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RESEARCH ARTICLE

Contribution of friction and adhesion to the reliable attachment of a gecko to smooth inclines

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Abstract: Geckos' ability to move on steep surfaces depends on their excellent adhesive structure, timely adjustments on locomotor behaviors, and elaborates control on reaction forces. However, it is still unclear how they can generate a sufficient driving force that is necessary for locomotion, while ensuring reliable adhesion on steep inclines. We measured the forces acting on each foot and recorded the contact states between feet and substrates when geckos encountered smooth inclination challenges ranging from 0° to 180°. The critical angles of the resultant force vectors of the front and hind-feet increased with respect to the incline angles. When the incline angle became greater than 120°, the critical angles of the front- and hind-feet were similar, and the averages of the critical angles of the front- and hind-feet were both smaller than 120°, indicating that the complicated and accurate synergy among toes endows gecko's foot an obvious characteristic of "frictional adhesion" during locomotion. Additionally, we established a contact mechanical model for gecko's foot in order to quantify the contribution of the frictional forces generated by the heel, and the adhesion forces generated by the toes on various inclines. The synergy between multiple contact mechanisms (friction or adhesion) is critical for the reliable attachment on an inclined surface, which is impossible to achieve by using a single-contact mechanism, thereby increasing the animal's ability to adapt to its environment.

Keywords: friction; adhesion; incline; frictional adhesion; gecko

1 Introduction

The reliable attachment between an animal's foot and the substrate over which it is moving forms the foundation of its movement. This is because reliable attachment is essential in providing a sufficient and continuous contact force to counteract resistance and enable locomotion [1]. Inclines constitute a common terrain over which legged animals could move [2]. Thus, a major challenge faced by a legged animal is how it can reliably attach itself to an incline while moving. During the course of evolution, animals have optimized several means (attachment organs) for conquering the challenge of climbing steep inclines, including the development of claws, and smooth, hairy adhesive pads [3, 4]. The ability of a claw to reliably attach itself to a substrate depends on the frictional coefficient between the claw and the substrate, as well as the angle with which the claw engages with the substrate asperities, and the depth of a claw as it penetrates into a surface. In plain terms, the claw is not suited to move over a smooth substrate [5, 6]. Therefore, adhesive pads have evolved to adhere to smooth substrates where claws fail to grip [7]. Smooth, deformable pads generate capillary-like forces, which allow organisms such as insects and tree frogs to remain attached to various substrates. This adhesive mechanism is known as "wet adhesion" [8–10]. Hairy pads of geckos require a fine proximal pull to establish intimate contact between the flat spatula-shaped tips

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and the substrate [11, 12]. This adhesive mechanism is known as "dry adhesion", which is based on van der Waals forces [13]. On the other hand, the hair found in several insects also operates in accordance to the mechanisms of wet adhesion. Thus, the underlying mechanisms of these smooth and hairy pads are different, but both generate adhesive forces.

Generally, the attaching organs of animals are both diverse and, in the case of some animals, hierarchical. Many insects have not only several claws but also some smooth or hairy pads on their extremities that can generate adhesive forces [14, 15]. The adhesion system of *Gekko gecko*s has an elaborate hierarchical structure. The extraordinary climbing ability of geckos on inverted inclines is not only due to the van der Waals forces between the submicron-sized spatulae and the substrate, but it is also partially attributed to the synergy between the hierarchical units [16–19]. For example, the flexible lamellae on the feet ensure that the setal arrays maintain intimate contact with almost all substrates [16, 20]. Furthermore, the coupling between the front limbs and hind limbs can generate opposite reaction forces that enhance the stability of the gecko on inverted surfaces [17, 21]. In regard to the mesoscale foot, which consists of five toes covered with setae and a nonadhesive heel, our aim was the determination of how geckos coordinate the functions of the separate parts, in order to achieve reliable attachment when considering the challenge of a wide range of smooth inclines (0° to 180°).

Under the influence of a preload and pulling forces, a single seta can generate a 200 μN shear force ($F_{\parallel}$, parallel to a substrate) and a 40 μN adhesion force ($F_{\perp}$, perpendicular to the substrate). If the angle of the resultant force vector ($\alpha = \tan^{-1}(F_{\perp}/F_{\parallel})$) is greater than 30°, then the setae detach from the substrate. This means that the critical angle (α^*) of the resultant force vector acting on an isolated seta is 30° [11, 22]. When the setal array is pulled along its natural path to generate normal adhesion forces, the critical angle (α^*) of the resultant force vector acting on the setal array is 24.6° [23, 24]. Geckos attached to a glass slide by a single toe became detached at an average critical angle (α^*) of 25.5° [23]. There is no significant difference between the critical angle (α^*) for a single toe and a setal array, which is less than that of a single seta.

Considering the direction of adhesion, the adhesion force ($F_{\perp}$) directly depends on shear force ($F_{\parallel}$) and is limited by the critical detachment angle. This adhesion characteristic is defined as the "frictional adhesion" model. By frictional adhesion, the adhesion force can be precisely controlled via the shear force, allowing attachment and detachment to occur with negligible forces. Studies have shown that a single seta, a setal array, and a toe, all exhibit a property known as "frictional adhesion" [23]. However, none of these studies has proven experimentally that a foot consisting of hierarchical frictional adhesion components at different scales exhibits this frictional adhesion characteristic.

Geckos can reliably attach themselves to inclines due to the combined effect of components at different scales [16, 17], with frictional adhesion being provided by hierarchical structures with transmissibility characteristics, from the micro-scale seta to the meso-scale toe [23]. We performed trials with *Gekko gecko* that could move freely over a rotated three-dimensional force-measuring array (FMA) [25], and investigated the forces acting on an individual foot, and on the foot's contact area with the substrate, in a wide range of smooth inclines (0° to 180°). Our aim was to verify by experiment whether the gecko's mesoscale foot exhibited the characteristic "frictional adhesion" in locomotion. Meanwhile, the cooperative mechanism, whereby the adhesion of the toes acts in cooperation with the friction of the heel was studied to reveal the deployment strategy of the adhesion system in response to the challenge of smooth inclines.

