Biomechanics of gecko locomotion: the patterns of reaction forces on inverted, vertical and horizontal substrates

2015 Bioinspir. Biomim. 10 016019

(http://iopscience.iop.org/1748-3190/10/1/016019)

IOP Publishing Bioinspir. Biomim. 10 (2015) 016019 doi:10.1088/1748-3190/10/1/016019

PAPER

Biomechanics of gecko locomotion: the patterns of reaction forces on inverted, vertical and horizontal substrates

CrossMark

RECEIVED
13 August 2014

REVISED
6 November 2014

ACCEPTED FOR PUBLICATION
14 January 2015

PUBLISHED
4 February 2015

Zhouyi Wang[1,4], Zhendong Dai[1,4], Aihong Ji[1], Lei Ren[2], Qiang Xing[1] and Liming Dai[3]

1 Institute of Bio-inspired Structure and Surface Engineering, Nanjing University of Aeronautics and Astronautics, Nanjing, 210016, People's Republic of China
2 School of Mechanical, Aerospace and Civil Engineering, University of Manchester, Manchester, M13 9PL, UK
3 Department of Chemical Engineering, Case Western Reserve University, Cleveland, Ohio, USA
4 These authors contributed equally to the work

E-mail: zddai@nuaa.edu.cn

Keywords: biomechanics, reaction forces, ceiling, wall, Tokay gecko

Supplementary material for this article is available online

Abstract

The excellent locomotion ability of geckos on various rough and/or inclined substrates has attracted scientists' attention for centuries. However, the moving ability of gecko-mimicking robots on various inclined surfaces still lags far behind that of geckos, mainly because our understanding of how geckos govern their locomotion is still very poor. To reveal the fundamental mechanism of gecko locomotion and also to facilitate the design of gecko-mimicking robots, we have measured the reaction forces (RFs) acting on each individual foot of moving geckos on inverted, vertical and horizontal substrates (i.e. ceiling, wall and floor), have associated the RFs with locomotion behaviors by using high-speed camera, and have presented the relationships of the force components with patterns of reaction forces (PRFs). Geckos generate different PRF on ceiling, wall and floor, that is, the PRF is determined by the angles between the direction of gravity and the substrate on which geckos move. On the ceiling, geckos produce reversed shear forces acting on the front and hind feet, which pull away from the body in both lateral and fore-aft directions. They use a very large supporting angle from 21° to 24° to reduce the forces acting on their legs and feet. On the floor, geckos lift their bodies using a supporting angle from 76° to 78°, which not only decreases the RFs but also improves their locomotion ability. On the wall, geckos generate a reliable self-locking attachment by using a supporting angle of 14.8°, which is only about half of the critical angle of detachment.

1. Introduction

Geckos (*Tokay*, *gecko*) can move freely on a vertical surface and crawl across a ceiling with various roughness (Maderson 1964, Russell 1975, Autumn *et al* 2000, Chen *et al* 2006, Wang *et al* 2010b, 2011). This ability is attractive for scientists to know how geckos adhere on various rough and inclined substrates by hierarchical seta on toes and by regulation reaction forces (RFs). The gecko's outstanding moving ability depends upon many synergetic effects, such as elaborate morphological micro-structure (Ernst and Ruibal 1967, Williams and Peterson 1982, Bauer and Russell 1988), super adhesive ability (Irschick *et al* 1996, 2006, Autumn *et al* 2000, 2002, Huber *et al* 2005), motion coordination among legs under stance phase in crawling posture (Li and Dai 2012) and fine perception to the contact and adhesive forces up to the resolution to mN (Guo *et al* 2012). The super adhesive ability depends largely on van der Waals forces and/or capillary forces of the half million hairs (or setae) on the toe (Autumn *et al* 2000, Huber *et al* 2005). The modulation on attaching and detaching procedure largely depend on the control the angle of attaching and detaching force, which was experimentally demonstrated by a single seta (Autumn *et al* 2000) and by a single toe (Autumn *et al* 2006) and the critical angle of detachment (α_{CD}) was obtained as 30°. These results were supported by mechanical models (Jagota and Bennison 2002, Arzt *et al* 2003, Tian *et al* 2006, Chen *et al* 2008). Inspired by the unique hierarchical seta structure and van der Waals mechanism, many dry adhesives were developed (Del Campo and Arzt 2007, Boesel *et al* 2010, Bartlett *et al* 2012, Hu *et al* 2013, King *et al* 2014) and some of them even reached ten times stronger adhesion force than its natural counterpart (Qu *et al* 2008). Even so, the moving ability of gecko-mimicking robots still lags far behind that of gecko, because any motion of an object is finally determined by the forces acting on it (Dickinson *et al* 2000) and we still lack of detail information about RFs during gecko locomotion. To understand the gecko's locomotion, or sprawl-postured legged locomotion, we need to know how geckos delicately coordinate the RFs among each foot under stance phase and how they modulate the RFs between feet and the substrates, namely, generating adhesion, detecting contact, modulating the attaching and detaching, especially, when the slope angle of the substrates changes. Theoretically, the knowledge can be obtained by modeling the legged locomotion and/or by measuring the RFs. Mathematically modeling the locomotion, RFs between each foot and substrate and many internal parameters, such as internal forces acting on each joint, can possibly be calculated (Wadden and Ekeberg 1998, Full and Koditschek 1999, Dickinson *et al* 2000, Holmes *et al* 2006), but the exact prediction by the models is much more difficult because the complex of the mechanism, for example, (1) the discontinuous constraint due to the changes between attaching the foot to and detaching the foot from the substrate (Dai and Sun 2007, Dai 2008), which introduce nonlinear impact and vibration to the legged mechanism; (2) the change of degrees of freedom (DoF) from a open-chain mechanism with a high DoF in the swing phase to a closed-chain mechanism with a low DoF in the stance phase (Dai *et al* 2007) results in an overdriven status among the legs under stance phase. Here the force coordination among the feet/legs becomes one of the most critical issues for not only efficient locomotion, but also for reliable attachments when adhesion is needed, unfortunately, the RFs can not be calculated out based on rigid body mechanics. So the direct experimental measurements of the RFs between each foot and substrate thus become one of the most effective ways to understand the legged locomotion.

Since the first force platform was invented in 1938 to measure the three-dimensional (3D) RFs of a cat moving on a horizontal substrate (Manter 1938), many researches have been conducted to measure the ground RFs (Sparrow and Tirosh 2005) or 3D RFs (Chateau *et al* 2009, Lin and Trimmer 2012). A 3D force platform was developed (Full and Tu 1990, 1991, Biewener and Full 1992) and has been employed to measure the 3D RFs of different animals (Autumn *et al* 2006, Chen *et al* 2006, Goldman *et al* 2006, Mcelroy and Reilly 2009, Welch *et al* 2009). Chen *et al* have measured the complete RFs of geckos (*Hemidactylus garnotii*) under trotting gait where the duty factor less than 0.5. Here the complete RFs mean the full procedure from very beginning attachment to very last detachment of a foot on substrate. The force platform can nether measure the full RFs of individual foot acting on substrate when the duty factor larger than 0.5, and nor the RFs of each single foot successively acting on substrate during locomotion. On the other hand, how does the inclined plane angle (from 0° horizontal floor to 90° vertical wall) influence animals' locomotion behaviors and RFs has become great interesting. The behaviors and RFs of upstanding quadrupeds (Dutto *et al* 2004, Gregor *et al* 2006, Lammers *et al* 2006, 2007, Schmidt and Fischer 2010, 2011), sprawl-postured quadrupeds (Jayne and Irschick 1999, Higham and Jayne 2004a, b, Autumn *et al* 2006, Wang *et al* 2011, Foster and Higham 2012, Endlein *et al* 2013, Foster and Higham 2012, Krause and Fische 2013) and insects (Lipp *et al* 2005, Goldman *et al* 2006) were studied. When the slope angle larger than 90°, the kinematics and behaviors were studied for gecko (Wang *et al* 2010b). However, the RFs were not measured for locomotion on inverted substrate. So the main questions addressed in this paper were: (i) How does the pattern of reaction forces (PRFs) change with change of three typical substrate orientations? (ii) How to present the difference of PRF clearly? (iii)What are the mechanical principles which govern the locomotion?

To answer above questions, we used a newly developed force measuring array (FMA) (Dai *et al* 2011), and have, for the first time, measured the RFs successively acting on the each individual foot when geckos move freely on inverted, vertical and horizontal substrate (i.e. ceiling, wall and floor) without the influence of duty factor. Based on the measured RF data on each individual foot, we proposed an approach to present the characteristics of RFs—the PRFs and set up mechanical models under different substrate positions (floor, wall and ceiling). The mechanical principles of how geckos modulate the PRFs to adapt to different substrate inclination revealed in this study may provide inspiration for the development of gecko-mimicking robots.

2. Materials and methods

2.1. Animals

Gecko lizards (*Tokay gecko*, Linnaeus) were obtained from a gecko feeding base in Guangxi Province, China. Animals were housed in a natural simulated room with fresh water and live insects as food. The animal house was kept with a natural light cycle with temperatures no lower than 15 °C during winter and no higher than 35 °C during summer, and a humidity of 50% ~ 70%, according to the rules of China Association of Wild Animal Protection. The experiments have been approved by animal care and use protocols committee of the University. The geckos used in this study have a body gravity (G) 632.1 ± 23.5 mN (N = 16, mean ± S.D. N presents number of animals), and the snout-to-vent length 140.2 ± 14.1 mm (N = 16). Before the experiments, the geckos were trained in two boxes connected by an aisle, which was similar to the aisle of the FMA (figure 6(a)).

