

RESEARCH ARTICLE

The whole is more than the sum of all its parts: collective effect of spider attachment organs

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ABSTRACT

Dynamic attachment is the key to moving safely and fast in a three-dimensional environment. Among lizards, hexapods and arachnids, several lineages have evolved hairy foot pads that can generate strong friction and adhesion on both smooth and rough surfaces. A strongly expressed directionality of attachment structures results in an anisotropy of frictional properties, which might be crucial for attachment control. In a natural situation, more than one leg is usually in contact with the substrate. In order to understand the collective effect of hairy foot pads in the hunting spider *Cupiennius salei* (Arachnida, Ctenidae), we performed vertical pulling experiments combined with stepwise disabling of the pads. We found the attachment force of the spider to be not simply the sum of single leg forces because with leg pair deactivation a much greater decrease in attachment forces was found than was predicted by just the loss of available adhesive pad area. This indicates that overall adhesion ability of the spider is strongly dependent on the antagonistic work of opposing legs, and the apparent contact area plays only a minor role. It is concluded that the coordinated action of the legs is crucial for adhesion control and for fast and easy detachment. The cumulative effect of anisotropic fibrillar adhesive structures could be potentially interesting for biomimetic applications, such as novel gripping devices.

KEY WORDS: Locomotion, Adhesion, Friction, Claw tuft, Scopula, Cuticle, Arthropoda, Arachnida, *Cupiennius salei*

INTRODUCTION

Among lizards, frogs and arthropods, several lineages have evolved specialized adhesive foot pads leading to impressive climbing abilities, even on very smooth surfaces. During the last decade, numerous attempts have been made to demonstrate the functional principles of these abilities, sometimes aiming at applying this knowledge to suitable technical applications (for reviews, see Gorb, 2001; Federle, 2006; Gorb et al., 2007; del Campo and Arzt, 2007; Autumn and Gravish, 2008).

The majority of biological reversible attachment organs include arrays of aligned separated fibres permitting a high adaptability to the substrate surface profile. This, in turn, results in a higher real contact area between the pad and substrate and, thus, in the effective contribution of intermolecular forces. In spiders, adhesive pads (scopulae) are present on the pretarsus, tarsus and metatarsus. In locomotion, primarily pretarsal pads (claw tufts) are involved. These

pads consist of dense arrays of hierarchical and directionally branched setae terminating in thin plate-like tips (spatulae). The pads exhibit highly anisotropic frictional properties (Niederegger and Gorb, 2006; Wolff and Gorb, 2013). Slight proximal shear movements cause an alignment of setae and their spatulae along the substrate surface, and this, in turn, generates strong friction and adhesion. Because of the specific anisotropic distribution of the spatulae on only one side of the seta, distal shearing induces both peel-off and separation of spatulae from the surface. This is the key feature for gaining both strong attachment and fast and effortless detachment. The combination of sloped spatula-terminated setae or thin-film-terminated fibres with applied shear force is a ubiquitous mechanism of the biological reversible attachment principle, as it also has been found in insects with both hairy and smooth adhesive pads (Beutel and Gorb, 2001; Gorb and Beutel, 2001; Federle, 2006; Bullock et al., 2008) and in geckoes (Autumn et al., 2000; Autumn et al., 2006).

However, shear forces can only be applied by an animal if an antagonistic shear force is generated elsewhere at the same time (Gorb, 2011). In stick insects, high muscle activity is observed when the position of the animal is altered from the horizontal to being upside down (Busshardt et al., 2011). This indicates that muscular forces have to be continuously applied, at least until the position is static. From experiments on leaf beetles standing on a ceiling, it is known that the loss of contact by single legs leads to a reorientation of the remaining legs, presumably for the purpose of optimizing the application of shear force (Gorb, 2011). With a single leg in contact, the beetle is not able to attach to a smooth glass ceiling, although adhesion of the foot pad might be sufficient to hold the beetle (Gorb, 2011). However, two opposing legs in contact are sufficient for ceiling adhesion. Thus, the radial arrangement of legs in arthropods (Gorb, 2011; Wolff and Gorb, 2013) and toes in lizards (Autumn et al., 2006) was hypothesized to fundamentally influence the adhesive forces of attachment pads. However, the joint action of opposing legs has never before been experimentally proven.

In this study, for the first time, we experimentally investigated the cumulative effect of opposing legs on resulting adhesion by successively disabling the adhesive pads of leg pairs in the banana spider *Cupiennius salei* Keyserling 1877 (Arachnida, Ctenidae). The morphology of attachment devices in this species was previously studied using scanning electron microscopy and reflection contrast microscopy (Gorb, 2001; Wolff and Gorb, 2012; Wolff and Gorb, 2013). We tested against the null hypothesis that the adhesion of the clinging spider is proportional to its contact area with the substrate.