2 Materials and methods

2.1 Animal

This study was carried out in accordance with the Guide of Laboratory Animal Management Ordinance of China. The experimental procedures were approved by the Jiangsu Association for Laboratory Animal Science (Jiangsu, China). A special room, which was under simulated wild environment of gecko habitat, including rock crevices, a water pool, a lighting system, and a ventilation system, was built to raise *Gekko geckos*, which were obtained from a supplier (*Jun-Hao* Wild

Animal Science & Technology Development Co. Ltd.) in Guangxi Autonomous Region, China. With the help of the lighting system and ventilation system, they were housed under simulated natural conditions with fresh water and live insects (cricket and locust, etc.) as food. A regular disinfection of the feeding room was performed by 1/1000 potassium permanganate solution every three days. The geckos were monitored daily to confirm their living states, which were revealed by indicators of food-intake, water drinking, and escape speeds.

Two to four years old adult male geckos (62.3 ± 1.8 g mass, mean ± s.d., snout-vent length: 128.3–139.5 mm, $N = 11$) were used in this study. During the experiments, there was almost no damage to the gecko. After the experiments, all of the experimental animals were again housed in animal room and were cared by professional nursing staff. In order to reduce the potential pain caused by experiments, geckos were lured to cross an FMA-like aisle that connected two boxes. During the experiment, a black box was fixed at the aisle end to lure them to climb fluently.

2.2 Experimental equipment and procedure

Details of force measurements and behavior recordings have been described in our previous work [17, 25] (Fig. 1(a)). Briefly, the forces acting on each foot were measured through the FMA which consisted of 3D force sensors, having a smooth square glass ($R_a = 0.008$ μm) at the top (30 mm × 30 mm with 1 mm clearance gap) (Fig. 1(b)) [25]. The aisle of FMA was rotated (30° per step) to imitate different inclined surfaces. Synchronously to the force measurement (NI, 500 Hz), a high-speed camera (iSpeed-3, Olympus, 1280 × 1024 pixels) recorded each trial at 500 fps. Two mirrors were placed at the two sides of the channel with angles of 45°, enabling us to see the lateral of the geckos from the side-on view. The forces acquisitions and video recordings were triggered by a pulse signal at the same time (Fig. 1(a)).

2.3 Analysis of force and video recordings

The gecko's toe adducts to attach to a substrate, and then abducts to detach itself. Video captured with a high-speed camera shows that the contact process between the foot and the substrate can be subdivided into three periods: the incipient period of contact (T_{IPC}), which starts when the heel makes contact with the substrate (t_1) and ends when the toes attach to the substrate (t_2); the stable period of contact (T_{SPC}), which starts when the toes, attached to the substrate (t_2), begin to abduct prior to detaching (t_3); and the released period of contact (T_{RPC}), which starts at the beginning of the abduction of the toe (t_3) and ends when all of the toes detach from the substrate (t_4) (Figs. 2(a) and 2(c)). Thus, the synchronous force data, as obtained with the FMA, is also subdivided into three periods (Figs. 2(b) and 2(d)).

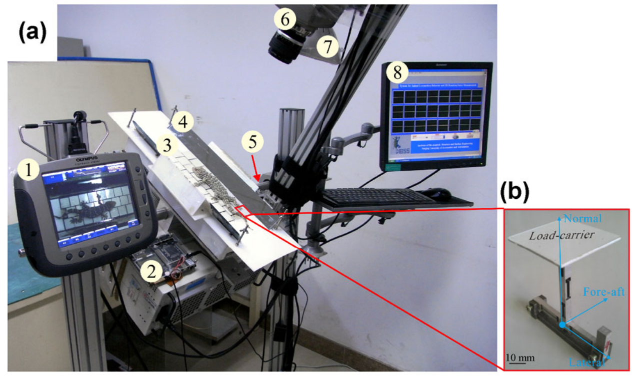

Fig. 1 Three-dimensional reaction force measuring and behavior observing system. (a) The system consists of a force-measuring array (FMA) and high-speed camera. 1, the control panel of high-speed camera; 2, synchronizer trigger; 3, an aisle of FMA; 4, mirrors; 5, rotating axis; 6, high-speed camera; 7, cold light illuminator; and 8, the control panel of FMA. The FMA can be rotated from horizontal to up-side-down to imitate different inclines. When a gecko moves through an aisle of the FMA, the dorsal view and two side-views in mirrors of locomotive behaviours were recorded by a high-speed camera located perpendicular to the FMA at 500 fps. (b) A single three-dimensional sensor for constructing FMA.

The force resulting from the combination of the lateral and fore-aft forces is a shear force ($F_{\parallel}$), which can be calculated by summing the components of the lateral and fore-aft forces in accordance to Eq. (1), which act parallel to the plane of the sensor array. The normal direction is defined as being perpendicular to the plane of the array, and the force is known as a normal force ($F_{\perp}$). To investigate the contribution of the friction of the heel and the adhesion of the toes to the reliable attachment when a gecko climbs different inclines, we focused on the video and force data for the feet in T_{SPC} (the pink points in Figs. 2(b) and 2(d)). The angle of the resultant force vector (α) of the foot was calculated from $F_{\perp}$ and $F_{\parallel}$ in T_{SPC} for each trial