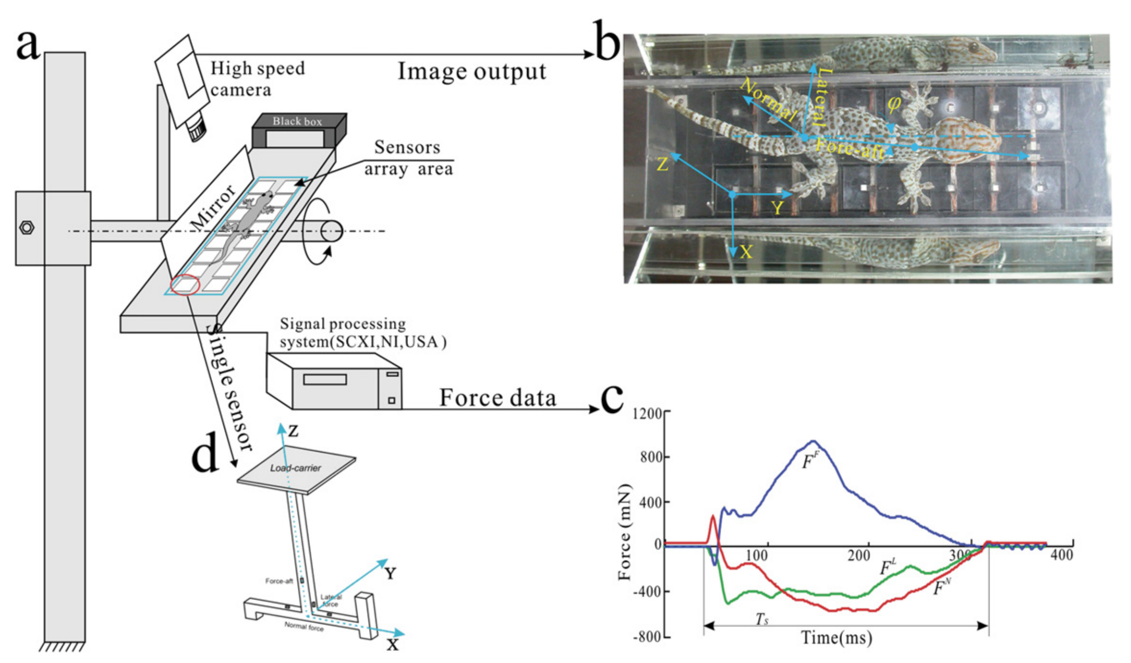

Figure 1. Three-dimensional reaction force measuring and behavior observing system and the measured forces. (a) The system consists with a force-measuring array (FMA) and high speed video-recording camera. The FMA consists of 16 separate 3D sensors. The FMA can be rotated from horizontal to up-side-down invert to simulate yield inclined substrates. (b) When a gecko moves through an aisle of the FMA, the vertical view and two side-views in mirrors of locomotive behaviors were recorded by a video camera located perpendicular to the FMA at 215 frames per second. (c) The reaction forces of a front left foot of a freely climbing gecko as a function of time, gecko generates a negative normal force (F^N), negative lateral force (F^L) and positive fore-aft force (F^F) by the left front limb between the vertical substrate (wall) and a foot during stance phase. (d) A single three-dimensional sensor for constructing FMA.

2.2. Experimental setup

We have developed a FMA, (figure 1(a)) to measure the 3D RFs (Dai *et al* 2011). The force measuring system consists of 16 3D sensors (figure 1(b)), manufactured by aluminum alloy. A thin glass load-carrier ($30 \times 30 \times 0.8$ mm) was glued onto the top of each sensor to act as a substrate. And the FMA could be rotated from horizontal to up-side-down to simulate the slope of substrates. The locomotive behaviors were recorded when geckos moved from one end of the aisle to a black box at another end of the aisle using high speed camera at 215 frames per second (figure 1(a)). To record the 3D locomotion behaviors, we mounted two mirrors on the left and right (figure 1(a)) of the sensor array to provide a possibility to record 3D locomotion behaviors by a high speed camera, namely, behaviors in lateral and fore-aft direction by the real image and side views in normal and fore-aft direction from the mirror images. The camera was mounted perpendicular to the sensor array and covered all array in the image. The force measuring and the image recording were synchronized by using a connected trigger.

2.3. Data analysis

We have performed 2176 test trials which the locomotion behaviors of unconstrained geckos and the RFs were recorded. Geckos do not always move smoothly from one end of measuring array to another end, we removed these trials and retained the 576 test trials (on ceiling: 176 trials, on wall: 207 trials, on floor: 193 trails and $N = 16$). With the help of simultaneous video-recording (figure 1(a)), we carefully checked the data of RFs and the recorded images to select those recordings which meet the conditions below for further analyses: (I) all toes of a foot acting on only one sensor or two sensors, when toes attached on two sensors, the components of RFs on each direction were algebraically added; (II) the selected data were only collected from the groups that geckos moved with near-steady velocity, and the difference between maximum and minimum velocity in one complete stride was below than 15% of the average velocity of the animal.

The RFs measured from the sensor-based coordinate system (X, Y, Z, figure 1(b). Y—length direction of the sensor array; X—width direction of the sensor array, Z—perpendicular to the sensor array and pointed out) were regulated into the gecko-body-based coordinate system (lateral, for-aft, normal, figure 1(b). Fore-aft—from tail to head and connecting the middle points of shoulder joints and hip joints; lateral—perpendicular to the fore-aft direction and through the middle point of shoulder joints; normal—perpendicular to the sensor array through the middle point of shoulder joints) by the deviation angle (φ), which comes from the video-record, to reduce the influence of the difference between two coordinates and evaluate the effect of RF on the gecko locomotion. The difference between two coordinate systems could be

Table 1. Three-dimensional reaction force peaks during gecko freely moving on inverted, vertical and horizontal substrates.

Force	Foot	N	Lateral reaction force(mN)	Fore-aft reaction force(mN)	Normal reaction force(mN)	Supporting angle α (°)	Driving angle β (°)
F_{RC}	Front	20	478.5 ± 123.5	737.4 ± 197.6	−407.2 ± 113.3	−24.81 ± 6.24	39.77 ± 11.48
	Hind	21	504.3 ± 173.0	−600.1 ± 204.7	−388.1 ± 93.8	−21.03 ± 9.60	136.42 ± 16.58
F_{RW}	Front	20	212.2 ± 116.4	466.7 ± 80.2	−149.1 ± 55.6	−14.80 ± 6.41	26.08 ± 11.53
	Hind	20	209.2 ± 134.7	455.1 ± 135.4	−94.3 ± 54.9 115.3 ± 55.6	−1.53 ± 10.85	13.78 ± 5.83
F_{RG}	Front	24	−29.7 ± 21.6 93.8 ± 35.2	−115.3 ± 63.9 69.2 ± 41.4	435.6 ± 87.4	78.13 ± 8.90	
	Hind	24	−31.4 ± 16.53 75.2 ± 21.6	−108.7 ± 72.3 96.6 ± 53.2	324.9 ± 91.7	76.23 ± 13.54	

calibrated by equation (1)

$$\begin{bmatrix} F^{L} \\ F^{F} \\ F^{N} \end{bmatrix} = \begin{pmatrix} \cos\varphi & -\sin\varphi & 0 \\ \sin\varphi & \cos\varphi & 0 \\ 0 & 0 & 1 \end{pmatrix} \begin{bmatrix} F^{X} \\ F^{Y} \\ F^{Z} \end{bmatrix}. \qquad (1)$$

The measured RF acting on a left front foot of a freely wall climbing gecko as a function of time over the stance phase (T_S) was shown in figure 1(c). The positive fore-aft force (F^F) drives the locomotion, while the negative lateral force (F^L) acting on left foot, pulling away from the gecko trunk, and the negative normal force (F^N) indicates adhesive force acting on the gecko's foot. The shear force (F^S) and overall RF (F^R) were also presented over stance phase (T_S) in figure 1(c). A larger supporting angle (α) indicates that overall RF (F^R) is closer to the normal direction of the substrate to support or hang the body gravity more effectively. A smaller driving angle (β) indicates that the F^R shifts more towards the moving direction to drive the animal moving forward more effectively (figure 1(d)). The lateral force (F^L), fore-aft force (F^F), and normal force (F^N) when the overall RF was maximum were selected out to present the RF; the average supporting angle (α) and driving angle (β) were calculated when shear force (F^S) and overall RF (F^R) were the maximum.

$$F^S = \sqrt{\left(F^L\right)^2 + \left(F^F\right)^2}, \qquad (2\text{-}1)$$

$$F^R = \sqrt{\left(F^L\right)^2 + \left(F^F\right)^2 + \left(F^N\right)^2}, \qquad (2\text{-}2)$$

$$\alpha = \arctan\left(F^N/F^S\right), \qquad \alpha \in (-90°, 90°), \qquad (2\text{-}3)$$

$$\beta = \left|\arctan\left(F^L/F^F\right)\right|, \qquad \beta \in (0°, 90°). \qquad (2\text{-}4)$$

2.4. Data filtering

We studied the influence of cut-off frequency of the signal regulation system (NI, USA) to the measured data from 50 to 1000 Hz, and selected the cut-off frequency of Butterworth filtering at 100 Hz.

2.5. Statistics

The moving speed of geckos on floor, wall and ceiling is different. What we are concerned here is the PRFs, or the internal relationship among the lateral, fore-aft and normal force. We do not try to dig out the relation of the value of RFs to the orientation of three substrates, but pay attention to the three RF components acting on each foot on various substrates only. We have selected data from 576 trials when the change of velocity no more than 15% of its average in trial. Data from all individuals were pooled, and SPSS software (SPSS15.0, Inc., Chicago, IL) was used for statistical analysis. Comparisons were made among data for front and hind foot using the co-variance analyses (ANCOVA) with a p value of 5%. For the ANCOVA analysis, the dependent variables were the lateral force, fore-aft force, normal force, supporting angle and driving angle respectively, the animal and velocity were considered as covariate variables. Differences were considered statistically significant when $p < 0.05$. The measurement data are presented in table 1 as mean ± standard deviation (mean ± s.d.).

