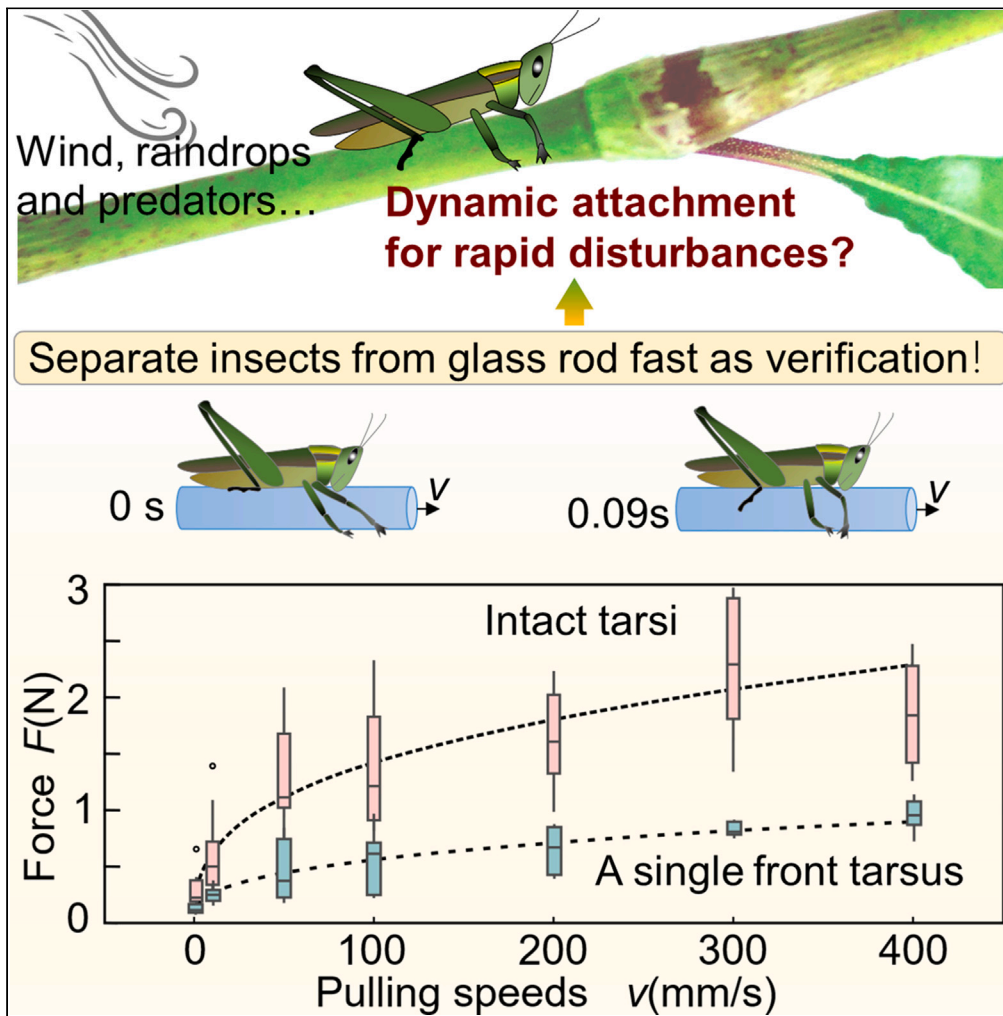


Article

Rate-dependent adhesion together with limb collaborations facilitate grasshoppers reliable attachment under highly dynamic conditions



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Highlights

Explore attachment of grasshopper on glass rod at separating speeds up to 400 mm/s

Insects reposition limbs to resist large loads and reduce shocks

Forces increased with the pulling speeds following power laws

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## Article

## Rate-dependent adhesion together with limb collaborations facilitate grasshoppers reliable attachment under highly dynamic conditions