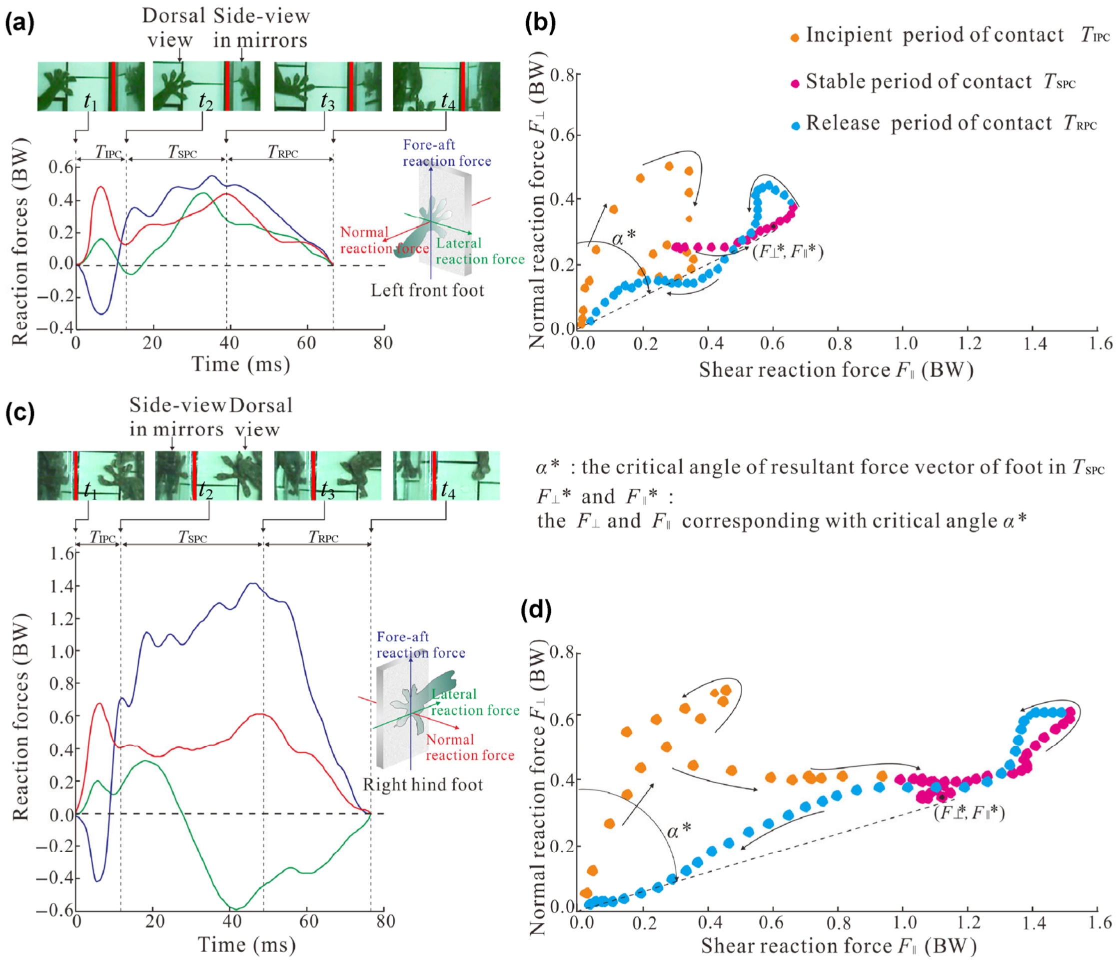

Fig. 2 State and reaction forces of feet of a freely climbing *Gekko gecko*. (a) The relationship between the state and reaction forces acting on the right front foot. (b) The normal reaction force ($F_{\perp}$) *vs.* shear reaction force ($F_{\parallel}$) acting on the left front foot. The force data for different periods of contact is indicated by different colors. We examined the data shown in pink (T_{SPC}) to investigate the effect of synergy between the friction and adhesion, or adhesion and adhesion on the reliability of the contact. (c) The relationship between the state and the reaction forces acting on the left hind foot. (d) The normal reaction force ($F_{\perp}$) *vs.* shear reaction force ($F_{\parallel}$) acting on the left hind foot.

in accordance to Eq. (2). The maximum angle was the critical angle (α^*) of the resultant force vector of the foot (Eq. (3)).

To congruously describe the data result of the critical angle (α^*), as collected from a gecko moving on different inclines, the normal direction of the substrate was defined as the starting position of α^*, with the clockwise direction being positive. The clockwise α^* defined in our research differs from that defined in previous studies [23], with the former and the latter having a phase difference of 90°. Moreover, the $F_{\perp}$ and $F_{\parallel}$ corresponding to α^* were selected as the critical normal force ($F_{\perp}^*$) and critical shear force ($F_{\parallel}^*$) (Figs. 2(b) and 2(d)).

$$F_{\parallel} = \sqrt{F_L^2 + F_F^2} \tag{1}$$

$$\alpha = \tan^{-1}(F_{\perp} / F_{\parallel}) \quad \alpha \in (0°, 180°) \tag{2}$$

$$\alpha^* = \max\{\alpha = \tan^{-1}(F_{\perp} / F_{\parallel})\} \quad \alpha^* \in (0°, 180°) \tag{3}$$

2.4 Statistics

Both the local velocities and the average velocities of a gecko were calculated for every trial to select available trails—if the interval velocity was 15% greater than or less than the average velocity, the trial was discarded. Data from all individuals were pooled, and the SPSS software (SPSS15.0, Inc., Chicago, IL) was used for all analyses. Force data were normalized by body weight (BW) in order to account for differences in body size across the sample population. In spite of our great efforts to obtain equivalent forward speeds on different inclines, the geckos slowed their forward motion when they encountered an increased angle of the incline [26]. Thus, the velocity was set as the covariate variables for each co-variance (ANCOVA) analyzed. We use the ANCOVA to compare among data for incline from 0° to 180°, where the incline was set as the independent variable and the dependent variables included α^*, $F_{\perp}^*$, and $F_{\parallel}^*$. We used ANCOVA again to compare the differences between the front and hind limb on incline; the grouping of the foot was set as the independent variable while the dependent variables were the same as above. The relationships between the $F_{\perp}^*$ and $F_{\parallel}^*$ on inclines were determined using least-squares linear regression. The similarity among α^* of feet collected from different inclines was evaluated by the Euclidean distance in hierarchical clustering and the dendrogram result was printed as figure. Because different animals were used for the seven inclines trials, we did not use repeated-measures ANOVA. Differences were considered statistically significant when $p \le 0.05$. The tested data are presented as mean ± standard deviation (mean ± s.d.).

3 Results

3.1 State of foot during stable period of contact

The image at the instant corresponding to α^* was selected from the video to show the contact state between the feet and the substrate (Fig. 3). On a horizontal substrate, the gecko abducts all of its toes to prevent the toes from adhering to the substrate (Fig. 3(a)), and uses its non-adhesive heels to place pressure on the substrate, thus generating a supporting force to oppose its weight and the friction force acting against propelling or braking locomotion. For an incline of 30° to 90°, the gecko continues to adduct some of its toes so that it can adhere to the substrate, relying on the higher adhesive and shear forces, although the heels remain in contact with the substrate (Fig. 3(b)). When the incline is greater than 90°, each of the toes of the foot adheres to the substrate, while the heel is pulled away from the substrate by gravity (Fig. 3(c)).