3. Results

The mean peaks and angles of 3D RFs are presented by figures 2 and 3, and table 1 which correspond to the measurements when geckos move on inverted, vertical and horizontal substrates respectively (i.e. ceiling, wall and floor). To reveal the essential PRF and the relationship among RF components—lateral force (F^L), fore-aft force $\left(F^F\right)$ and normal force $\left(F^N\right)$, we plot F^L versus F^F and shear force $\left(F^S\right)$ versus normal force $\left(F^N\right)$ to present the relationship of the lateral force to the fore-aft force, and the shear force to the normal force respectively, which we defined as PRFs. To show the pattern clearly, we take three group data of RFs from a gecko freely moving on ceiling, wall and floor over one step cycle respectively, as graphic illustration and showed the results in figures 4–6, and presented the 3D RFs in videos 1–3, respectively. These figures and videos illustrated the relationship of the essential pattern of RF and the substrate orientations.

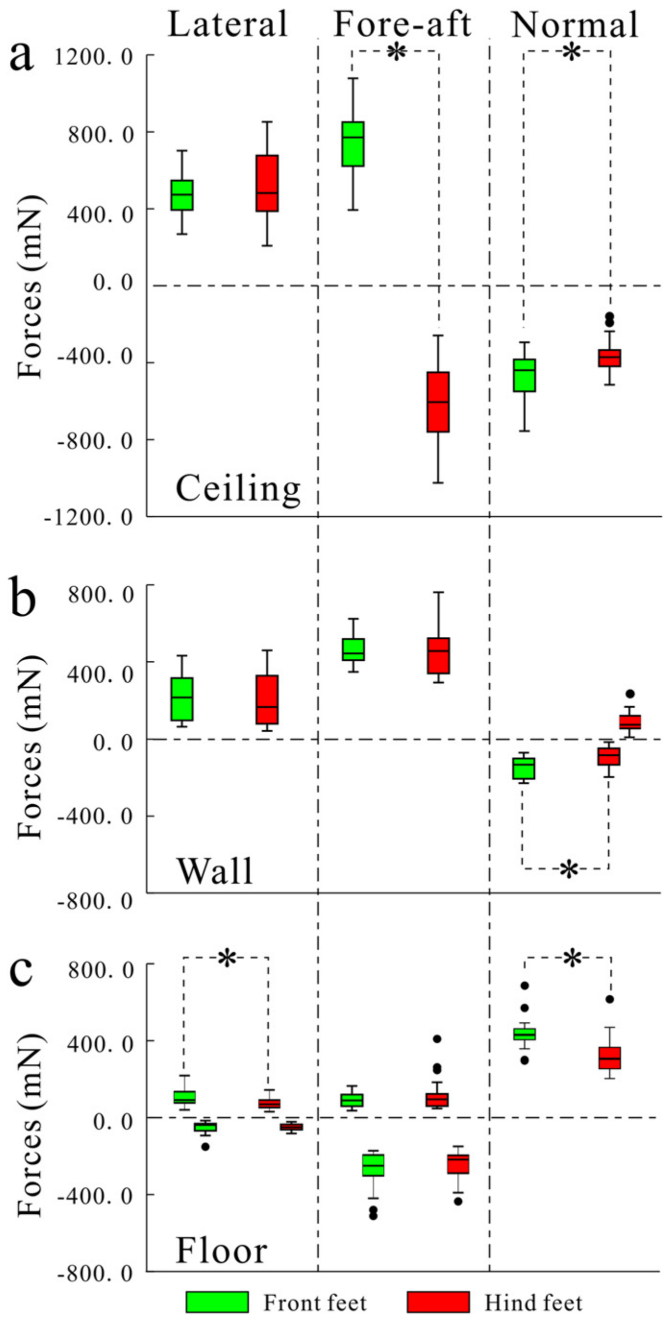

Figure 2. Box and whisker plots of peak of reaction forces during gecko moving on inverted, vertical and horizontal substrates (i.e. ceiling, wall and floor). (a) On ceiling (inverted substrate); (b) on wall (vertical substrate); (c) on floor (horizontal substrate). In order to unifiedly describe the peak of lateral reaction forces of left and right feet, the lateral force directing the body middle line is defined as positive lateral force (foot pushes away from the body), whereas, as negative lateral force. Each box represents 50% of the data, and the line within the box represents the median. Each whisker corresponds to 25% of the data. Black points represent outlier. Asterisks (*): significantly different between the peak of reaction forces of front and hind feet, $p < 0.05$.

3.1. Pattern and 3D RFs when crawling on inverted substrate (ceiling)

When a gecko crawls on ceiling, the measured RFs show that all the feet adhere to the substrate by negative normal forces (figures 2(a), 4(a), (b), (g) and (h)) and all the limbs pull toward the center of the body and generate lateral forces and fore-aft forces acting on the feet directed away from the body (figures 4(c)–(f)). The lateral forces $\left(F^{L}\right)$ acting on the left foot and the right foot direct reversed direction, so do the fore-aft forces $\left(F^{F}\right)$ acting on the front foot and the hind foot, which makes the gecko's body hang from the ceiling. The RF components acting on the left foot are statistically without difference with those on the corresponding right ones, but the RFs generated by front foot and hind foot are significant different. Geckos adhere to the ceiling with average peak of adhesive forces F^{N} -407.2 ± 113.3 mN ($n = 20$, n presents number of test trials) by front foot that is larger than the F^{N} -388.1 ± 93.8 mN ($n = 21$) by hind foot ($p < 0.001$, $F = 1.096$, d.f. = 39). Geckos generate

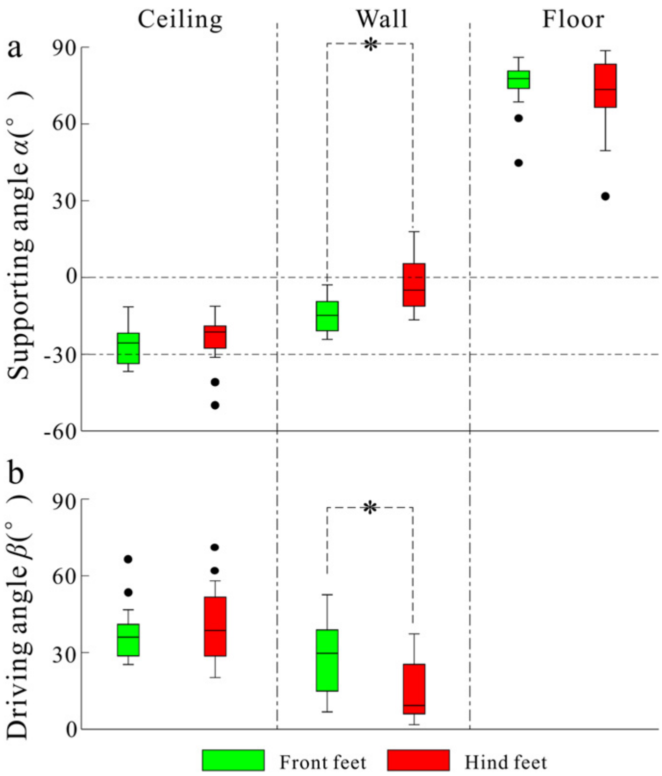

Figure 3. Box and whisker plots of supporting angle and driving angle during gecko moving on ceiling, wall and floor. (a) The supporting angles; (b) the driving angles. In order to understand the influence of lateral forces to the locomotion during gecko moving on ceiling, here, comparisons were made between driving angle of front foot and supplementary angle of driving angle of hind foot. Black points represent outlier. Asterisks (*): significantly different between angles of front and hind feet, $p < 0.05$.

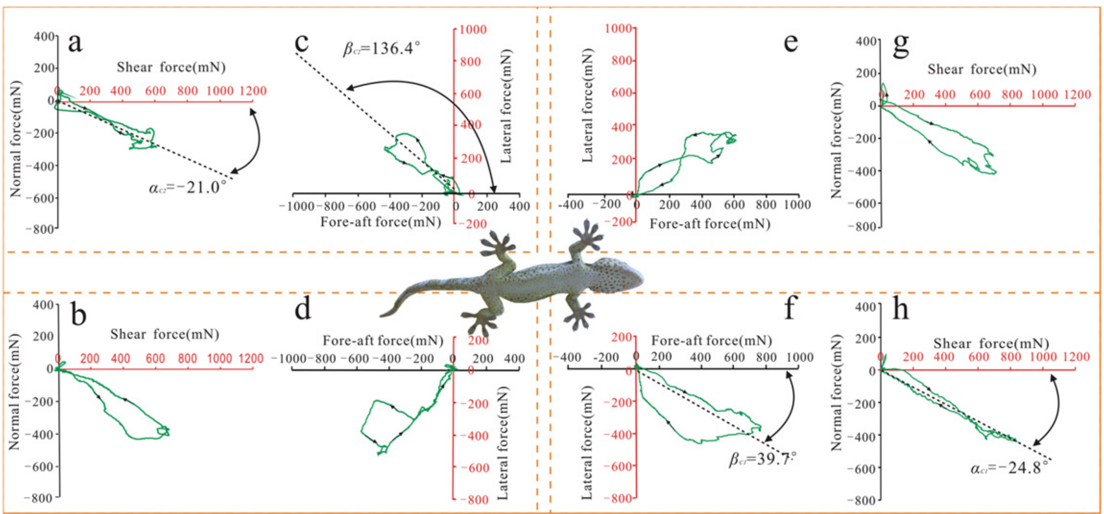

Figure 4. Diagrams of three-dimensional reaction forces when geckos crawl freely on a ceiling (inverted substrate). (c)–(f) The relation of lateral and fore-aft forces. RFs acting on four feet pull away from body and form opposing shear forces in the locomotion surface. (a), (b), (g) and (h) The diagrams of shear and normal forces. All feet generate adhesive (negative) forces, and the overall RF acting on uniformed directions during stance phase. The supporting angle of the RF acting on front and hind feet is slightly smaller than critical detach angle of seta array.

