wider framework, it can be observed that long-legged jumping insects, which exert lower ground reaction forces with respect to short-legged ones, are less subject to inefficient jumping, especially when interacting with

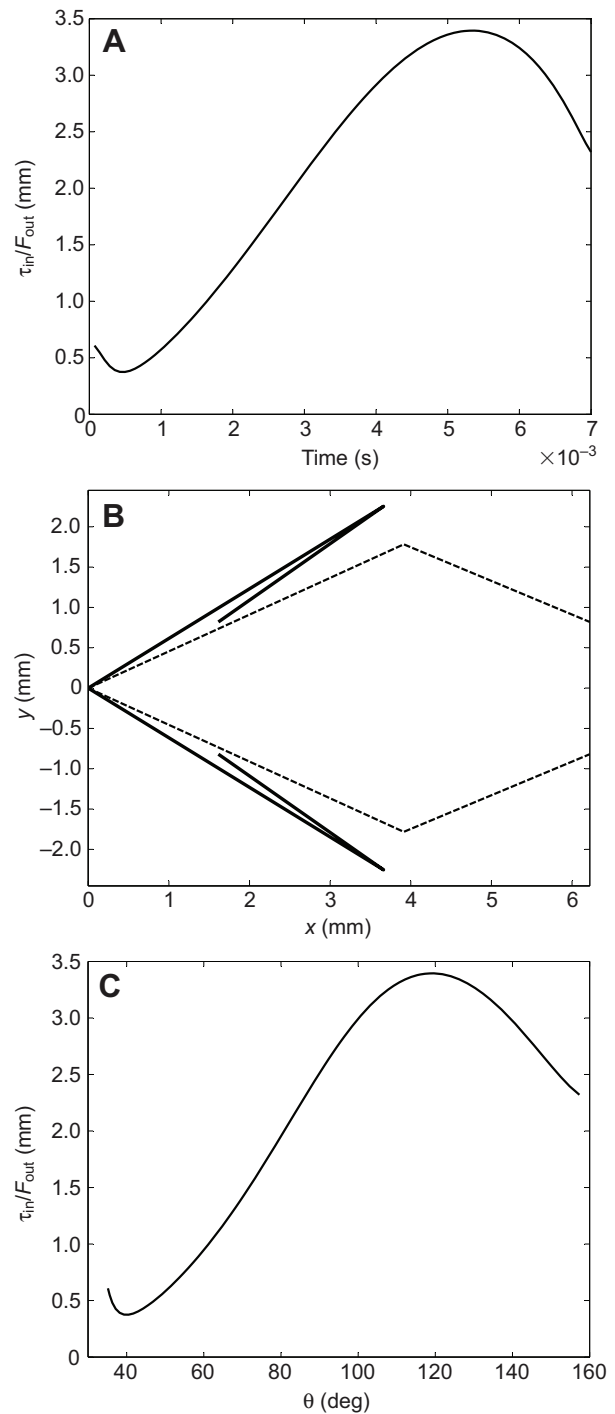


Fig. 11. *Cicadella viridis* legs act as a variable transmission ratio between the musculo-elastic action and the output thrusting force. (A) The ratio between the input torque (τ_{in}) and output force (F_{out}). Because the purpose of the mathematical model was to show the effect of leg motion, the morphology of the muscles actuating the joint was not simulated, thus preserving the simplicity and general validity of the model. (B) The starting (dashed lines) and final (solid lines) positions of the simulated model. (C) The τ_{in}/F_{out} ratio with respect to the angular position of the legs.

compliant substrates (Burrows and Sutton, 2007). If compared with the jump of *P. spumarius* (Burrows, 2003; Burrows, 2007b), the *C. viridis* jump is slower (4.7 and 0.9 ms^{-1} , respectively), but in contrast, it is cheaper in terms of energy consumption, by as much as 33%

(Burrows, 2007b). The fact that the insect adopts this strategy is of further interest when considering that jumping with constant thrust force is very close to the optimum strategy (Scarfogliero et al., 2009). Constant acceleration, and hence constant force, which minimizes stress in the legs and soil (Scarfogliero et al., 2009), could be considered as another solution to reduce possible breakage of the structures involved, from the legs to any surface used for take-off. In terms of escaping efficiency, this mechanism could ensure more successful jumps and a greater capacity for survival over different substrates.

Overall, it can be assumed that the evolution of the hind legs in *C. viridis* has been directed towards optimization of jumping locomotion. This peculiar locomotion strategy is achieved not only through complex neuro-physiological mechanisms that require time-consuming activation, but also through passive morphological mechanisms, which are always available without the need for any kind of activation. This is also confirmed by a recent analysis published by Li et al. (Li et al., 2012), in which similar results on take-off velocity and acceleration were obtained by means of a robotic platform reproducing the insect's leg mechanism and spatial arrangements. This passive optimization of processes, which is essential for survival, is not isolated to the case of *C. viridis* jumping locomotion. Another example of passive stabilisation is the reflex, defined by Brown and Loeb (Brown and Loeb, 2000) as an intrinsic neuromusculoskeletal response to disturbances with absolute absence of system delay. For instance, reflexes in cockroaches are important components of a locomotion stabilisation system independent from the neuro-physiological system, and completely intrinsic in their leg's structure (Full et al., 1998; Clark et al., 2001).

We believe that our findings could be the starting point for a kinematic analysis of a wide variety of biological actuation systems, with the aim to reveal what could be defined as a sort of intrinsic capability of materials, joints and structures to enable some of the most amazing abilities in the animal world. Finally, this new knowledge could be the basis for the design of high-performance machines whose mechanisms take inspiration from that of nature.

LIST OF SYMBOLS

\vec{a}_i	acceleration of a generic body
d	distance between the two coxo-trochanteral joints
E	femoro-tibial joint
F	coxo-trochanteral joint
$\vec{F}_{i \rightarrow j}$	force generated by the i th body on the j th body
G_c	<i>C. viridis</i> centre of mass
G_i	generic body centre of mass
I	moment of inertia
\hat{k}	unit vector perpendicular to the plane where the leg lies during jumping
l_a	tibial length
l_b	femur length
m	mass
O	point of contact between the feet and the ground modelled as a rotational joint
\vec{R}	reaction force of one leg on the ground
t_0	the instant of the first movement of the hind leg just before jumping
t_{fin}	the instant when the hind legs lose contact with the ground
(x_c, y_c)	<i>C. viridis</i> position coordinates of the centre of mass in the plane of trajectory
γ	angle between the tibia and the ground
θ	angle between the femur and the longitudinal axis of the <i>C. viridis</i> body
λ	estimated transformation parameter in the Box-Cox power transformation
τ	torque generated at the coxo-trochanteral joint

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