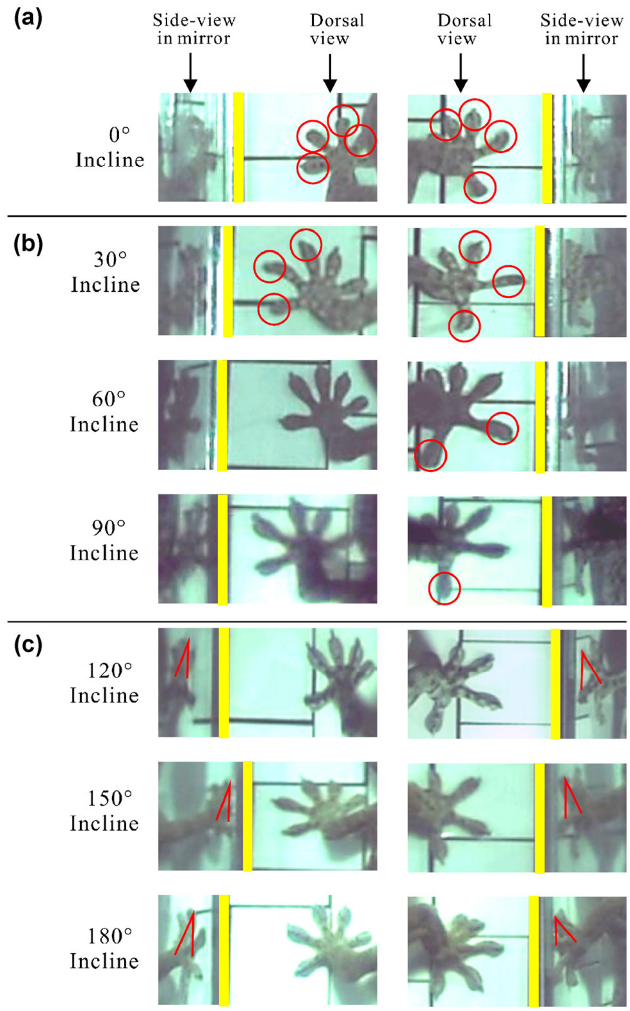

Fig. 3 Foot contact with the substrate during a stable period of contact (T_{SPC}) for an incline of 0° to 180°. (a) Only the heel contacts the substrate. (b) Concomitant contact state involving both the heel and toe. (c) Toes contact the substrate while the heel is held away from the substrate. The state of the left front foot is shown in the left column of the figure, while the state of the right hind foot is shown in the right column of the figure. The red circle indicates that the toes are not in contact with the substrate. The red bevel indicates that the heel is not in contact with the substrate.

3.2 Critical angle of resultant force vector of foot (α^*)

The critical angles of the resultant force vector (α^*) for the front and hind feet increased with respect to the incline, and α^* for the front foot ($\alpha^* = 0.632\theta + 22.607$, $F = 754.477$, $R^2 = 0.842$, $d.f. = 136$, $p < 0.001$) increased faster than that for the hind foot ($\alpha^* = 0.595\theta + 26.124$, $F = 795.014$, $R^2 = 0.856$, $d.f. = 136$, $p < 0.001$) (Fig. 4(a); Table 1). Remarkably, α^* for the front foot exhibited no significant difference for any of the

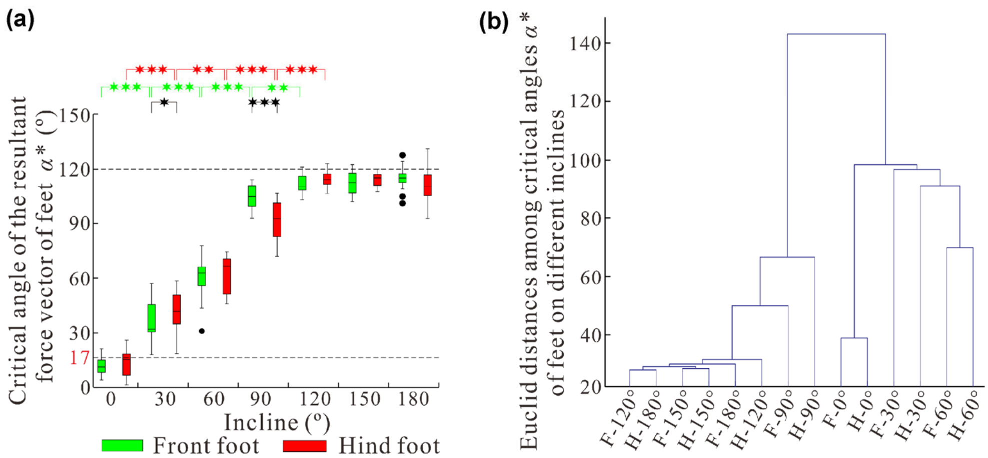

Fig. 4 Critical angle of the resultant force vector and the critical forces corresponding to the critical angle. (a) Box and whisker plots of the critical angle of the resultant force vector of the feet as related to the incline. (b) The results of hierarchical clustering analysis of the α* on different inclines. In (b), the horizontal coordinates indicate the data of the α* of the front and hind feet from 0° incline to 180° incline. For example, the F-0° means the data of α* of the front foot on 0° incline; the H-0° means the data of α* of the hind foot on 0° incline.

Table 1 Mean of forces and angles of front and hind feet of gecko at different inclines.

Subjects	Inclines						
	0°	30°	60°	90°	120°	150°	180°
$F_\perp$* of front foot (BW)	0.68 ± 0.14(20)	0.64 ± 0.15(19)	0.42 ± 0.18(20)	–0.21 ± 0.09(20)	–0.42 ± 0.13(21)	–0.54 ± 0.24(22)	–0.68 ± 0.22(20)
$F_\perp$*of hind foot (BW)	0.51 ± 0.15(20)	0.71 ± 0.18(19)	0.51 ± 0.17(20)	–0.01 ± 0.16(20)	–0.30 ± 0.10(21)	–0.44 ± 0.09(22)	–0.50 ± 0.17(20)
$F_{\parallel}$* of front foot (BW)	0.14 ± 0.06(20)	0.42 ± 0.19(19)	0.72 ± 0.27(20)	0.81 ± 0.12(20)	0.98 ± 0.21(21)	1.17 ± 0.33(22)	1.31 ± 0.29(20)
$F_{\parallel}$* of hind foot (BW)	0.16 ± 0.12(20)	0.73 ± 0.31(19)	0.95 ± 0.36(20)	0.75 ± 0.22(20)	0.69 ± 0.26(21)	0.83 ± 0.31(22)	1.11 ± 0.32(20)
α* of front foot (°)	11.86 ± 4.86(20)	33.00 ± 12.67(19)	63.57 ± 10.72(20)	104.50 ± 6.41(20)	112.77 ± 6.17(21)	114.51 ± 7.63(22)	117.68 ± 7.43(20)
α* of hind foot (°)	17.31 ± 10.82(20)	44.00 ± 12.06(19)	61.24 ± 12.83(20)	92.16 ± 11.11(20)	114.36 ± 5.91(21)	117.75 ± 4.87(22)	114.68 ± 9.75(20)