the opposite lateral forces of 478.5 ± 123.5 mN ($n = 20$) and 504.3 ± 173.0 mN ($n = 21$) without significant difference ($p = 0.557$, $F = 2.518$, d.f. = 39) in amount and the opposite fore-aft forces acting on front foot 737.4 ± 197.6 mN ($n = 20$) are larger than that on hind foot -600.1 ± 204.7 mN ($n = 21$) in amount ($p < 0.001$, $F = 0.165$, d.f. = 39). The mean supporting angle (α, defined by equations (3)–(5)) is $-24.81 \pm 6.24°$ ($n = 20$) on front foot (figures 3(a), 4(a) and (b)) and $-21.03 \pm 9.60°$ ($n = 21$) on hind foot (figures 3(a), 4(g) and (h)) respectively, without significant difference ($p = 0.276$, $F = 0.628$, d.f. = 39),

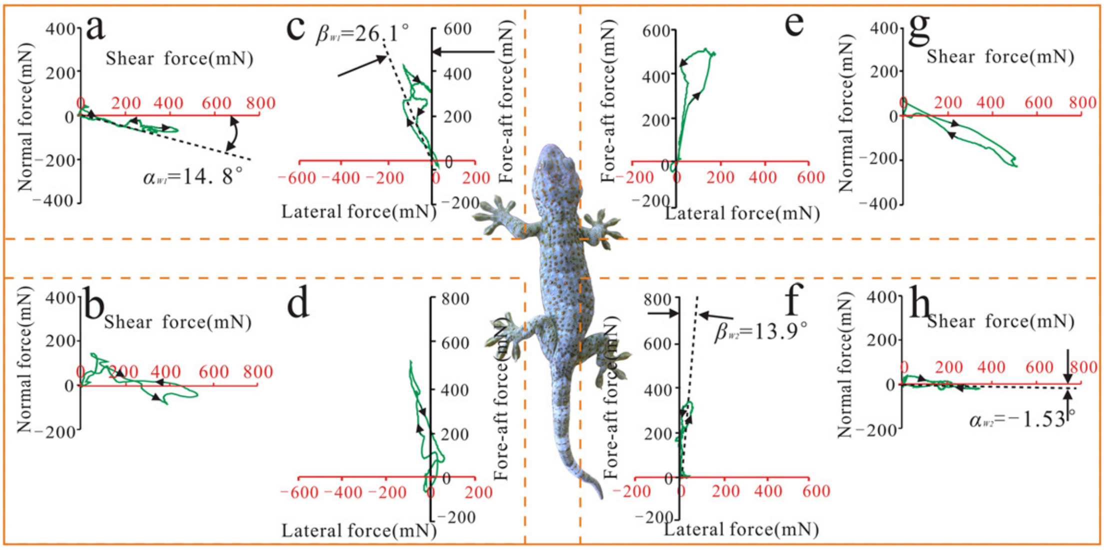

Figure 5. Diagrams of three-dimensional reaction forces when geckos climb on a wall (vertical substrate) and the corresponding mechanical models. (c)–(f) Lateral forces acting on all feet pull away from body and the fore-aft forces direct upward to balance the body gravity for a up-climbing gecko motion. (a) and (g) The front feet generate adhesive forces at the half of the critical supporting angle. (d) and (h) The hind feet may push away from or adhere to the wall.

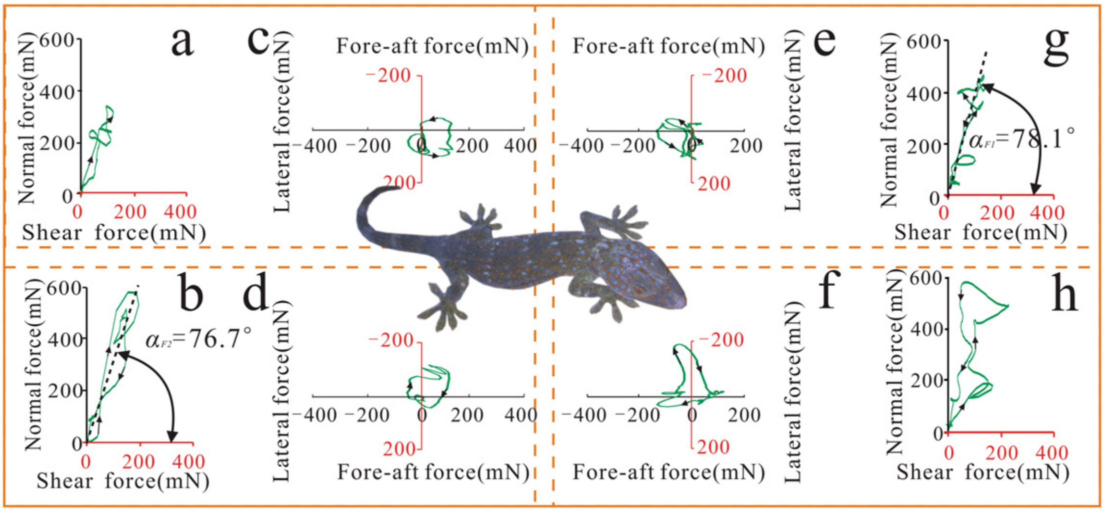

Figure 6. Diagrams of three-dimensional reaction forces when geckos move on a floor (horizontal substrate) and the corresponding mechanical models. (c)–(f) All four feet may push away from or pull toward the body and generate very small lateral and fore- aft forces; (a), (b), (g) and (h) The normal forces act on the front and hind feet push toward floor almost perpendicular to the floor at the supporting angle 78.1° and 76.7°.

which are slightly less than the critical angle of detachment −30° (Autumn *et al* 2000 and 2006). The negative values of support angle were obtained by the attractive normal RF divided by over-all RF and suggested the pulling force acting on gecko foot. The mean driving angles (β, defined by equations (4) and (5)) of F^R acting on front and hind feet are 39.77 ± 11.48° and 136.42 ± 16.58° without significant difference ($p = 0.079$, $F = 4.209$, d.f. = 39) (in order to understand the influence of lateral forces to the locomotion during gecko moving on ceiling, comparisons were made between driving angle of front foot and supplementary angle of driving angle of hind foot (43.58 ± 16.58°)) (figures 3(b), 4(e) and (f)). The values of driving angles were calculated by the fore-aft RFs and the shear forces, if less than 90°, suggested the force acting on the direction from tail to head, otherwise, if larger than 90°, suggested the force acting on the direction from head to tail. The curved surfaces generated by the vector of F^R acting on each foot were shown in figure 7(c) and the variation of the 3D RF vector by a stereo-video film was shown in video 1.

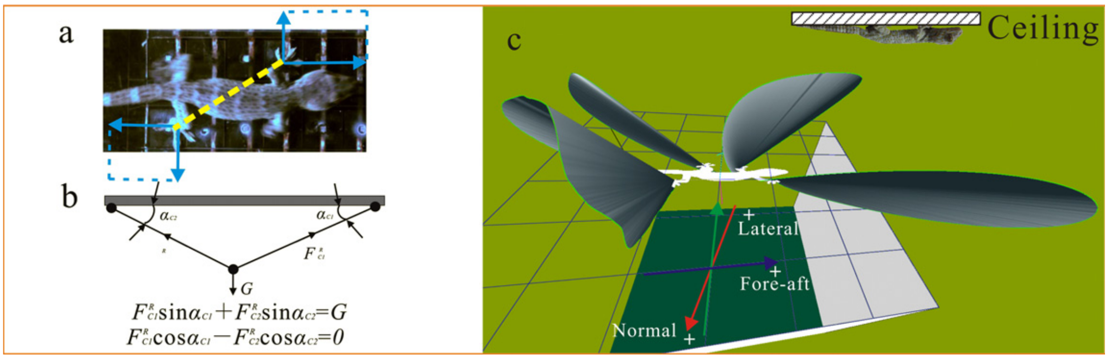

Figure 7. The corresponding mechanical model when geckos crawl freely on a ceiling (inverted substrate). (a) The locomotion image and the forces acting on feet in the substrate plane, the yellow line shows a projection line of which projection-plane is perpendicular to the substrate. (b) A simplified mechanical model is represented by the overall RF acting on front and hind feet in projection-plane, the corresponding force support angle and gecko's body gravity. (c) A sectional drawing from video of three-dimensional diagram of consecutive moving force-vectors when a gecko freely crawls on up-side-down ceiling.

3.2. Pattern and 3D RFs when climbing on vertical substrate (wall)

When geckos climb on wall, the measured RFs reveal that front foot adhere to wall (figures 2(b), 5(a) and (g)) at average F^N -149.1 ± 55.6 mN ($n = 20$) to avoid turning the body over. The F^N acting on the hind foot was repulsive at 115.3 ± 55.6 mN ($n = 20$) or attractive at -94.3 ± 54.9 mN ($n = 20$) (figures 2(b), 5(b) and (h)). The adhesive RF acting on front foot is clearly larger than that acting on hind foot ($p = 0.039$, $F = 0.4905$, d.f. = 38). All limbs pull toward the body laterally and the F^L acting on the front foot and hind foot direct away from the body at 212.2 ± 116.4 mN ($n = 20$) and 209.2 ± 134.7 mN ($n = 20$) for front and hind limbs and without significant difference was found between the F^L generated by front foot and hind foot ($p = 0.920$, $F = 1.039$, d.f. = 38). The F^F acting in moving direction on the front foot and hind foot are 466.7 ± 80.2 mN ($n = 20$) and 455.1 ± 135.4 mN ($n = 20$) respectively to balance the gravity (figures 2(b), 5(c)–(f)) and without significant difference between the two group of data ($p = 0.763$ $F = 2.896$, d.f. = 38). It is apparent that geckos use a much smaller supporting angle (α), forces acting on front foot at $\alpha = -14.80 \pm 6.41°$ ($n = 20$), which is clearly larger than that on hind foot on $\alpha = -1.53 \pm 10.85°$ ($n = 20$) ($p < 0.001$, $F = 7.317$, d.f. = 38) (figure 3(a)). The negative supporting angles mean the adhesive force acting on gecko foot. The mean driving angle (β) of forces acting on front foot is $26.08 \pm 11.53°$ ($n = 20$), clearly larger than that on hind foot $13.78 \pm 5.83°$ ($n = 20$) ($p = 0.033$, $F = 4.125$, d.f. = 38) (figures 3(b), 5(c) and (f)), which are much smaller than the corresponding angles for crawling on ceiling. The driving angles less than 90° mean that the fore-aft forces acting on gecko foot direct from tail to head, The RF was represented by a 3D curved surface, generated by the vector of F^R acting on each foot (figure 8(e)), while the variation of the 3D RF with time for climbing was shown in a stereo-video film (video 2).