RESULTS

During the test, spiders attempted to actively enhance their attachment to glass. At the beginning of the test, they moved around and tried to find an uneven surface to cling to. After further lifting, they tended to spread their legs away from the body and grip the surface. When one leg slid towards the centre of the body, the spider

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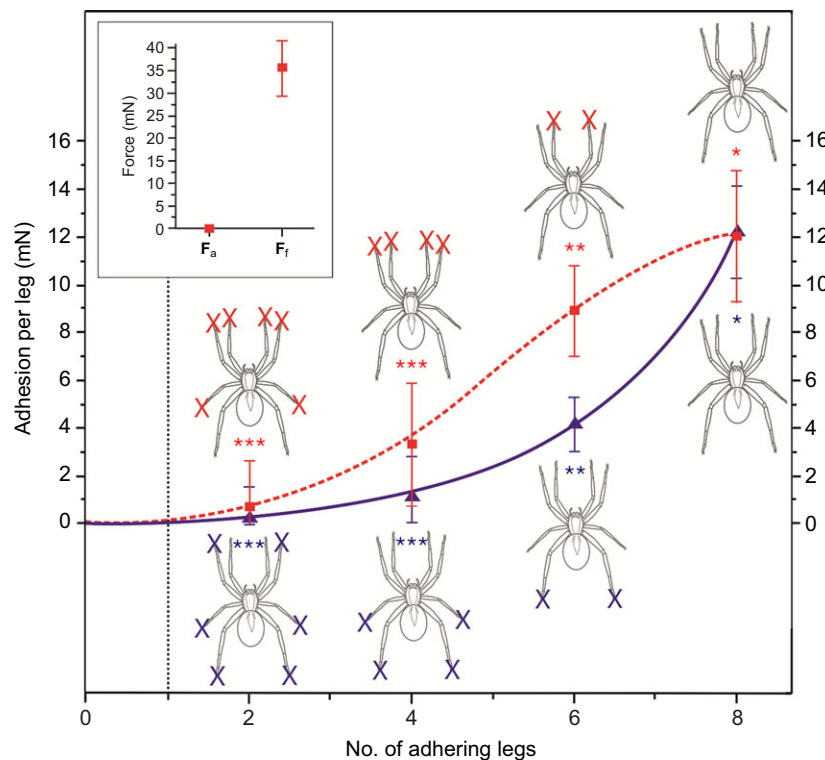


Fig. 1. Adhesion force per leg obtained in the vertical pull-off tests on glass. Treatment sequences are displayed from right to left. Squares depict mean values obtained in measurements with stepwise disabling of pads from anterior to posterior leg pairs. Triangles show those obtained with stepwise disabling of pads from posterior to anterior leg pairs. Bars show standard deviations of means. X indicates disabled legs. Different numbers of asterisks indicate significant differences between different treatments within each of the two ablation experiments (pair-wise Wilcoxon test with FDR alpha adjusting and $P < 0.01$; performed with R software package). The inset shows both adhesion (F_a , without shear preload) and friction forces (F_f , proximal sliding) of the claw tuft of a freshly ablated tarsus at preloads comparable to the weight of the spider [based on data published elsewhere (Wolff and Gorb, 2013)].

immediately moved it back distally and renewed the grip. As soon as several legs began to slide, the measured force decreased considerably.

For all eight legs in contact, an average force of 97 mN was measured, which is three times higher than the average spider body weight. With the decreased number of intact legs, attachment force decreased more rapidly than would be predicted due only to the loss of available adhesive pad area (Fig. 1). If the adhesive surface of the first pair of legs was disabled, the mean force was reduced to 74% of its original value (77% predicted). Interestingly, when the fourth pair of legs did not attach to the substrate, the mean force was reduced to 27% (71% predicted). For two pairs of legs with disabled adhesive surfaces, the attachment forces were reduced to 27% of their original value for disabled front legs (53% predicted) and 9% for disabled hindlegs (47% predicted). With only the first leg pair remaining intact, initial forces dropped to 2% (23% predicted) and for the last pair of legs remaining intact they dropped to 6% (28% predicted) of the attachment force obtained with untreated animals.

DISCUSSION

Our results indicate that shear forces generated by contralateral legs are crucial for spider attachment to smooth surfaces. When individual legs were disabled from adhering, the measured pull-off force decreased more strongly than might be expected simply from the reduction of the contact area. Shear forces should primarily act between the opposing legs (i.e. between first left anterior and last right posterior leg). Thus, disabling the leg pairs led to the loss of the primary antagonists in the opposite leg pairs. This effect provides evidence that adhesion is influenced not only by the area covered by adhesive hairs but also by the manner of applying load to them.

The difference between the two series of pad deactivation (Fig. 1) indicates that the fourth pair of legs adheres most strongly and that adhesion gradually decreases from the third, to second, to first pair of legs. This is presumably because of the fact that the contact area

increases from anterior to posterior legs (Wolff and Gorb, 2012). First and second leg pairs are also presumably more specialized for prey capture, while posterior legs are more important for running and attachment to the substrate while resting.

A second benefit of the antagonistic activity of hairy adhesive pads on opposing legs might be the lowering of the pad's peeling angle, which, according to the Kendall peeling theory, results in higher adhesion (Kendall, 1975; Varenberg et al., 2010). This conclusion is also well supported by the recent theory of multiple peeling (Pugno, 2011). This theory predicts higher adhesive forces between a smooth surface and two interconnected tapes, simultaneously peeled off in two opposing directions, than would be found for the peeling off of two non-interconnected tapes. The interconnected tapes are capable of keeping the peeling angle small (Gorb, 2011). Our behavioural observations on spiders show that they actively use this principle: when the vertical pulling distance in experiments increased, spiders spread their legs in order to decrease the peeling angle and increase the adhesive force.