Values are means ± s.e.m.; *n* values are given in parentheses; BW is body weight

120°, 150°, and 180° inclines, as did the α* of the hind foot (Table S1 in the Electronic Supplementary Material (ESM)). Meanwhile, there is no significant difference between α* for the front and hind feet (Table S2 in the ESM). When the incline exceeded 120°, the data for α* for the front and hind feet are clearly similar (Fig. 4(b)), and the average α* of both the front and hind feet did not exceed 120°.

3.3 Critical normal forces and shear force corresponding to critical angle

The critical normal forces ($F_\perp$*) of the front and hind feet decreased with respect to the incline (front foot: $F_\perp^* = -0.009\theta + 0.761$, $F = 787.364$, $R^2 = 0.848$, $d.f. = 134$, $p < 0.001$; hind foot: $F_\perp^* = -0.007\theta + 0.734$, $F = 528.071$, $R^2 = 0.796$, $d.f. = 134$, $p < 0.001$). The critical shear force ($F_{\parallel}$*) of the front and hind feet decreased with respect to the incline (front foot: $F_{\parallel}^* = 0.006\theta + 0.234$, $F = 382.638$, $R^2 = 0.730$, $d.f. = 134$, $p < 0.001$; hind foot: $F_{\parallel}^* = 0.003\theta + 0.441$, $F = 52.925$, $R^2 = 0.278$, $d.f. = 134$, $p < 0.001$) (Fig. 5; Table 1). Note that when incline ranges from 0° to 90°, there were no significant correlations between the $F_\perp$* and $F_{\parallel}$*. Alternatively, the $F_\perp$* was significantly affected by the $F_{\parallel}$* when the incline ranges from 120° to 180° (Table 2).

4 Discussion

Geckos can move freely on steep inclines, because of the excellent adhesion performance of their toes, the real-time adjustment of the locomotive behavior, and precise control over reaction forces. As a result, geckos continually modulate the reaction force acting on their feet in response to the challenge posed by

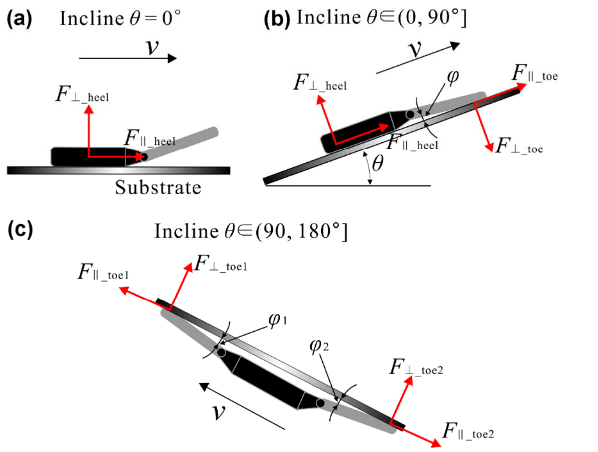

Fig. 5 The planar mechanical model of contact between foot and the inclined substrate. θ: incline of the substrate; v: locomotive direction. (a) A mechanical model of contact for 0° incline. Only the heel pushes away from the substrate to generate a supporting force ($F_{\perp\_heel}$) and friction force ($F_{\parallel\_heel}$) on a level surface. (b) A mechanical model of contact when incline does not exceed 90°. The state of contact is a concomitant contact of friction and adhesion. The toe pulls toward the substrate to generate adhesive friction force ($F_{\parallel\_toe}$) and adhesion force ($F_{\perp\_toe}$), while the heel pushes away the substrate. φ: angle between the toe and the substrate. (c) A mechanical model of contact when the incline exceeds 90°. More toes adhere to the substrate to generate adhesion and friction forces, whereas the heel does not make contact with the substrate. $F_{\perp\_toe1}$ and $F_{\perp\_toe2}$: the adhesion forces acting on toe1 and toe2; $F_{\perp\_heel1}$ and $F_{\perp\_heel2}$: the adhesive friction forces acting on toe1 and toe2; φ_1 and φ_2: the angles between the toe1/2 and the substrate.

changing incline [17]. Therefore, we questioned how geckos generate corresponding reaction forces to meet the requirement for locomotion, while ensuring reliable attachment between the foot and the inclined substrates.

4.1 Synergy between friction and adhesion according to incline

The measured results of the variable α^* of the feet may imply turning points in the attachment mechanism (friction and adhesion) of the foot (Fig. 4). A planar mechanical model was established to describe the change in the attachment mechanism of the foot in response to the incline, and reveal the contribution of the synergy between the friction and adhesion to a reliable attachment. As it can be seen from the results, the toes abduct to keep the foot away from a horizontal (0° incline) substrate (Figs. 3 and 5(a)). This contact approach not only reduces the number of toes adhering to the substrate to protect the setae [23, 27], but also avoids the unnecessary deployment of adhesion, and thus improves the maneuverability [26, 28]. A gecko's heel is covered with scales, making it a nonadhesive and nonlubricated system. This indicates that its frictional properties are similar to those of a typical dry solid. Thus, the α^* ($\alpha^* = \tan^{-1}\mu$) of the foot is

Table 2 The linear regression of critical normal reaction force ($F_{\perp}$*) on critical shear reaction force ($F_{||}$*) acting on front and hind feet of gecko at different inclines.

