

Dynamic biological adhesion: mechanisms for controlling attachment during locomotion

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The rapid control of surface attachment is a key feature of natural adhesive systems used for locomotion, and a property highly desirable for man-made adhesives. Here, we describe the challenges of adhesion control and the timescales involved across diverse biological attachment systems and different adhesive mechanisms. The most widespread control principle for dynamic surface attachment in climbing animals is that adhesion is ‘shear-sensitive’ (directional): pulling adhesive pads towards the body results in strong attachment, whereas pushing them away from it leads to easy detachment, providing a rapid mechanical ‘switch’. Shear-sensitivity is based on changes of contact area and adhesive strength, which in turn arise from non-adhesive default positions, the mechanics of peeling, pad sliding, and the targeted storage and controlled release of elastic strain energy. The control of adhesion via shear forces is deeply integrated with the climbing animals’ anatomy and locomotion, and involves both active neuromuscular control, and rapid passive responses of sophisticated mechanical systems. The resulting dynamic adhesive systems are robust, reliable, versatile and nevertheless remarkably simple.

1 In contrast to conventional man-made glues, the adhe-
2 sive systems of many animals can be switched rapidly be-
3 tween strong attachment and easy detachment, enabling lo-
4 comotion in environments that require firm surface attach-
5 ment, such as the canopy of forests, or the intertidal zone.
6 Throughout the lifetime of a climbing animal, such cycles
7 between strong attachment and rapid detachment have to
8 occur millions of times with no loss of adhesive force [1].
9 The ability to control adhesion is therefore a fundamen-
10 tal property of natural adhesive systems. Indeed, four out
11 of the seven benchmark properties for the performance of
12 gecko adhesives defined by Autumn [2], relate to the con-
13 trollability of adhesion (namely, anisotropic attachment,
14 low detachment force, non-sticky default state, high pull-
15 off to preload ratio; the remaining three are self-cleaning,
16 anti-self-matting, and material independence). As control-
17 lability is also a highly desirable feature for synthetic ad-
18 hesives, animal adhesive structures have become models
19 for worldwide efforts to fabricate controllable ‘biomimetic’
20 adhesives, which may have a wide range of applications,
21 including but not limited to industrial pick up-and-release
22 manipulation at the macro- and microscale, and climbing
23 robots [for recent reviews, see 3–5].

24 An adhesive system is ‘controllable’ if large variations
25 in adhesive force can be achieved via the variation of sys-
26 tem parameters, and ‘dynamic’ if such changes can be re-
27 alised within short periods of time. In biological adhesive
28 systems, these changes are not merely binary, but many
29 animals can adjust their attachment systems in a grad-
30 ual manner to respond to external forces resulting from
31 climbing on substrates with various slopes, and from waves,
32 wind, or additional loads [6–12]. In this article, we provide
33 a brief overview of the mechanisms which allow adhesion
34 control in biological adhesive pads.

Control of adhesion: from permanent glues to dynamic adhesives

35
36
37 Attachment and detachment of adhesive contacts is a fun-
38 damental requirement for locomotion. Protraction of one
39 body part, such as a leg or part of a foot, requires other
40 body parts to remain in contact, in order to resist gravity
41 or other external forces, and to produce the forward thrust
42 which powers locomotion. The feet of moving animals go
43 through a coordinated cycle of ‘stance’ and ‘swing’, and
44 at the start and end of each stance phase, the adhesive
45 contacts will have to be formed and broken.¹

46 Although the time required to form and release adhesive
47 contacts may often represent only a fraction of the stance
48 and swing phase, it is likely that at least in some animals,
49 the speed of attachment and detachment imposes a limit
50 to the stepping frequency and hence the speed of move-
51 ment. Animal adhesive systems range from permanent to
52 highly dynamic, reflecting the animals’ lifestyle and speed
53 of locomotion. Table S1 in the supplementary information
54 (SI) summarises the limited data available on the timing
55 of stance-swing cycles in animals that use adhesion during
56 locomotion. Temporary adhesion is used by animals differ-
57 ing in “stride frequency“ (defined here as the inverse of the
58 time of one complete pad attachment-detachment cycle) by
59 more than two orders of magnitude (see also Fig. 1). This
60 large variation in stride frequencies may be based on sev-
61 eral factors, including the medium in which the adhesive
62 organs operate (air or water), the adhesive mechanism, and
63 the dimension of individual adhesive contacts.