3.3. Pattern and 3D RFs when running on horizontal substrate (floor)

When geckos run on floor, tendency of both F^L and F^F does not been presented clearly (figures 6(c)–(f)), which show that the PRFs of F^L and F^F for horizontal locomotion obviously differ from the corresponding patterns for vertical wall climbing and up-side-down ceiling crawling. The F^L acting on the front foot may push away from or pull toward the body at 93.8 ± 35.2 mN ($n = 24$) or -29.7 ± 21.6 mN ($n = 24$), and the F^L acting on the hind foot push away at 75.2 ± 21.6 mN ($n = 24$) or pull toward body -31.4 ± 16.53 mN ($n = 24$). The value of F^L pushing away from the body on front foot and hind foot are clearly larger than those pulling toward ($p = 0.021$, $F = 3.022$, d.f. = 46 and $p = 0.008$, $F = 5.190$, d.f. = 46 respectively). The F^L pushing away from the body acting on front foot is clearly larger than that on hind foot ($p = 0.007$, $F = 2.783$, d.f. = 46). The F^F acting on the front foot at -115.3 ± 63.9 mN ($n = 24$) and hind foot at -108.7 ± 72.3 mN ($n = 24$) directed against the gecko's motion at beginning of the corresponding attachments, and no statistical difference ($p = 0.264$, $F = 0.663$, d.f. = 46). Then it transfers the direction to push forward at 69.2 ± 41.4 mN ($n = 24$) and 96.6 ± 53.2 mN ($n = 24$) respectively without difference ($p = 0.495$, $F = 3.049$, d.f. = 46). The value of F^F acting on front foot against moving direction is clearly larger than that along the moving direction ($p < 0.001$, $F = 6.493$, d.f. = 46). The values of both F^L and F^F were much smaller than the corresponding forces for the vertical climbing and up-side down crawling. The much higher F^N, comparing with F^F and F^L, acting on front foot at 435.6 ± 87.4 mN ($n = 24$) is much larger than that on hind foot at 324.9 ± 91.7 mN ($n = 24$) ($p < 0.001$, $F = 0.601$, d.f. = 46) (figures 6(a), (b), (g)

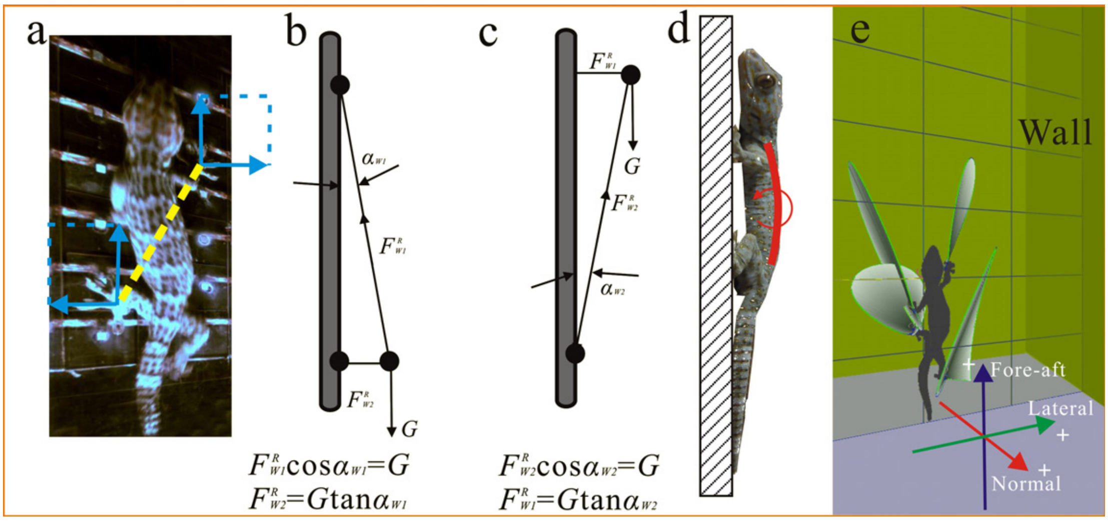

Figure 8. The corresponding mechanical models when geckos climb on a wall (vertical substrate). (a) The locomotion image and the forces acting on feet in the plane of the substrate, the yellow line shows a projection line of which projection-plane is perpendicular to the substrate. (b) and (c) Correspond to two mechanical models in projection-plane, only front feet bear the body gravity or only hind feet bear the body gravity. (d) The internal moment generated by muscles; (e) a sectional drawing from video of three-dimensional diagram of consecutive moving force-vectors when a gecko freely climbs on vertical wall.

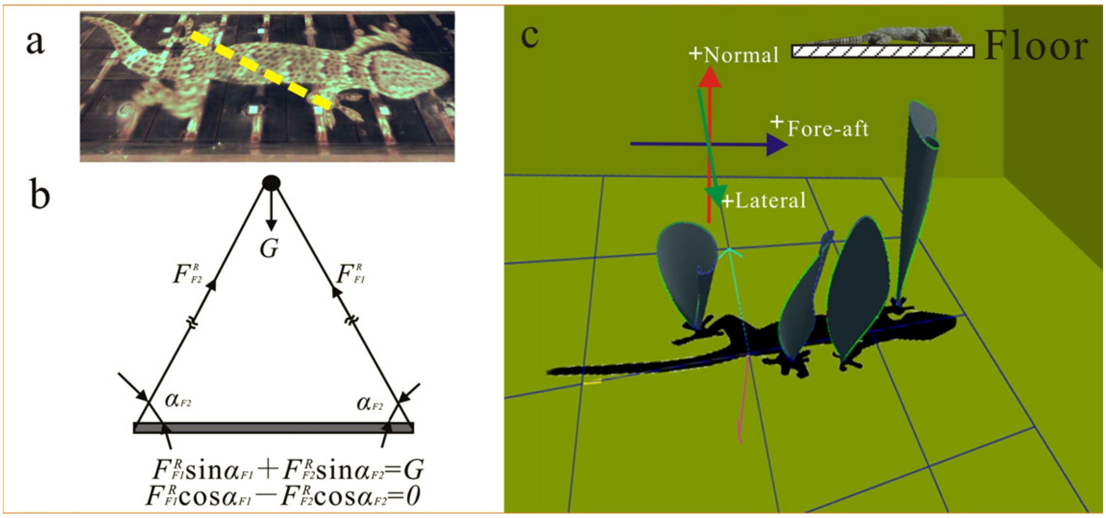

Figure 9. The corresponding mechanical models when geckos move on a floor (horizontal substrate). (a) and (b) Show how the mechanical model was set up in projection-plane. (c) A sectional drawing from video of three-dimensional diagram of consecutive moving force-vectors when a gecko freely runs on horizontal floor.

and (h)), makes the supporting angles (α) 78.13 ± 8.90° ($n = 24$) and 76.23 ± 13.54° ($n = 24$) for the front foot and hind foot (figures 3(a), 6(b) and (g)) respectively, and there is without significant difference ($p = 0.092$ $F = 3.321$, d.f. = 46). The positive supporting angles mean that the RF acting on gecko push the foot away from substrate. A 3D curved surface generated by the vector of F^N acting on each foot throughout a step cycle was introduced to present the change of RF (figure 9(c)), while the variation of the 3D RF for horizontal locomotion is presented in a stereo-video film (video 3).

4. Discussion and conclusion

4.1. Mechanical models and the analysis

To reveal the mechanical mechanism of how geckos govern the locomotion through modulating the RFs on various substrates, namely up-side-down ceiling, vertical wall and horizontal floor, and to illustrate the fundamental relationship between the RF and body gravity-three mathematical models were established.

When geckos crawl on ceiling, the mean peak of RFs acting on front and hind feet F^R_{C1} and F^R_{C2} almost fall in a plane which passed through two feet under stance phase and perpendicular to the substrate (figures 7(a) and (b)), so a two-dimensional mechanical model was presented.

The force-value balance in the plane should be $F_{C1}^{R}\sin\alpha_{C1} + F_{C2}^{R}\sin\alpha_{C2} = G$ in the direction perpendicular to the substrate to balance the gravity of gecko and $F_{C1}^{R}\cos\alpha_{C1} - F_{C2}^{R}\cos\alpha_{C2} = 0$ in the direction defined by two foot under stance phase (figure 7(b)) to balance the components of RFs along the connection line of two feet under stance phase if we omitted the influence of inertial forces acting on the direction perpendicular to the plane. The RFs acting on front foot F_{C1}^{R} and hind foot F_{C2}^{R} can be calculated by equation (3):

$$F_{C1}^{R} = \frac{G\cos\alpha_{C2}}{\left(\cos\alpha_{C2}\sin\alpha_{C1} + \cos\alpha_{C1}\sin\alpha_{C2}\right)},$$
$$F_{C2}^{R} = \frac{G\cos\alpha_{C1}}{\left(\cos\alpha_{C2}\sin\alpha_{C1} + \cos\alpha_{C1}\sin\alpha_{C2}\right)}, \quad (3)$$

where α_{C1}, α_{C2} are the corresponding supporting angles; and G is the gravity.