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## SUMMARY

**Dynamic attachment is indispensable for animals to cope with unexpected disturbances. Minor attention has been paid to the dynamic performance of insects' adhesive pads. Through experiments pulling whole grasshoppers off a glass rod at varying speeds, surprising findings emerged. The feet did not always maintain contact but released and then reconnected to the substrate rapidly during leg extension, potentially reducing the shock damage to pads. As the pulling speeds increased from 1 to 400 mm/s, the maximum forces of single front tarsus insects and entire tarsi insects were nearly proportional to the 1/3 power of pulling speeds by 0.11 and 0.29 times, respectively. The force of some individuals could be even 800 times greater than their weight, which is unexpectedly high for smooth insect pads. This work not only helps us to understand the attachment intelligence of animals but is also informative for artificial attachment in extreme situations.**

## INTRODUCTION

Many arthropods and vertebrates have developed the ability to attach to and move across various surfaces (such as plants and rocks) by utilizing their specialized feet, providing engineers with innovative solutions to the technical systems requiring fast connection and release.<sup>1,2</sup> Studies on the biological attachment devices that consider topographic features of substrate surfaces, such as slopes,<sup>3</sup> roughness,<sup>4–7</sup> compliance,<sup>8–10</sup> slipperiness,<sup>11,12</sup> or discontinuity,<sup>12,13</sup> have not only elucidated the morphological and functional intelligence of animals<sup>11,14–19</sup> but also contributed to the development of advanced artificial adhesive systems<sup>20–25</sup> and novel methodology for biomimetic research.<sup>26–28</sup> Nevertheless, many functional advantages of the biological attachment systems remain unclear.

Animals typically use interlocking claws<sup>29</sup> and spines<sup>13</sup> and/or adhesive pads<sup>14,15</sup> as parts of their attachment system. Even though understanding these components' contribution is very important, we are more interested in this paper in the overall performance of the adhesive system or even the entire animal for several reasons. As previously demonstrated, the distributed control among the components allows the whole system to perform in intelligent and sometimes even unexpected ways.<sup>12,30</sup> Some static and quasi-static tests with insects indicated that different legs and different attachment elements in the feet have the potential to work together, therefore allowing the system to generate forces greater than the direct sum of the same number of components.<sup>19,31,32</sup> However, the synergy of gecko toes does not appear to increase the magnitude of force<sup>33,34</sup> but allows feet to withstand loads from different directions.<sup>3,12</sup>

On the other hand, we are also interested in the dynamic performances of the attachment systems because strong but highly dynamic surface adhesion is crucial for animals,<sup>10</sup> especially when they are exposed to disturbances, such as unexpected substrate oscillations and intense jerky wind pulses or when they must move quickly to escape predators. Claws and spines can produce instantly repeatable and releasable engagements<sup>29</sup> through friction and mechanical interlocking that appear independent of loading rate.<sup>35</sup> As to the adhesive pads (both smooth and hairy), they have been shown to be rate-dependent in relatively slow cases (smooth pads,  $\leq 1.3$  mm/s<sup>36</sup>) or *in vitro* (gecko seta,  $\leq 160$  mm/s<sup>37</sup>). Whereas how the multiple limbs function together under highly dynamic situations is rarely understood.

As the first step to understanding the dynamic attachment of the system with multiple controllable components, we focused on the insects' adhesive pads, which function well on smooth substrates. Using the grasshoppers (*Oxya chinensis*) as the experimental animals, we test their attachment force on a glass rod (6 mm in diameter) that mimics the plant stem while imitating dynamic disturbance by varying the moving speeds. The assessment of dynamic adhesion in the whole foot and the whole animal promises a better understanding of animal-environment interactions, which in turn can provide interesting ideas for biomimetic adhesion systems.