Inclines	Foot	*d.f.*	*F*	R^2	*p*-value	
0°	front	19	0.007	0.001	0.935	
	hind	19	1.464	0.068	0.400	
30°	front	18	0.015	0.003	0.906	
	hind	18	0.474	0.026	0.500	
60°	front	19	1.916	0.084	0.181	
	hind	19	0.073	0.004	0.790	
90°	front	19	0.743	0.040	0.400	
	hind	19	0.061	0.003	0.807	
120°	front	20	11.849	0.389	0.033	$F_{\perp}^* = -0.384F_{\parallel}^*-0.118$
	hind	20	17.303	0.449	0.001	$F_{\perp}^* = -0.423F_{\parallel}^*-0.106$
150°	front	21	11.382	0.361	0.003	$F_{\perp}^* = -0.445F_{\parallel}^*-0.019$
	hind	21	69.781	0.786	<0.001	$F_{\perp}^* = -0.569F_{\parallel}^*-0.301$
180°	front	19	13.461	0.461	0.029	$F_{\perp}^* = -0.501F_{\parallel}^*-0.286$
	hind	19	10.962	0.448	0.039	$F_{\perp}^* = -0.422F_{\parallel}^*-0.360$

determined by the frictional coefficient μ between the heel and the substrate on a 0° incline [29], while the average α^* values for the front and hindfeet are 11° and 17°, respectively (Fig. 4(a) and Table S1 in the ESM). These values are smaller than the values of frictional angles ranging between 19° to 28° ($\tan^{-1}(0.339–0.551)$) between a snakeskin and a glass surface [30].

A larger driving force is required to overcome the increase in the component of the weight parallel to the substrate ($W^{\parallel} = W \cdot \sin\theta$) with the increase in the incline, while the component of the weight perpendicular to the substrate ($W^{\perp} = W \cdot \cos\theta$) decreases [17]. As a result, the frictional force between the heel and the substrate is not sufficient to provide the driving force required to allow the geckos successfully move on an incline, i.e., geckos could not climb inclines of more than 17° by relying solely on the friction of their heels, without deploying the adhesion of their toes. Thus, the toes gradually increase their role in making contact with the substrate, and provide a driving force. Correspondingly, the contact between the foot and the substrate enters a concomitant contact state involving both the heel and the toes (Fig. 5(b), in which the forces acting on all the toes are simplified to equivalent forces acting on a single toe in the planar mechanical model).

The α^* value for the foot is determined based on the friction of the heel and the adhesion of the toe (Eq. (4), detailed derivation process refers to the ESM).

$$\alpha^* = \tan^{-1}\left(\frac{\mu r_{\mathrm{h\_t}} + 1/\tan\varphi}{r_{\mathrm{h\_t}} - 1}\right) = \tan^{-1}\left(\mu + \frac{\mu + 1/\tan\varphi}{r_{\mathrm{h\_t}} - 1}\right),$$

$$r_{\mathrm{h\_t}} > 0, r_{\mathrm{h\_t}} \neq 1 \tag{4}$$

Here, μ is the frictional coefficient between the heel and the substrate; φ is the angle between the toe and the substrate, and the contribution ratio ($r_{\mathrm{h\_t}}$) is used to evaluate the contribution of the friction generated by the heel and the adhesion generated by the toes to achieve reliable attachment.

When a gecko moves on a wall and across a ceiling, the angle between each single toe and the substrate is approximately 20° [31], that is, not greater than the α^* value for each toe. Herein, μ = 0.31 = tan17°, and φ = 20°, are used to calculate the α^* of the foot for different deployments of friction and adhesion (Fig. 6(a)). The

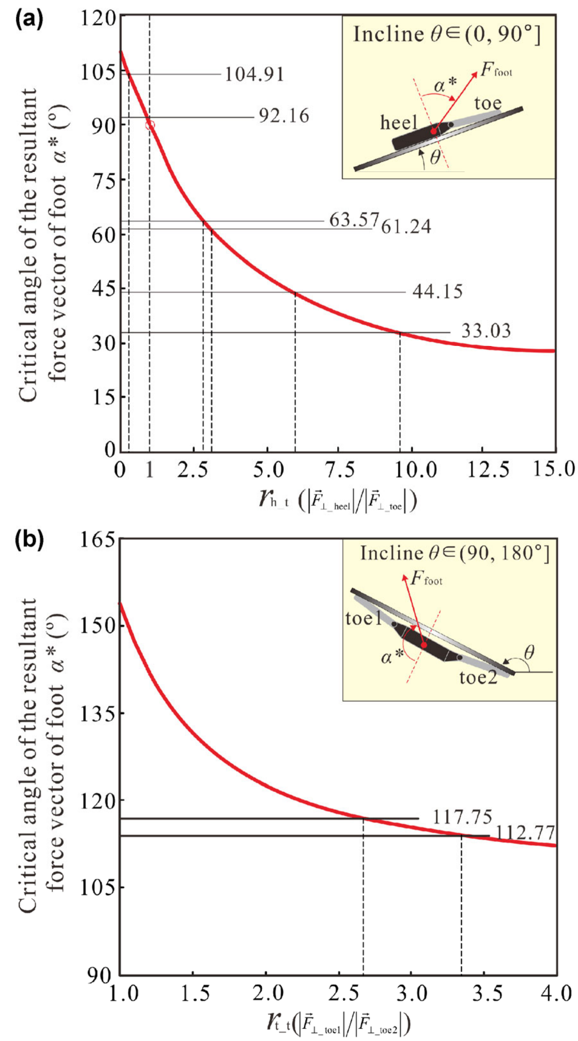

Fig. 6 Critical angle (α^*) of the resultant force vector of the foot, calculated by the mechanical model of contact between the foot and the substrate. F_{foot}: the resultant force vector acting on foot. (a) The critical angle of the foot as calculated by the mechanical model when the incline does not exceed 90°. The average value of α^* for the front and hind feet on inclines not exceeding 90°, as measured by experiment, were shown to be level lines in the figure (detail data in Table 1). (b) The critical angle of the foot as calculated by the mechanical model when the incline exceeds 90°. The maximum and minimum average value of α^* for the feet, as measured by experiment, are shown in the figure for inclines exceeding 90°.