The mechanical models (equation (3)) basically represent the static force balance, and they clearly indicate that overall RFs $\left(F^{R}\right)$ acting on both the front feet and hind feet (F_{C1}^{R} and F_{C2}^{R}) have to pull away from the body, thus resulting in opposing forces in both lateral and fore-aft directions, which correspond well with the measured RFs. Moreover, the models show that overall RFs acting on legs and feet under the support phase will decrease with increasing supporting angle ($\alpha \in (-90°, 0°)$), thus decrease the forces (that is, the stresses) acting on legs and feet during locomotion. But a higher supporting angle will reduce the attachment reliability and result in detaching. From this study, we can see that geckos use a supporting angle (α), slightly smaller than the critical detaching angle ($-30°$), which may be helpful to ensure a reliable attachment and to decrease the RF simultaneously. We introduced measured supporting angle for both front and hind legs, and obtained correspondent RF predicted by the model is 26% and 18% lower than the corresponding experimental data.

There are few studies which study the RF of animals move on an upside-down substrate (Wang *et al* 2010a, b, Dai *et al* 2011) or bat landing on ceiling and fly adhering on ceiling (Gorb 2005, Riskin *et al* 2009). Here our measurements, for the first time, show a unique PRFs which ensure gecko adhering on ceiling. The technique used by geckos to obtain multi-benefits functions such as to reduce the forces acting on feet and legs and at the same time to ensure a reliable attachment may inspire the robot design for a better ceiling crawling.

When geckos climb on wall, the F^{R} is considered acting in a plane perpendicular to the substrate passing through the two attached feet (figure 8(a)). This forms a closed-loop system consisting of the animal body and the substrate, which make it impossible to work out the load distribution between the two stance feet directly. Based on the observation and the RFs measurements—the front and hind limbs equivalently share the body gravity, we developed a two-dimensional model by assuming that: (1) the front feet bear the half gravity $F_{W1}^{R}\cos\alpha_{W1} = 0.5G$ and $F_{W2}^{R} = 0.5G\tan\alpha_{W1}$ (figure 8(b)), and (2) the hind feet bear the half gravity $F_{W1}^{R} = 0.5G\tan\alpha_{W2}$ and $F_{W2}^{R}\cos\alpha_{W2} = 0.5G$ (figure 8(c)). The RFs can be presented by equation (4):

$$F_{W1}^{R} = 0.5G\left(\tan\alpha_{W2} + \frac{1}{\cos\alpha_{W1}}\right),$$
$$F_{W2}^{R} = 0.5G\left(\tan\alpha_{W1} + \frac{1}{\cos\alpha_{W2}}\right), \quad (4)$$

where F_{W1}^{R}, F_{W2}^{R} are RF acting on the front and hind feet; α_{W1}, α_{W2} are the corresponding supporting angles; and G is the gecko's body gravity. We obtained the predicted F_{W1}^{R} and F_{W2}^{R}, which differs by only 5% and 11% from those of measured. These models also suggest that RF decreases with decreasing supporting angle (α). Therefore, a special PRFs has been employed by wall-climbing geckos to decrease the RFs and also to enhance the reliability of the attachment simultaneously.

Our measurements and models on the RFs acting on front feet are adhesive, which well correspondent to the studies previously on gecko (*Hemidactylus garnotii*) (Autumn *et al* 2006) and cockroach (Goldman *et al* 2006). The RFs acting on hind feet when moving vertically are repulsive, as previously proposed mechanical model (Autumn *et al* 2006), but also are adhesive, which have never been reported before demonstrating the complexity of the animal locomotion. To understand the measurements, we proposed several possible factors which result in the adhesive forces acting on hind feet. First factor—the tail support, studies show that a *treecreeper* uses tail support to balance external forces and torques at rest, clinging to a vertical trunk (Norberg 1986). Geckos have long and sturdy tail, which was proposed as 5th leg during aerial descent and gliding (Jusufi *et al* 2008, Libby *et al* 2012). If geckos actively support by tail, the adhesive forces acting on hind feet are reasonable. In fact, in our measurements, we did not find the obvious RFs during gecko tail contacting with substrate, which suggest that the 5th leg may play a role in emergency only. Second factor—the body deformation due to muscle contraction. The biggest muscle *Puboischiotibialis*, around 1.094% of the body weight (Liu *et al* 2005), which connects the gecko's (Tokay) vertebra, may generated bending deformation of the animal body. This may lead to changes in the RFs at both stance feet. It has been reported that salamander's lateral hypaxial musculatures generate both torsional moments to counteract ground RFs generated by forelimb support, and torsional moments to counteract ground RFs from hindlimb support (Bennett *et al* 2001). So, the body deformation of a gecko caused by muscle contractions may induce positive RF at the front foot and the adhesive RF on the hind feet (figure 8(d)). The inertia force may tend to make the gecko moving away from vertical substrate and thus the hind feet will generate adhesive force to secure the body. This suggests that modeling a gecko as a rigid body may be insufficient to represent the characteristics of its bendable body, and also the muscle actuation and the inertia forces need to be considered.

The measured RFs of freely moving gecko on vertical surface revealed that geckos use much smaller supporting angle −14.8° and −1.53° to adhere, which is only half the critical angle of detachment −30° (Autumn *et al* 2000, 2006) or even smaller. The results means that geckos will receive a more reliable attachment on the vertical substrate because the limit detaching force increases with decrease of supporting angle (Qu *et al* 2008, Tian *et al* 2006). The model show geckos reduce the RF acting on feet and legs and enhance the driving efficiency at the same time. In short, geckos have obtained a multi-benefit approach during locomotion. The technique used by freely moving gecko on vertical surface, both fore-limbs and hind-limbs share the body gravity almost half to half, will reduce the forces acting on feet and legs. How geckos modulate their muscles to maintain the share rate is still unclear, it may be owed to the modulation of nervous system.

When geckos run on floor, a mechanical model was set up in a projection plane which passed through two feet under stance phase (figure 9(a)) and perpendicular to the substrate. $F_{F1}^{R}\sin\alpha_{F1} + F_{F2}^{R}\sin\alpha_{F2} = G$ and $F_{F1}^{R}\cos\alpha_{F1} - F_{F2}^{R}\cos\alpha_{F2} = 0$, similar to the equations describing the mechanics of crawling on the ceiling (figure 9(b)), the RFs can be presented by equation (5):

$$F_{F1}^{R} = \frac{G\cos\alpha_{F2}}{\left(\cos\alpha_{F2}\sin\alpha_{F1} + \cos\alpha_{F1}\sin\alpha_{F2}\right)} \text{ and }$$
$$F_{F2}^{R} = \frac{G\cos\alpha_{F1}}{\left(\cos\alpha_{F2}\sin\alpha_{F1} + \cos\alpha_{F1}\sin\alpha_{F2}\right)}. \quad (5)$$

The model predicted F_{F1}^{R} and F_{F2}^{R} of the front and hind feet differed from the corresponding experimental data by 15.6% and 16.7%. The mechanical model shows clearly that gecko obtain several benefits at the same time—to reduce the RF acting on the legs and to enhance the locomotion ability on the ground by only lifting the body up and using a bigger supporting angle. The measured results show that characteristics of the ground RFs, esp. the fore-aft forces and normal forces, when geckos run on horizontal substrate match with those when quadruped even human run on floor (Manter 1938, Full and Tu 1991, Dickinson *et al* 2000, Chen *et al* 2006, Zumwalta *et al* 2006, Dai *et al* 2011). It is interesting that the support angle is as large as 76°–78° when geckos move on horizontal substrate, which make the RFs falling into the frictional angle and received a frictional self-locking contact (Stoecker 2003).

To move safely and efficiently sometime is trade-off. To move safely is essential for animals' survival. Our measurements show clearly that geckos ensure safe locomotion first by regulating the RFs. When crawling on ceiling, geckos regulate the RFs and keep the supporting angles never larger than the critical detach angle (30°). At the same time, geckos regulate the supporting angles as large as possible to reduce the force acting on limbs and feet. When climbing on wall, the smaller supporting angles is better for both reliable attachment and small RFs, so geckos regulate the supporting angles much smaller than those crawling on ceiling to obtain both benefit of safety attachments and lower forces acting on limbs and feet. When running on floor, larger supporting angles have advantages to both reducing RFs and increasing frictional self-locking ability, but vary larger supporting angle will limit the stride, thus reduce the locomotion speed, so geckos use supporting angles that fall into the frictional cone, but not too large.

Therefore, the patters of RFs used by geckos during locomotion are dependent on the orientation of the substrates. They attempt to balance the gravitational force of their body, to decrease the forces acting on their limbs and feet, and also to maintain their locomotion speed simultaneously.

4.2. Comparing the RFs measured by FMA and by the force platform

Animals' locomotion is finally determined by the RFs acting on the animals' body, so accurately measuring the RFs acting on each foot is a key step for understanding locomotion. Full and his group has made great contribution by developing force platform (Full and Tu 1990) and carrying out a lot of measurements on RFs of various legged animals (Full and Tu 1991, Biewener and Full 1992, Chen *et al* 2006, Goldman *et al* 2006). They have measured the complete RFs acting on a single foot of gecko (*Hemidactylus garnotii*) when duty factor is below 0.5 (0.42–0.5) (Chen *et al* 2006). Only very beginning and/or very last part of the RFs can not be detected by the force platform because the overlapping of front foot and hind foot when duty factor is larger than 0.5. When one front foot attached on force platform, it is possible to measure the RF from zero to maximum and then decreasing, but it is impossible to obtain the RF decreasing to zero, because the duty factor >0.5 means that another foot must attached on the force platform before the first one detachment. For the same reason, it is also impossible to measure the RFs while the hind foot detaching from the force platform, because another front foot must not detached from the force platform when duty factor larger than 0.5. When geckos (*Tokay*) moved on vertical surface along different directions, the duty factor decreases from 0.8

to 0.5 with increasing of speed from 0.2 to 0.8 m s^{-1}, larger than 0.5 (Wang *et al* 2011). Russell and Higham studied the kinematics of gecko with adhesive capabilities (*Tarentola mauritanica*) and one without (*Eublepharis macularius*), and the duty factor is also larger than 0.5 (Russell and Belsb 2001, Russell and Higham 2009). Biewener studied the locomotion behaviors of six different quadrupedal animals and found that the duty factor decreases from 0.7 to 0.3 with increasing of locomotion speed up to 6 m s^{-1}, and the duty factor will less than 0.5 at the trot-gallop transition speed (Biewener 1983).