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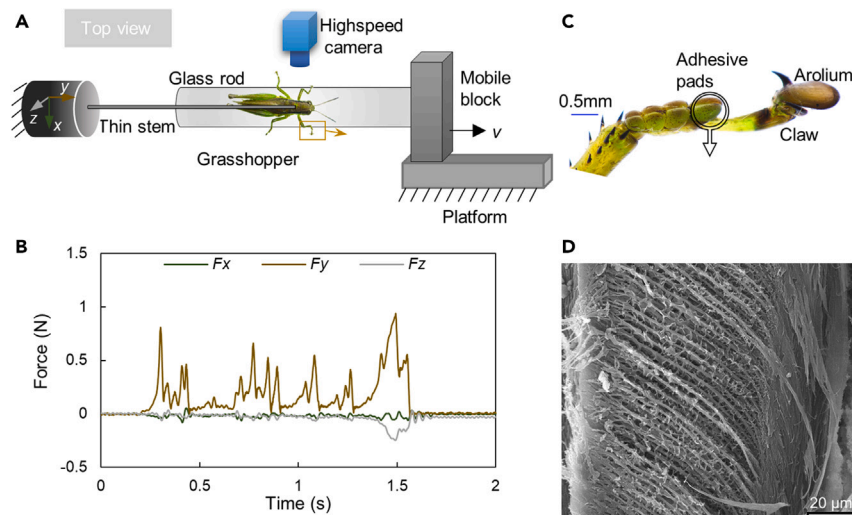
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**Figure 1. The experimental approach**

(A–D) (A) Scheme of the experimental procedure; (B) An example force result (100 mm/s); (C) The tarsus of the insect; (D) The interior structure of the adhesive pads (Adopted from our previous work<sup>35</sup>). Fig. C were taken using an ultra-depth-of-field microscope (VHX-600E, Keyence, Japan). In A, the grasshoppers were glued with their dorsal thorax surface to a thin stem, which was then attached to a multi-axis force transducer. A glass rod (diameter 6 mm) was used to mimic convex substrates typical for the habitat of this animal. The substrate was first moved toward the animal until its thorax touched it. After several seconds for the insects to establish an initial contact, we moved the glass rod away from the animal at different speeds and measured the forces.