contribution ratio ($r_{\mathrm{h\_t}}$) value cannot exceed 10, which indicates that the friction of the heel plays a major role in the reliable attachment on 30° inclines. However, even a relatively low toe adhesion can notably improve the reliability of the attachment. As the incline continues to increase, the climbing resistance increases with the gravity component parallel to the incline, whereas the frictional force decreases because of the decrease in the gravity component perpendicular to the incline. The adhesion and shear forces generated by the toes play an important role in ensuring a reliable attachment, since the $r_{\text{h\_t}}$ value is only 2.5 when the incline is 60°. A smaller $r_{\text{h\_t}}$ value can improve the reliability of the attachment, but the internal moment caused by the difference between the forces acting on the heel and toe increases owing to a decrease in $r_{\text{h\_t}}$, which may result in a more difficult movement. On a nearly vertical substrate, the front foot gradually pulls the body close to the substrate and provides adhesion to satisfy the requirement of ensuring movement stability [17], which results in a $r_{\text{h\_t}}$ value of less than 1. To-date, the contribution of the friction generated by the heel has been very obscure, but the deployment of the adhesion of the toe plays a key role. The average critical angle of the front foot on a 90° incline is approximately 104° during the movement, similar to the result obtained by Autumn et al. [23]. The hindfoot is required to push away or pull towards the substrate in order to provide either a pushing or an adhesion force, respectively, in order to maintain the dynamic stability during movement [18, 32], thereby leading to an $r_{\text{h\_t}}$ value of the foot close to 1. The foot has to withstand a large internal moment during movement.

The adaptability of this concomitant contact state is severely limited by the adhesive capability of the toe and the friction coefficient of the heel. When the incline is larger than 90°, the non-adhesive heel will be pulled away from the substrate by gravity, leaving only the toes attached to the substrate (Fig. 3). Geckos can safely remain attached to an inverted surface by stretching their first and fifth toes into a *Y*-configuration, thus avoiding the failure of the adhesion of a single toe [17, 31]. The forces acting on each toe of the foot are equally deployed to toes 1 and 2 in a planar mechanical model (Fig. 5(c)). The α^* of the foot is determined by the combined adhesion between the toes (Eq. (5), detailed derivation process refers to the ESM).

$$\alpha^* = \tan^{-1}\left(\frac{r_{\text{t\_t}}/\tan\varphi_1 - 1/\tan\varphi_2}{r_{\text{t\_t}}+1}\right) \tag{5}$$

Here, φ_1 and φ_2 are the angles between the toe 1/2 and the substrate respectively; the contribution ratio ($r_{\text{t\_t}}$) is defined to evaluate the contribution of the adhesions generated by different toes to the attachment.

The gecko modulates the orientations of the toes and alters the number of attachment toes, resulting in the change in $r_{\text{t\_t}}$, thus adapting the motion requirement [17, 31, 33]. As the number of toes adhering to the substrate increases, the load on the adhesive toe will decrease, since this will reduce the risk of detachment of the gecko. Therefore, when the incline is larger than 90°, all five toes of the foot adhere to the substrate (Fig. 3) to share the load, and thus increase the reliability of the attachment. As a result, the locomotive performance worsens, an outcome that is exemplified by a decrease in the speed and stride frequency [26], manifested as a trade-off between locomotive safety and performance. To form a *Y*-configuration with the five toes, the $r_{\text{t\_t}}$ of the foot ranges from 1 to 4. In fact, the scope of adjustment between any adjacent toe is limited by the morphology and structure of the toes [27, 31]. Thus, the $r_{\text{t\_t}}$ of the foot is less than 4. On the other hand, if the $r_{\text{t\_t}}$ of the foot is too small, one toe would be overtaxed, and the muscles in the foot would have to produce a larger internal moment, which would be detrimental to the locomotion. We found that the load share ratio ($r_{\text{t\_t}}$) was within a range of 2.6 to 3.3 when the inclined angle was larger than 120° (Fig. 6(b)).

The synergy between friction and adhesion, or adhesion and adhesion, in response to an incline illustrates that the synergy between multiple contact mechanisms can achieve a reliable attachment on an incline, while a single-contact mechanism cannot. This increases the animal's ability to adapt to its environment, but also explains the importance of the reasonable deployment of the adhesion system when faced with the challenge of an inverted incline. This characteristic of the synergy of friction and adhesion was found in the attachment mechanism of tree frogs and insects [10, 34], which embodies the functional convergent evolution in animal survival.

4.2 Frictional adhesion of foot

The adhesion system of a gecko consists of hierarchical adhesive units including setae, arrays of setae, lamellae, toes, and feet [24, 35]. Previous research has revealed that the α^* values of the setae, arrays of setae, and toes, were not relevant to the exerted force, and that the adhesion force is a function of the shear force [23, 24]. This adhesion capability was characterized as a frictional adhesion [23]. The roles of the feet were changed to respond to an increase in the incline, which led to a significant change in the forces acting on the feet [17]. However, the α^* of the foot did not change significantly when the incline changed from 120° to 180°, i.e., during locomotion the α^* value of the foot was not affected by the forces acting on the foot (Fig. 4(a), Tables S1 and S2 in the ESM). In addition, there is an apparent linear relationship between the critical adhesive force ($F_\perp{}^*$) and the critical shear force ($F_\parallel{}^*$) acting on the toes (Fig. 7, Table 2). During locomotion, the complicated and accurate synergy between the toes endows a gecko's foot with obvious characteristics of frictional adhesion, i.e., the adhesive force is a function of the shear force. When a gecko climbs steep and inverted inclines, the mean value of α^* of the foot ranges from 114° to 117° (Fig. 4(a)), similar to the α^* values of the arrays of setae and the toes. However, it does not exceed the α^* value (α^* = 120° = 90° + 30°) of a single seta, which may imply the extremes values of the α^* of a foot.

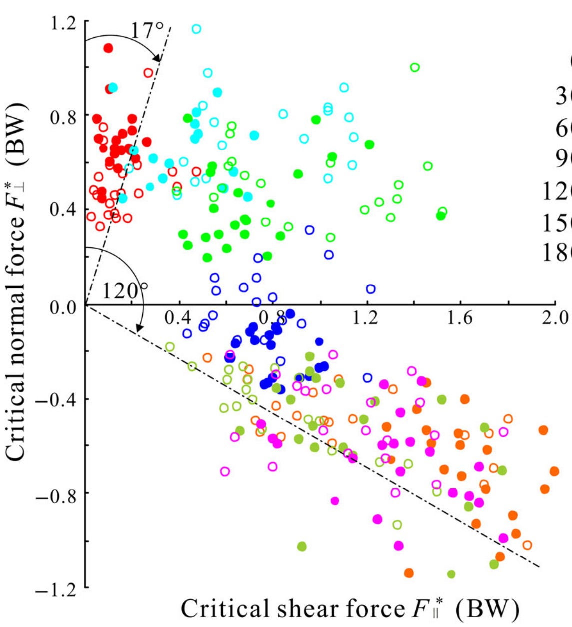

Fig. 7 The critical normal force ($F_\perp$*) *vs.* the critical shear force ($F_\parallel$*) corresponding to the critical angle when the gecko moves on different inclines. The solid points represent the variables for the front foot, whereas, the hollow points represent the variables for the hind foot.