On the other hand, FMA independently detects the RFs acting on each foot by separated 3D sensor (Dai *et al* 2011), this character makes it possible to measure the completed RFs through attaching to detaching procedure—preloading, attaching and detaching procedure and the coordinate forces among four legs, which means the RFs continuously acting on each foot without the influence of duty factor. So FMA provided biologists a new technique to measure the RFs of legged locomotion. The measured RFs acting on each foot provide a possibility to draw the PRFs.

4.3. Approaches to present the RFs

In order to understand the effects of RFs to legged locomotion, curves of normalized RFs versus normalized time were introduced, where the forces were divided by body gravity and the time was divided by step-circle (Biewener 1983, Cartmill 1985, Biewener and Full 1992, Blob and Biewener 2001, Alexander 2002, Autumn *et al* 2006, Chateau *et al* 2009). The approach shows the force change clearly during step-circle. On the anther hand, Cavagna measured two-dimensional RFs acting on dog's foot (Cavagna *et al* 1977), which is right for upright postured locomotion. Full *et al* measured two-dimensional (Full and Tu 1990) and 3D (Full *et al* 1995, Autumn *et al* 2006, Goldman *et al* 2006) RFs of the sprawl-postured locomotion. Dickinson *et al* presented the relationship between RFs and locomotion by using the vectors of two-dimensional RF for sprawl- and upright- postured locomotion (Dickinson *et al* 2000), which seems not perfect to reveal this relationship because the vector of RF in one direction was ignored in this approach. Autumn presented the relationship of shear and normal forces in isolated gecko setal arrays on a glass surface (Autumn *et al* 2006), but he did not connect this presentation with gecko locomotion.

To clearly present the inter-relationship of the components of RFs and the relationship among the RFs acting on each foot, we introduce PRFs, and show the PRFs in figures 4(a)–(h), 7(c); 5(a)–(h), 8(e) and 6(a)–(h) and 9(c). In fact, phrase of PRFs was used to present the characteristic of the force versus time curve (Dutto *et al* 2004, Koditschek *et al* 2004, Gottschall and Kram 2005, Goldman *et al* 2006, Nicholls *et al* 2006) Nicholls studied the influence of baseball bat material, namely metal and wooden, on the ball exit velocity, they used PRF to show the difference of the RFs when a baseball interacted with bat (Nicholls *et al* 2006). The phrase used by the authors is different with PRF defined here.

The effects of force action are determined by its magnitude, direction and force-acting point. The curve of normalized RFs versus normalized time presents the magnitude clearly, but does not show the change of direction. The PRF introduced in this paper extends previous approach (Dickinson *et al* 2000), and presents the three key parameters clearly. A vector connecting the coordinate origin and any point on the curve of PRF presents the magnitude of force, the direction and the force-acting point. At the same time, the PRF presents the overall changes clearly. There are small change of supporting angles during ceiling crawling (figures 4(a), (b), (g) and (h)) and wall climbing (figures 5(a), (b), (g) and (h)), so do the driving angle when geckos climb on wall (figures 5(c)–(f)). Those findings support our proposal to set up two-dimensional mechanical models and suggest that the RFs acting on animals' body on a definite direction may be a way for animals to simplify the regulation for the locomotion and to save energy. The PRF presented in figures 6(c)–(f) suggests that the forces needed to drive animals' locomotion on floor and to balance in lateral direction is very small, the change of direction is very complex. The 3D presentation shows the change (figure 9(c)). Combining the PRF with locomotion behavior provide us a new technique to vividly understand legged locomotion.

4.4. Conclusions

We have measured the detailed 3D RFs on an individual foot of a freely moving gecko and linked the forces with locomotor behavior. It was demonstrated that gecko obtains multi-benefits by developing PRF to reduce the overall RF and to secure highly reliable attachment on ceiling or to enhance the locomotion ability on the floor. On a ceiling, geckos bear opposing shear forces, which pull from body both laterally and fore-aft with diagonal front and hind feet. It hangs on the ceiling at a very big supporting angle which reduces the force acting on the legs, but the angle is always slightly smaller than the critical detaching angle to ensure reliable attachment. When running on the floor, geckos lift its body from a floor at bigger supporting angle, which obtain several benefits at the same time—decreasing the RFs acting on feet, reducing forces in muscles and enhancing the ability to get across rough substrate because the increase of the distance between gecko's trunk to the substrate make geckos easier to move across bigger obstacles. When climbing on a wall, geckos secure a reliable self-locking attachment by modulating the supporting angle to only half the critical detaching angle and at the same time reduce the RF acting on feet and legs. The above strategies governing the gecko's locomotion should inspire human to develop a better gecko-mimicking robot. In addition, different species of geckos have different morphological features including body shapes, sizes, or toe-pad morphologies, which might result in different PRF, however, it is still unclear.

Acknowledgment

Supported by National Natural Science Foundation of China (Nos. 51435008 to Z D Dai and 60910007 to Z D Dai and L M Dai) and Funding from State Key Laboratory of Solid Lubrication of China. L M Dai thanks the partial support from National Science Foundation (CMMI-1047655) and the Fundamental Research Funds for the Central Universities (Grant No. CXZZ11_0198 and BCXJ10_10).

Author contributions

Z D designed research; Z W, A J, and Q X performed research; Z D, Z W, L R and L D analyzed data; Z D and Z W wrote the paper.

Conflict of interest

The authors declare no conflicting financial interests.

References

Alexander R M 2002 Energitics and optimization of human walking and running: the 2000 raymond pearl memorial lecture *Am. J. Hum. Biol.* **14** 641–8

Arzt E, Gorb S and Spolenak R 2003 From micro to nano contacts in biological attachment devices *Proc. Natl. Acad. Sci. USA* **100** 10603–6

Autumn K, Dittmore A, Santos D, Spenko M and Cutkosky M 2006 Frictional adhesion: a new angle on gecko attachment *J. Exp. Biol.* **209** 3569–79

Autumn K, Hsieh S T, Dudek D M, Chen J, Chitaphan C and Full R-J 2006 Dynamics of geckos running vertically *J. Exp. Biol.* **209** 260–72

Autumn K, Liang Y, Hsieh S T, Zesch W, Chan W P, Kenny T, Fearing R and Full R J 2000 Adhesive force of a single gecko foot–hair *Nature* **405** 681–5

Autumn K *et al* 2002 Evidence for van der Waals adhesion in gecko setae *Proc. Natl. Acad. Sci. USA* **99** 12252–6

Bartlett M, Croll A B, King D R, Irschick D J and Crosby A J 2012 Looking beyond fibrillar features to scale gecko-like adhesion *Adv. Mater.* **24** 1078–83

Bauer A M and Russell A P 1988 Morphology of gekkonoid cutaneous sensilla, with comments on function and phylogeny in the Carphodactylini (Reptilia: Gekkonidae) *Can. J. Zoo.* **66** 1583–8

Bennett W O, Simons R S and Brainerd E L 2001 Twisting and bending: the functional role of salamander lateral hypaxial musculature during locomotion *J. Exp. Biol.* **204** 1979–89

Biewener A A 1983 Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size *J. Exp. Biol.* **105** 147–71

Biewener A A and Full R J 1992 Force platform and kinematic analysis *Biomechanics: Structures and Systems, a Practical Approach* ed A A Biewener (Oxford: IRL Press) pp 45–73

Blob R W and Biewener A A 2001 Mechanics of limb bone loading during terrestrial locomotion in the green iguana (*Iguana iguana*) and American alligator (*Alligator mississippiensis*) *J. Exp. Biol.* **204** 1099–122

Boesel L F, Greiner C, Arzt E and del Campo A 2010 Gecko-inspired surfaces: a path to strong and reversible dry adhesives *Adv. Mater.* **22** 2125–37

Cartmill M 1985 *Functional Vertebrate Morphology* ed M Hildebrand, M Bramble, K F Liem and D B Wake (Cambridge, MA: Harvard University Press) pp 73–88

Cavagna G A, Heglund N C and Taylor C R 1977 Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure *Am. J. Physiol.* **233** R243–61

Chateau H, Robin D, Simonelli T, Pacquet L, Pourcelot P, Falala S, Denoix J M and Crevier-Denoix N 2009 Design and validation of a dynamometric horseshoe for the measurement of three -dimensional ground reaction force on a moving horse *J. Biomech.* **42** 336–400

Chen B, Wu P D and Gao H 2008 Hierarchical modellingmodeling of attachment and detachment mechanisms of gecko toe adhesion *Proc. R. Soc.* A **4** 1639–52

Chen J J, Peattie A M, Autumn K and Full R J 2006 Differential leg function in a sprawled -posture quadrupedal trotter *J. Exp. Biol.* **209** 249–59

Dai Z D 2008 Biomimectics on discontinous-constraint metamorphic legged mechanism: biological roles for locomotion gait and control design *Chin. Sci. Bull.* **53** 618–22 (in Chinese)

Dai Z D and Sun J R 2007 A biomimetic study of discontinuous-constraint metamorphic mechanism for gecko-like robot *J. Bionic Eng.* **4** 91–5

Dai Z D, Wang Z Y and Ji A H 2011 Dynamics of gecko locomotion: a force-measuring array to measure 3D reaction forces *J. Exp. Biol.* **214** 703–8

Dai Z D, Zhang H, Zhang M, Dai L Q and Sun J R 2007 Biomimectics on discontinous-constraint metamorphic legged mechanism: concepts and models *Chin. Sci. Bull.* **52** 236–9 (in Chinese)

Del Campo A and Arzt E 2007 Design parameters and current fabrication approaches for developing bioinspired dry adhesives *Macromol. Biosci.* **7** 118–27

Dickinson M H, Farley C T, Full R J, Koehl M A R, Kram R and Lehman S 2000 How animals move: an integrative view *Science* **288** 100–8