## RESULTS

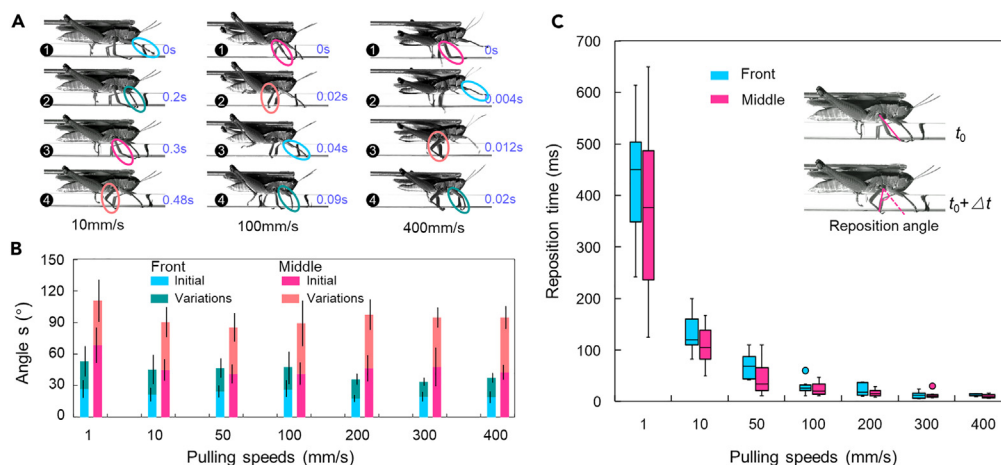
To study the dynamic adhesion of the insects, we connected the grasshoppers (*Oxya chinensis*, Figure 1A) to a force sensor using a thin stem and then attached them equipped with adhesive tarsi (Figure 1C) to a glass rod and separated them with different speeds (from 1 mm/s to 400 mm/s; Figure 1A). Video S1 shows examples of the pulling experiments. During the preparation stage, the grasshoppers with intact tarsi and grasshoppers with a single front tarsus behaved similarly. The grasshoppers tried to grasp the glass rod with their front and middle limbs. When viewed from the side, the initial angle between the front leg and the rod was 25°–45°, and the middle portions 100°–150°. Instead of grasping the glass rod like the front and middle legs, the hind legs may attach to the rod at the proximal side with the tarsi or unused. Pulling the glass rod (fast or slow) changed the insects' posture similarly (Figure 2A, Video S1). In particular, all tarsi in contact with the rod moved with the rod first. As soon as the legs were straightened, in addition to sliding their tarsi on the glass rod, the grasshoppers could also detach the legs and tried to restore the original position and generate new contact (circles in Figure 2A). As the pulling speed increased from 1 mm/s to 400 mm/s, the angles between the front limbs and the trunk when they started to move slightly decreased from  $27.1 \pm 7.8^\circ$  to  $19.1 \pm 5.6^\circ$  (Cyan bars in Figure 2B; Mixed model,  $F_{(6,50,2)} = 3.13$ ,  $p = 0.011$ ), so did the angles they moved (Light green bars in Figure 2B; Mixed model,  $F_{(6,50,4)} = 2.80$ ,  $p = 0.02$ ). In comparison, the angles between the front limbs and the trunk when they started to move ( $68.5 \pm 16.8^\circ$ ) for the 1 mm/s case were larger than those in other cases ( $\sim 42^\circ$ , magenta bars in Figure 2B;  $F_{(6,56)} = 5.63$ ,  $p < 0.001$ ) whereas the angular variations of the middle limbs showed no differences (light pink bars in Figure 2B;  $F_{(6,55,17)} = 0.685$ ,  $p = 0.66$ ). Figure 2C shows the time costs for repositioning the front and middle legs. In slow-pulling experiments (1 mm/s), the time costs to reposition limbs fluctuated largely among trials (241.7–614.3 ms for the front limbs and 125–572.2 ms for the middle legs). With the increase in the pulling speeds, the repositioning time for both front and hind limbs significantly decreased (Front: cyan boxes,  $F_{(6,51)} = 100.4$ ,  $p < 0.001$ ; Middle: magenta boxes,  $F_{(6,55,47)} = 29.47$ ,  $p < 0.001$ ).

Figure 3 shows the maximum resultant force of the grasshopper pulled by the glass rod. When we pulled the rod, the force was not constant but varied non-monotonically with time (Figure 1B). When we tested with grasshoppers that possessed a single front tarsus, the force ( $F_s$ ) increased from  $0.12 \pm 0.04$  N ( $v = 1$  mm/s) to  $0.95 \pm 0.13$  N ( $v = 400$  mm/s), also flowing a power law ( $F_s = 0.11v^{0.33}$ ,  $p < 0.001$ ,  $R^2 = 0.98$  when calculated using averaged data, Figure 3A). Surprisingly, the force for the whole animals ( $F_a$ ) also followed a power law ( $F_a = 0.29v^{0.34}$ ,  $p < 0.001$ ,  $R^2 = 0.98$  when calculated using averaged data, Figure 3B), from  $0.29 \pm 0.16$  N to  $2.16 \pm 0.41$  N.

## DISCUSSION

### Grasp with limbs helps to achieve better original attachment

There has been some interest in insect walking strategies on rod-shaped substrates, and it has been shown that insects tend to bend their tarsus and even legs<sup>32,39–41</sup> to conform to the rod-shaped surface for stable locomotion. Here, we also find that the grasshopper held the rod by wrapping it with their front and middle legs, even when their tarsi were removed (Video S1). When a grasshopper holds a stick, its tarsus does not match its legs. When the leg is pulled, the load transferred from the portion to the tarsus can be divided into parallel pulling and compression rather than separation due to the curvature of the substrate. In other words, the limb could convert the macro separation load



**Figure 2. Results of the speed-force experiments**

(A) Sequence diagrams of pulling tests at velocities of 10 mm/s (left), 100 mm/s (middle) and 400 mm/s (right).