Conclusions

Our results indicate that spider attachment forces, generated by adhesive pads, are dependent not only on the apparent contact area of pads but also on the muscle-generated shear force. That is why the force of two opposite legs working together is more than the sum of the forces of two separate individual legs. It is shear force that activates the generation of high real contact area by properly aligning the spatulae. Through the antagonistic activity of opposing legs, friction and adhesion generation as well as fast and effortless detachment can be efficiently achieved. This principle could be worthy of biomimetic applications, such as the design of novel gripping devices.

MATERIALS AND METHODS

Six adult *C. salei* females were obtained from a laboratory stock at the University of Vienna (Austria). Adhesion measurements on living spiders

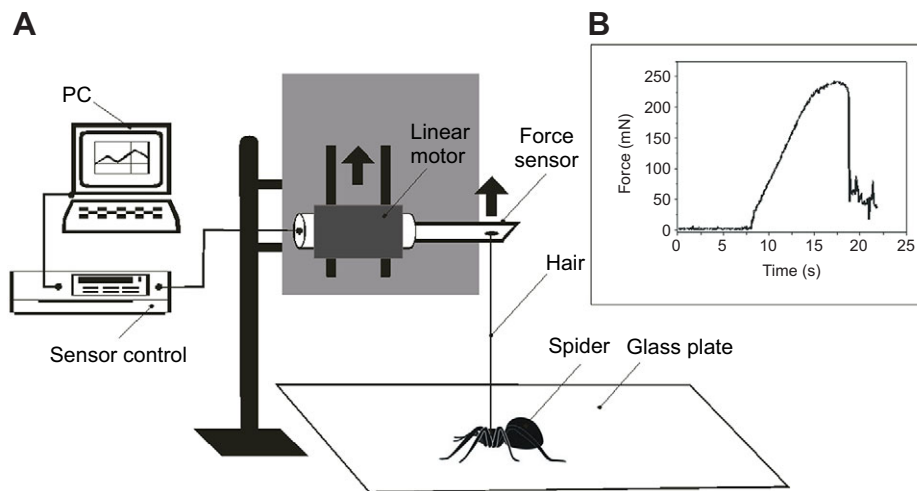


Fig. 2. Experimental set-up for vertical pull-off tests of living spiders (A) and a typical force–time curve obtained (B).

were carried out on plane glass (SiO_2 with 12:16 weight:% $\text{Na}_2\text{CO}_3/\text{K}_2\text{CO}_3$, 10:15 weight:% CaCO_3 and 2:5 weight:% fining and bleaching agents, 30×40 cm) using a load cell force transducer (100 g capacity; Biopac Systems Ltd, Santa Barbara, CA, USA). The spiders were anaesthetized with CO_2 and then attached to the force sensor by means of a human hair glued to the dorsal surface of the prosoma with a drop of a molten mixture of rosin gum and beeswax (1:1). The experiment was carried out at least 2 h after this preparation procedure under laboratory room conditions (temperature 25°C , relative humidity 20%). The force sensor was attached to the motorized pulling unit and positioned above the spider (Fig. 2). By means of the motor, the sensor was moved upwards at a speed of 1.3 mm s^{-1} until the spider was lifted off the glass. Glass surfaces were cleaned with dry Kimwipes (34133 EX-L delicate task wipes, Kimberly-Clark Professional, Roswell, GA, USA), rinsed with deionized water and 70% ethanol, and finally dried in a nitrogen jet.

The performance of intact spiders was compared before and after disabling their claw tufts on different numbers of legs. The adhesive setae were disabled by gluing them together using warm beeswax, leading to the complete loss of adhesive ability. Two different kinds of experiments were performed, with three spiders each. In the first one, the adhesive pads were successively deactivated, pair-wise, from anterior to posterior leg pairs; in the second, pads were deactivated from posterior to anterior leg pairs. After each treatment the pull-off force was measured five times in each individual. Dragline attachment onto the glass was prevented by placing a loose piece of paper below the spinnerets. Forces, measured in different experimental situations, were normalized to the number of legs in adhesive contact. Hypothetical force reduction by reduction of contact area was calculated on the mean surface area of the adhesive pads, as previously published (Wolff and Gorb, 2012). This slightly increases from anterior to posterior legs: pads in leg pair L1 amount to 23.1% of the whole area of all foot pads, 23.7% in L2, 24.5% in L3 and 28.7% in L4. As the density of setae and contact elements (spatulae) does not differ significantly between the foot pads of all legs, we assume the contact area is comparable.

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Competing interests

The authors declare no competing financial interests.

Author contributions

S.N.G., E.W. and E.A. conceived and designed the experiments. E.W. performed the experiments. E.W. and J.O.W. analyzed the data. J.O.W., E.W. and S.N.G. wrote the paper.

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