Dutto D J, Hoyt D F, Cogger E A and Wickler S J 2004 Ground reaction forces in horses trotting up an incline and on the level over a range of speeds *J. Exp. Biol.* **207** 3507–14

Endlein T, Jia A H, Samue D, Yao N, Wang Z Y, Barnes W J P and Dai Z D 2013 Sticking like sticky tape: tree frogs use friction forces to enhance attachment on overhanging surfaces *J. Roy. Soc. Interface* **10** 1743–52

Ernst V V and Ruibal R 1967 The structure and development of the digital lamellae of lizards *J. Morphol.* **120** 233–66

Foster K L and Higham T E 2012 How forelimb and hindlimb function changes with incline and perch diameter in the green anole, *Anolis carolinensis J. Exp. Biol.* **215** 2288–300

Full R J and Koditschek D E 1999 Templates and anchors: neuromechanical hypotheses of legged locomotion on land *J. Exp. Biol.* **202** 3325–32

Full R J and Tu M S 1990 The mechanics of six-legged runners *J. Exp. Biol.* **148** 129–46

Full R J and Tu M S 1991 Mechanics of a rapid running insect: two-, four-and six-legged locomotion *J. Exp. Biol.* **156** 215–31

Full R J, Yamauchi A and Jindrich D 1995 Maximum single leg force production: cockroaches righting on photoelastic gelatin *J. Exp. Biol.* **198** 2441–52

Gregor R J, Smith D W and Prilutsky B I 2006 Mechanics of slope walking in the cat: quantification of muscle Load, length change, and ankle extensor EMG Patterns *J. Neurophysiol.* **95** 1397–409

Goldman D I, Chen T S, Dudek D M and Full R J 2006 Dynamics of rapid vertical climbing in cockroaches reveals a template *J. Exp. Biol.* **209** 2990–3000

Gorb S N 2005 Uncovering insect stickiness: structure and properties of hairy attachment devices *Am. Entomol.* **51** 31–5

Gottschall J S and Kram R 2005 Ground reaction forces during downhill and uphill running *J. Exp. Biol.* **38** 445–52

Guo C, Sun J R, Ge Y B, Wang W B, Wang D P and Dai Z D 2012 Biomechanism of adhesion in gecko setae *Sci. China Life Sci.* **55** 181–7

Higham T E and Jayne B C 2004a Locomotion of lizards on inclines and perches: hindlimb kinematics of an arboreal specialist and a terrestrial generalist *J. Exp. Biol* **207** 233–48

Higham T E and Jayne B C 2004b *In vivo* muscle activity in the hindlimb of the arboreal lizard, *Chamaeleo calyptratus*: general patterns and the effects of incline *J. Exp. Biol.* **207** 249–61

Holmes P, Full R, Koditschek D and Guckenheimer J 2006 Dynamics of legged locomotion: models, analyses, and challenges *SIAM Rev.* **48** 207–304

Hu S, Xia Z and Dai L 2013 Advanced gecko-foot-mimetic dry adhesives based on carbon nanotubes *Nanoscale* **5** 475–86

Huber G *et al* 2005 Evidence for capillarity contributions to gecko adhesion from single spatula nanomechanical measurements *Proc. Natl. Acad. Sci. USA* **102** 16293–6

Irschick D J, Austin C C, Petren K, Fisher R N, Losos J B and Ellers O 1996 A comparative analysis of clinging ability among pad-bearing lizards *Biol. J. Linn. Soc.* **59** 21–35

Irschick D J, Herrel A and VanHooydonck B 2006 Whole-organism studies of adhesion in pad-bearing lizards: creative evolutionary solutions to functional problems *J. Comp. Physiol.* A **192** 1169–77

Jagota A and Bennison S 2002 Mechanics of adhesion through a fibrillar microstructure *Integr. Comp. Biol.* **42** 1140–5

Jayne B C and Irschick D J 1999 Effects of incline and speed on the thee-dimensional hindlimb kinematics of a generalized iguanian lizard *(Dipsosaurus dorsalis) J. Exp. Biol.* **202** 143–59

Jusufi A, Goldman D I, Revzen S and Full R J 2008 Active tails enhance arboreal acrobatics in geckos *Proc. Natl. Acad. Sci. USA* **105** 4215–9

King D R, Bartlett M B, Gilman C, Irschick D J and Crosby A J 2014 Creating gecko-like adhesives for 'real-world' surfaces *Adv. Mater.* **26** 4345–51

Koditschek D E, Full R J and Buehler M 2004 Mechanical aspects of legged locomotion control *Arthropod Struct. Dev.* **33** 251–72

Krause C and Fischer M S 2013 Biodynamics of climbing: effects of substrate orientation on the locomotion of a highly arboreal lizard (*Chamaeleo calyptratus*) *J. Exp. Biol.* **216** 1448–57

Lammers A R, Earls K D and Biknevicius A R 2006 Locomotor kinetics and kinematics on inclines and declines in the gray short-tailed opossum Monodelphis domestica *J. Exp. Biol.* **209** 4154–66

Lammers A R 2007 Locomotor kinetics on sloped arboreal and terrestial substrates in a small quadrupedal mammal *Zoology* **110** 93–110

Li H K and Dai Z D 2012 Motion coordination strategy of quadruped robot inspired by the locomotion of animal *Adv. Reconfigurable Mech. Robots I* **6** 717–25

Libby T, Moore T Y, Chang-Siu E, Li D, Cohen D J, Jusufi A and Full R J 2012 Tail-assisted pitch control in lizards, robots and dinosaurs *Nature* **481** 181–4

Lin H T and Trimmer B A 2012 A new bi-axial cantilever beam design for biomechanics force measurements *J. Biomech.* **45** 2310–4

Lipp A, Harald W and Fritz-Olaf L 2005 Walking on inclines: energetics of locomotion in the ant *Camponotus. J. Exp. Biol.* **208** 707–19 (in Chinese)

Liu X Y, Dai Z D, Zeng X L and Xie C L 2005 A quantitative measurement research on Tokay gecko's appendicular muscle *Anat Res.* **27** 292–5 (in Chinese)

Maderson P F A 1964 Keratinized epidermal derivatives as an aid to climbing in Tokaynid lizards *Nature* **203** 780–1

Manter J T 1938 The Dynamics of quadrupedal walking *J. Exp. Biol.* **15** 522–40

Mcelroy E J and Reilly S M 2009 The relationship between limb morphology, kinematics, and force during running: the evolution of locomotor dynamics in lizards *Biol. J. Linn. Soc.* **97** 634–51

Nicholls R L, Miller K and Elliott B C 2006 Numerical analysis of maximal bat performance in baseball *J. Biomech.* **39** 1001–9

Norberg R Å 1986 Tree creeper climbing: mechanics, energetics and structural adaptations *Ornis. Scand.* **17** 191–209

Qu L T, Dai L M, Stone M, Xia Z H and Wang Z L 2008 Carbon nanotube arrays with strong shear binding-on and easy normal lifting-off *Science* **322** 238–42

Riskin D K *et al* 2009 Bats go head-under-heels: the biomechanics of landing on a ceiling *J. Exp. Biol.* **212** 945–53

Russell A P 1975 A contribution to the functional analysis of the foot of the Tokay, Tokay gecko (Reptilia: Tokaynidae) *J. Zool. London* **176** 437–76

Russell A P and Belsb V 2001 Biomechanics and kinematics of limb-based locomotion in lizards: review, synthesis and prospectus *Comp. Bioch. Phys.* A **131** 89–112

Russell A P and Higham T G 2009 A new angle on clinging in geckos: incline, not substrate, triggers the deployment of the adhesive system *Proc. R. Soc.* B **276** 3705–9

Schmidt A and Fischer M S 2010 Arboreal locomotion in rats—the challenge of maintaining stability *J. Exp. Biol.* **213** 3615–24

Schmidt A and Fischer M S 2011 The kinematic consequences of locomotion on sloped arboreal substrates in a generalized (Rattus norvegicus) and a specialized (Sciurus vulgaris) rodent *J. Exp. Biol.* **214** 2544–59

Sparrow W A and Tirosh O 2005 Gait termination:a review of experimental methods and the effects of ageing and gait pathologies *Gait and Posture* **22** 362–71

Stoecker H 2003 *Handbook of Physics, Verlag Harri Deutsch* translated by Wu X Z, Li Z X and Chen X P (Beijing: Press of Beijing University)

Tian Y, Pesika N, Zeng H B, Rosenberg K, Zhao B X, McGuiggan P, Autumn K and Israelachvili J 2006 Adhesion and friction in gecko toe attachment and detachment *Proc. Natl. Acad. Sci. USA* **103** 19320–5

Ting L H, Blickhan R and Full R J 1994 Dynamic and static stability in hexapedal runners *J. Exp. Biol.* **197** 251–69

Wadden T and Ekeberg O 1998 A neuro-mechanical model of legged locomotion: single leg control *Biol. Cybern.* **79** 161–73

Wang Z Y, Gu W H, Wu Q, Ji A H and Dai Z D 2010a Morphology and reaction force of toes of geckos freely moving on ceilings and walls *Sci. China Technol. Sci.* **53** 1688–93

Wang Z Y, Wang J T, Ji A H and Dai Z D 2010b Locomotion behavior and dynamics of geckos freely moving on the ceiling *Chin. Sci. Bull.* **55** 3356−3362

Wang Z Y, Wang J T, Ji A H, Zhang Y Y and Dai Z D 2011 Behavior and dynamics of gecko locomotion: effects of moving directions on vertical surface *Chin. Sci. Bull.* **56** 573–83

Welch J M, Wade J A, Hillberry B M and Weaver C-M 2009 Force platform for rats measures fore and hind forces concurrently *J. Biomech.* **42** 2734–8

Williams E E and Peterson J A 1982 Convergent and alternative designs in the digital adhesive pads of scincid lizards *Science* **215** 1509–11

Zumwalta A C, Hamrick M and Schmitta D 2006 Force plate for measuring the ground reaction forces in small animal locomotion *J. Biomech.* **39** 2877–81