(B) The variations in angles between limbs and the trunk of insects while the insects reposition their limbs.

(C) Temporal expenses for repositioning of limbs. In A, the circles indicate the positional variations of the front and middle limbs. In B, the deep color bars indicate the angles of limbs when they start to move, while the light bars indicate the variations of limb angles. Data are presented as mean  $\pm$  SD.

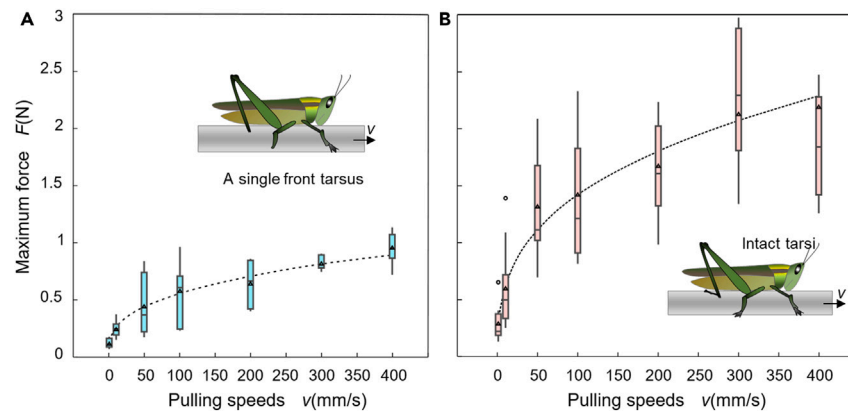
into local tangential force and enhance the local tangential force through the local friction caused by local pressure, as we have found in our previous works.<sup>7,42</sup> Though the grasp with limbs helps to achieve better original attachment on curved surfaces, a comprehensive force measurement (for example, using substrates with triangle sections on which the limbs can add pressure but will be pulled parallel to the surfaces) is still needed to understand such grip better and will be our subsequent step.

### Tarsi repositioning for safe adhesion

Before pulling the rod away from the insects, we assumed the limbs would remain immobile, resisting the force until the end. However, once the front and middle limbs were engaged with the rod (front  $\sim 43^\circ$ ; middle  $\sim 95^\circ$ ), the corresponding tarsi first moved along with the rod (Figure 2A), reducing the angles between the front limbs and the trunk to  $\sim 22^\circ$  and those between the middle limbs and the trunk to  $\sim 45^\circ$ . At first glance, such an alternation in the limb positions indicates that the trochanters seem not to be able to withstand large moments. However, from a mitigation perspective, this positional adjustment is beneficial. As the relative position between the glass rod and the grasshoppers changed suddenly, the relative acceleration could theoretically be infinite, as can the force at the tarsus and the moment at the basis of the leg. Such high forces and torques can damage pads and limbs if the animal tarsi remain in the same position. Conversely, by moving the tarsus with the glass rod, the grasshopper can effectively absorb the impact force and avoid damage to the body structure. As a result, when we started to pull the glass rod, the measured force did not increase immediately, especially in the fast pull test (Figure 1B).

Surprisingly, limbs were prone to detach from the rod immediately or after sliding on the rod for a period when the limbs were straightened, resulting in the forces decreasing instantly from a relatively large value (Figure 1B). Presumably, the detachment of limbs is beneficial for avoiding damage to animals caused by excessive force. After detaching from the rod, the limbs tried to reattach to the substrate by turning the front limbs backwards for  $\sim 20^\circ$  and the middle limbs for  $\sim 50^\circ$  in less than 0.7 s to resist the pulling. Due to the repeated detachment and reattachment, the recorded forces varied non-monotonously during the experiments (Figure 1B).