64 Permanent attachment is predominantly achieved by glues,
65 which allow animals to remain firmly attached in the same
66 place for extended periods of time [e. g. sessile marine an-

¹During the locomotion of some gastropods, muscular waves moving along the underside of the foot switch different parts of the foot between stationary adhesive contact (‘stance’) and forward sliding over mucus (‘swing’), so that the protracted part is not completely detached but remains in surface contact [13].

Figure 1: Animal adhesive systems range from permanent to temporary and highly dynamic. While permanent adhesive systems are glue-based, slow temporary adhesive systems use releasable glues or suction, and the most dynamic adhesive systems employ interfacial forces. Image sources are provided in the SI.

imals including sponges, cnidarians, cirripede crustaceans, bivalves, polychaetes, bryozoans and tunicates, but also terrestrial phoretic mites and insect pupae that attach themselves to substrates, see ref. 14–16]. Glues may be defined as secretions, often consisting of multiple components, which are applied in liquid form, but then solidify in contact with the substrate. Well-studied systems include the byssus thread of mussels, and barnacle cement [17]. However, glues do not have to be permanent, and indeed are also used for locomotion in temporary underwater adhesive systems. For example, flatworms and echinoderms achieve repeated attachment and detachment by the subsequent release of adhesive and de-adhesive secretions, each produced by distinct glands or cells [14, 18–20]. Glue-based adhesion and de-adhesion require (i) the secretion of the adhesive, (ii) contact formation, (iii) solidification, (iv) secretion of the release agent, (v) its diffusion into the adhesive, and (vi) reaction with it. Contact formation in particular is a key challenge for adhesive systems employed in water, as it requires water to be removed beneath the adhesive organ. Water is initially squeezed out via hydrodynamic forces, but complete removal by dewetting requires the thin remaining water films to be thermodynamically unstable, which is unlikely for many polar natural substrates [21]. Some mussels and cyprid larvae can displace water via the secretion of lipids into the contact zone instead [22, 23]. As an alternative, viscous secretions such as the glycoprotein footprints of temporarily adhering cyprid larvae may strengthen underwater adhesion by effectively replacing the water film [24].

The numerous steps involved in attachment-release cycles of glue-based adhesives are time-consuming, and probably only feasible if diffusion distances are short; even for microscopic contacts they may therefore impose a speed constraint on attachment-detachment cycles. Water displacement, secretion of lipids or glycoproteins, and viscous adhesion will result in further speed constraints, together explaining why glue-based adhesive systems of aquatic animals are generally less dynamic than those of terrestrial animals that do not rely on glues (TableS1). One strategy to reduce the time needed for underwater attachment and detachment may be the miniaturisation of individual adhesive contacts (as seen in flatworms and cyprid larvae; TableS1), which helps to accelerate both fluid drainage and diffusion-based processes [24, 25].

A potentially faster type of controllable attachment is suction, which lacks the speed and size constraints of diffusion. A clear definition of suction for biological attachment systems is still missing (and beyond the scope of this review); here we use the term to refer to attachment produced by reducing the pressure beneath the attachment organ, excluding pure capillary or viscous adhesion. Suction in this sense is used by diverse primarily aquatic animals including limpets, leeches, clingfish, remora fish, water-fall

climbing gobies, octopus, squid, net-winged midge larvae, and diving beetles [26–34]. These animals produce suction either by muscular action (active suction), or by the recoil of elastic elements (passive suction). Both strategies have in common that they tend to expand the volume underneath the suction organ. Suction organs share with other underwater adhesive systems the need to drain water from the outer rim of the contact zone, in order to achieve a tight seal. However, they are likely more tolerant to small amounts of residual water, as even leaky suction organs can allow for sufficient attachment over the timescales required for locomotion, and leakage rates can be reduced by the secretion of mucus [34]. In fact, the almost exclusive occurrence of suction among aquatic animals probably arises because the presence of an incompressible fluid such as water or mucus beneath the suction cup has the advantage that large variations in pressure can be produced by miniscule displacements. Whereas suction in air is limited by the atmospheric pressure, water can also resist tensile forces, so that even negative pressures can be achieved [27].