4.3 Contact state of foot and adjustment of position

When the action force falls within the scope of the frictional angle to attain frictional self-locking contact, the action force [29] will not affect the contact between the two objects. During locomotion, the reaction force is always in the direction corresponding to the minimum moment of force [36]. Herein, by ignoring the action of the moment of the force, we regard the limbs as being two force bars to allow a discussion of the relationship between the contact state and the adjustment of posture. On a horizontal surface, a gecko gathers up its limbs towards its body, and lifts them to the height COM (h) [26]. In turn, this limits the angle between the limbs and the substrate (β) to values within the range of the foot's α^* values in order to ensure that the foot reliably contacts the substrate without any slip (Fig. 8(a)). While in contact with a steep surface, the gecko reduces the value of h to reduce the risk of overturning, which in turn results in a decrease in β. Thus, the gecko involves more toes in the deployment of adhesion to enlarge the α^* of the

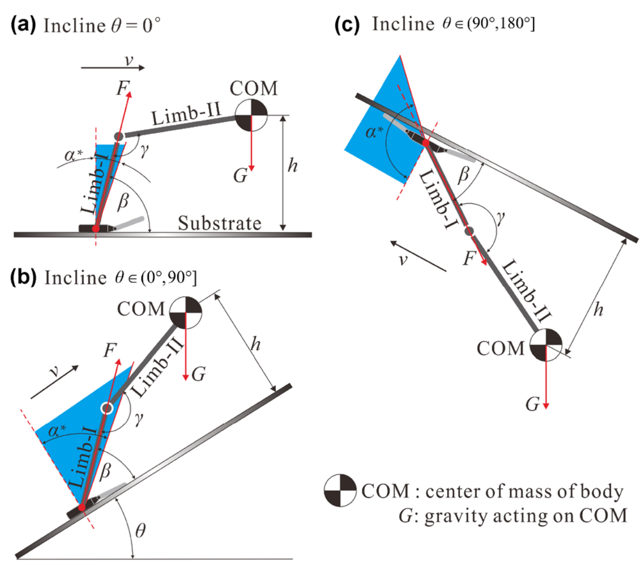

Fig. 8 Contact state of the foot and adjustment of the position in response to the incline. (a) Critical angle (α^*) of the foot and the position of the gecko limb on a horizontal substrate. (b) α^* of the foot and the position of the gecko limb on inclines of less than 90°. (c) α^* of the foot and the position of the gecko limb on inclines greater than 90°. The limb is simplified to two parts, limb-I and limb-II, with limb-I being closest to the foot. β: angle between limb-I and the substrate; γ: angle between limb-I and limb-II; h: distance between COM and the substrate; F: force acting on limb-I.

foot. This ensures the reliability of the contact between the foot and the substrate, while the limbs have plenty of active space (Fig. 8(b)). However, excessive deployment of the toes' adhesion may lead to a decrease in the locomotive performance [28].

Unlike common friction, where the shear force is a function of the normal force, a gecko's foot is characterized by frictional adhesion, where the adhesive force is a function of the shear force. This type of frictional adhesion provides a useful means of precisely controlling the adhesive force by controlling the shear force, and enables attachment and detachment to occur using only minute forces [23]. Geckos skilfully utilize this frictional adhesion by controlling the angle of the limb, thereby pulling the foot in such a way to allow a successful climb onto inverted inclines [18]. When the incline is larger than 90°, the h value will be enlarged owing to the effect of gravity, resulting in an increase in β (Fig. 8(c)). To ensure that the force acting on the limb falls into the critical scope of attachment, i.e., β becomes smaller than α^* (shaded areas in Fig. 8(c)), the gecko extends its limbs outwards to decrease the values of h and β [26]. Similarly, tree frogs and locusts can attach themselves to inverted inclined surfaces using this mechanism [6, 37], possibly owing to the limited adhesiveness in their feet.

5 Conclusion

Geckos rely on the friction between their heels and substrates to generate the forces required for movement across a horizontal substrate. On steep inclines, moderate deployment of toe adhesion enhances the reliability of attachment of feet. However, excessive deployment of toe adhesion results in the lower maneuverability of locomotion, even though the reliability is enhanced. These characters inspire us in the design of climbing robots or adhesion systems with more controllable freedom on adhesive units for the sake of a favorable trade-off between reliability and performance of locomotion. The adhesive ability of a special Y-configuration is limited by the performance of the adhesive units, resulting in the α^* value of the foot being approximately 120°, i.e., geckos could not hang from an incline at an angle exceeding 120° with the use of a single foot. Correspondingly, geckos exploit the characteristic of "frictional adhesion" in their feet to allow successful climbing on inverted inclines through cooperation of high-level units, including limbs and body. This fully reflects the fact that the locomotion system of animals is not a simple splice of units but their organic integration. Therefore, when designing a climbing robot or an adhesion system, we should not blindly pursue the improvement of one of the units, but rather carefully integrate each unit into an overall system, while correctly endowing the basic units with more controllable freedom, in order to allow a significant improvement in the performance of a climbing robot or an adhesion system.

Ethical statements

This manuscript adheres to the appropriate reporting guidelines and community standards for data availability. This manuscript has not been published or presented elsewhere in part or in entirety. All contributing authors are aware of and agree to the submission of this manuscript. All study participants provided informed consent, and the study design was approved by the appropriate ethics review boards. This study was carried out accordance with the Guide of Laboratory Animal Management Ordinance of China. The experimental procedures were approved by the Jiangsu Association for Laboratory Animal Science (Jiangsu, China).

Competing interest statement

The authors declare no competing financial interests.

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