We were also interested in whether the limb adjustment was achieved through active control or passive feedback. The feedback speed can depend on the contraction speed of the muscle. We recently observed the jump behaviors of the grasshoppers and discovered that their hind limbs could extend in less than 25 ms (unpublished data). Full et al.<sup>43</sup> found that the cockroach (*Periplaneta americana*) could freely run as fast as  $\sim 30$  steps per second with duty factors of about  $\sim 0.5$ , indicating that their muscles could reposition in  $\sim 16$  ms. Thus, it can be extrapolated that if the repositioning behaviors are achieved through neural control, their time costs must be at least longer than 16 ms. As demonstrated in Figure 2C, increasing the pulling speeds from 1 mm/s to 400 mm/s reduced the average limb repositioning time from 400 ms (range from 125 ms to 650 ms) to 10 ms (range from 6 ms to 25 ms), with no significant differences identified between the front and middle limbs. The trials in which the repositioning time was less than 16 ms were even discovered when the pulling speeds increased to 50 mm/s (Figure 2C). Therefore, we tended to support the hypothesis that this type of postural adjustment is achieved through neuronal control when the pulling speeds are less than 50 mm/s, but a combination of mechanical feedback and neuronal feedback in faster-pulling experiments. As Spagna et al.<sup>13</sup> pointed out, passive mechanical feedback coming from the synergy of leg configuration, leg motion, and attachment might swiftly build coupling with the environment and overcome the inherent delays of neural feedback, allowing for the handling of unforeseen disruptions. When the pulling was slow, neuronal cooperation could aid in achieving exact repositioning. Limbs collaborate well and generate large forces without harming themselves, utilizing mechanical and neural feedback.



**Figure 3. The dynamic attachment force of grasshoppers**  
(A) Insects with a single front tarsus; (B) Insects with intact tarsi. The triangles represent the mean values.

### Dynamical attachment to cope with extremity

As previously stated, once straightened, the engagements of the front and middle legs with the glass rod can be released immediately, reducing the number of limbs that effectively resist the glass rod and the forces (Figure 2A). However, as the circles in Figure 2A indicate, the grasshoppers attempted to re-establish contact with the rods soon, leading to increases in force (Figure 1B). This regulation reflects an attempt by grasshoppers to control their attachment. However, the reattachment of limbs did not always restore overall adhesion to the initial level. Besides, due to repeated attachment and detachment, determining the exact link between the real-time force and the rod motion is challenging. Therefore, we selected the maximum force in each trail to represent the grasshoppers' best performance (Figure 3). Here, we would like to highlight the dynamic attachment of the whole insects. As seen in Figure 3, the forces of some insects with intact tarsi could be 800 times greater than the insects' weight in the fastest-pulling experiments and more than 50 times larger than the insects' weight in our slowest tests. The insects could even hold their body on the smooth convex with a single tarsus. More surprisingly, the forces for insects with a single tarsus and those with intact tarsi were proportional to the  $1/3$  power of pulling speeds by 0.11 times and 0.29 times, respectively.

As shown in Figures 1A and 1C, the grasshoppers use smooth pads that release secretion to generate wet adhesion.<sup>44</sup> For the ants that develop adhesion using similar methods, Federle et al. studied the normal and tangential adhesion of *Oecophylla smaragdina* under sliding conditions and found that the friction of smooth pads increased linearly with sliding speed.<sup>36</sup> Such differences might be caused by the differences in substrate conditions and the test speeds. The ants were tested on a flat smooth substrate at relatively low loading rates ( $0.3 \text{ mm} \cdot \text{s}^{-1}$  -  $1.3 \text{ mm} \cdot \text{s}^{-1}$ ), whereas here, we used a convex substrate and much higher speeds. As mentioned previously, the convex substrates allow the insects to grasp instead of merely adhere. On the other hand, for the geckos using hairs to generate dry adhesion,<sup>45</sup> Gravish et al. found that setae's attachment force on a flat substrate grew logarithmically with the load velocity ( $500 \text{ nm s}^{-1}$  -  $158 \text{ mm s}^{-1}$ ).<sup>37</sup> Aside from the differences in substrate circumstances (flat vs. convex), the fundamental adhesion mechanisms (dry adhesion vs. wet adhesion) and structural variances in adhesive systems may all have effects on the nonlinear correlations between maximum forces and pulling speeds. The grasshoppers can secrete secretions that could act as lubricants in our studies. According to some boundary friction research, the frictional force may rise with sliding speeds following power laws due to the presence of organic solutions. As illustrated in Figure 1D, the adhesive pads had rods and branch-like microarchitectures in addition to tissue fluid, resulting in viscoelastic properties of the pads<sup>46</sup> and acting like rubber in which power laws between shear force and sliding speeds were also reported.<sup>47</sup> To clarify the effects of fundamental adhesion mechanisms on dynamic attachment, experiments with insects using hairs that function through different mechanisms<sup>44</sup> (e.g., hairs for dry adhesion vs. hairs for wet adhesion) will be informative. To further clarify the effects of the viscoelasticity of pads on adhesion, experiments with artificial pads<sup>48</sup> will be helpful. In addition to the dynamical properties of the adhesive pads, the action of limbs may also contribute to the dynamical adhesion found in whole animals.

Some previous static and quasi-static tests with insects indicated that the force of the whole animal is larger than the direct sum of forces measured with single limbs,<sup>19,31,32</sup> revealing the synergy among limbs. In comparison, the forces measured with insects possessing full limbs were around three times greater than those for insects with a single front tarsus. Such kind of discrepancy was supposed to be caused by the dynamics and the test method. As previously stated, as we pushed the rod away parallel to the insects, they regularly shifted their limbs. As a result, it was difficult to determine the exact condition with each leg in contact, hence the force reported here may be slightly underestimated compared to the maximum of the grasshoppers' attachment performance.

Anyway, such velocity-dependent adhesion in whole animals indicated animals' potential to repel rapid and substantial perturbations like intense jerky wind pulses, fast substrate oscillations and heavy rainfalls.

### Limitations of the study

Several limits must be asserted. In the current investigation, we chose a smooth round rod to simulate plant stems, whereas the natural substrates are sometimes of roughness and unevenness, in which case the claws may also function. As a result, the maximum force may be

understated. The influence of rod diameter was also overlooked. Furthermore, instead of being assessed in their natural states, the insects were fastened to a thin rod and tested. This may result in some discrepancies in the results.

## STAR★METHODS

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

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.108264>.

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## AUTHOR CONTRIBUTIONS

S.Y.: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft and writing – review and editing; D.Z.: Formal analysis, methodology, resources, and writing—review and editing; J.A.: Investigation, methodology, resources, validation and writing—review and editing; W.H.: Data curation, validation, visualization and writing—review and editing; G.S.: Conceptualization, funding acquisition, project administration, software, supervision and writing – review and editing.

## DECLARATION OF INTERESTS

The authors declared no competing interests.

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## STAR★METHODS

## KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
Grasshopper ( <i>Oxya chinensis</i> )	Captured from Purple Mountain, Nanjing, China	N/A
Software and algorithms		
MATLAB (version 2022b)	The MathWorks Inc.	<a href="https://www.mathworks.com/">https://www.mathworks.com/</a> <a href="https://www.rz.uni-kiel.de/en/our-portfolio/software">https://www.rz.uni-kiel.de/en/our-portfolio/software</a>
Spss (version 25)	IBM SPSS software	<a href="https://www.ibm.com/spss">https://www.ibm.com/spss</a> <a href="https://www.rz.uni-kiel.de/en/our-portfolio/software">https://www.rz.uni-kiel.de/en/our-portfolio/software</a>
Other		
Force sensor	Song et al. <sup>3</sup>	N/A
Mobile platform	Guangdong Kainike Automation Equipment Co., Ltd	<a href="http://www.gdknk.com/">http://www.gdknk.com/</a>
DAQ (NI 9237)	National Instruments Corp.	<a href="https://www.ni.com/">https://www.ni.com/</a>
Cameras (BFS-U3-16S2M-CS)	FLIR Systems Inc.	<a href="https://www.flir.com/">https://www.flir.com/</a>

## RESOURCE AVAILABILITY

## Lead contact

Further information and requests for resources and reagents should be directed and will be fulfilled by the lead contact, Stanislav N Gorb ([sgorb@zoologie.uni-kiel.de](mailto:sgorb@zoologie.uni-kiel.de)).

## Materials availability

This study did not generate any new unique reagents.

## Data and code availability

- All necessary data was provided in the text. Other data can be at Mendeley Data: <https://doi.org/10.17632/fyh8b96g2b.1>.
- This paper does not report original code.
- Any additional information required is available from the [lead contact](#) upon request.

## EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

In this study, 26 adult grasshoppers (*Oxya chinensis*, body mass 0.3–1.0g, snout-event length LSV: 2–4 cm, 10 males and 16 females) captured at Purple Mountain (Nanjing, China) were tested. Eighteen grasshoppers with intact tarsi and 12 grasshoppers with a single front tarsus were tested. Four individuals were tested in both cases. The insects with a single tarsus were allowed to rest for at least 48 h after the surgery and were fed with fresh grass.

The experiments done at NUAA followed the ASAB guidelines for the treatment of animals in behavioral research, were approved by the Jiangsu Association for Laboratory Animal Science and Jiangsu Forestry Department, and were performed under the Guide of Laboratory Animal Management Ordinance of China.

## METHOD DETAILS

Experiments were carried out in an isolated room at 25°C and ~50% humidity. Grasshoppers were glued with their dorsal thorax surface to a thin stem, which was subsequently linked to a multi-axis force transducer.<sup>3</sup> A glass rod (diameter 6 mm) was used to mimic convex substrates typical for the habitat of this animal. The substrate was attached to a two-dimensional mobile platform to control its displacement and velocity (Figure 1). The glass rod was first brought toward the animal until its thorax came into contact with it. The stem connecting the insects and the force sensor has a high respect ratio (300), resulting in a low radial stiffness. After touching the glass rod, the insects could freely move their limbs and modify their positions by exerting a tiny force to the glass rod. After several seconds given for the insects to establish an initial contact, we moved the rod away from the animal at different speeds (1 mm/s, 10 mm/s, 50 mm/s, 100 mm/s, 200 mm/s, 300 mm/s or 400 mm/s), then collected the force signals through an NI DAQ model (NI 9237, USA) at a rate of 1662–5000 Hz and monitored the motion by a high-speed camera (BFS-U3-16S2M-CS, FLIR Systems Inc., USA) at 500fps. Eighteen grasshoppers with intact tarsi and 12 grasshoppers with a



single front tarsus were tested. Notably, four individuals were tested in both cases. Removing the tarsi did not affect the action of limbs significantly, except for the ability to generate adhesion. Thus, the grasshoppers with a single front tarsi behave similarly to the insects with intact tarsi during the initial contact stage (as shown in [Video S1](#)). The insects were allowed to rest for at least 15 min before varying the pulling speed for a new test. The rod was cleaned using 75% alcohol before each test to minimise the effects of secretion stains from the insect's pads.

### QUANTIFICATION AND STATISTICAL ANALYSIS

The behaviors of the insects were determined from the high-speed video images using image processing (MATLAB 2022b, The MathWorks Inc., USA). Because the forces vary largely in the experiments, we calculated the resultant forces and then selected the maximum force to characterize the performance of insects. Statistical analysis was performed with SPSS 25.0 (IBM, USA) to determine the effects of the pulling speeds. Specifically, the mixed model with individuals as random effects and regression models were used.