Little is known about the mechanisms of detachment in natural suction organs. Generally, voluntary detachment takes place once the reduced pressure inside the sucker cavity is neutralised; the fastest way for this to occur may be by relaxation of the muscle(s) that produce(s) the suction for ‘active’ suction systems, but movements by other muscles might be needed to release passive suction. In net-winged midge larvae (*Blephariceridae*), attachment is achieved by raising a ‘piston’ in the centre of the suction disc. Detachment, in turn, can occur by rapidly ‘flooding’ the sucker through the opening of a V-shaped notch located at the anterior rim of the disc, with the piston still in its upper position [41].

By far the most dynamic control of adhesion occurs in adhesive systems which rely on interfacial forces, including both ‘dry’ van der Waals interactions and ‘wet’ capillary forces. Most terrestrial climbing animals belong to this category [a contribution of van der Waals forces has also been discussed for the temporary underwater adhesion of barnacle cyprid larvae, see ref. 24]. There has been substantial convergence both in the morphology of the adhesive systems of terrestrial climbing animals, and in the control mechanisms they employ [12, 42–53]. Detachment in these adhesive systems does neither require chemical release agents (as for glues), nor muscular action to neutralize pressure gradients (as for suction). Instead, rapid control of adhesion is achieved through mechanical systems. The universal strategy for rapidly reversible attachment is the control of adhesion via shear forces, which we review in detail in the following sections.²

Control of adhesive forces in dynamic biological adhesive systems

The maximum force an adhesive can carry is the product of its adhesive strength, and the area of contact. Animals could thus potentially control how well they adhere in two ways: first, they could alter the fraction of the available

²Many insects possess several attachment pads per leg. Unless otherwise stated, we are referring to distal adhesive pads in this review, and only briefly discuss the role of proximal friction pads.

Figure 2: In all non-aquatic animals climbing with adhesive pads tested to date, adhesion, F_A , is approximately half of the shear force, F_S , acting during detachment (see panel (d)); the dashed line visualises this approximate ‘rule of thumb’, which appears to hold for (a) geckos [*Gekko gecko*, seta, array and toe-level data; 35, 36], (b) tree frogs [*Litoria caerulea*, whole body data; 37], (c) dock beetles (*Gastrophysa viridulae*, single pad data, D Labonte & JMR Bullock, unpublished data), (e) stick insects [*Carausius morosus*, single pad data; 38], (f) cockroaches [*Nauphoeta cinerea*, single pad data; 39], and (g) ants [*Oecophylla smaragdina*, single pad data; 40]. Shear force therefore appears to be a universal control mechanism independent of pad morphology (smooth or hairy), adhesive mechanism (wet or dry), or contact size. Detailed regression results for (a-c) & (e-g) can be found in the SI.

adhesive area which they bring in contact with a surface; second, they could vary the strength of the contact, i. e. alter the force required to detach a unit area of their sticky pads.

In dynamic biological adhesive systems, the universal control parameter for both variables is shear force, i. e. a force acting in parallel to the adhesive interface. The typical effects of shear force on contact area, adhesive strength and hence net adhesive force can be summarised as follows: ‘Pushing’ pads away from the body results in an unstable contact, reflected in a dramatic decrease in contact area and thus effortless detachment, whereas ‘pulling’ pads towards the body results in a stable or increasing contact area, and strong attachment [54–60]. This ‘shear-sensitivity’ of adhesion is widespread across terrestrial climbing animals, including flies [54, 61, 62], spiders [12, 63], bees [55], bush-crickets [64], geckos [2, 35, 36, 65], stick insects [38, 57, 60], bats [66], cockroaches [52, 58], ants [11, 55, 67], leafhoppers [68], tree frogs [37, 38, 69], and beetles [49, 57]. Climbing animals can therefore control attachment simply by shearing their adhesive pads along the surface; pulling results in strong attachment, whereas pushing enables easy detachment (an important exception to this rule are ‘friction pads’; see below).

Control of adhesive strength

In all adhesive pads of climbing animals tested to date, the adhesive force, i. e. the perpendicular force required to detach the pads, increases when pads are pulled towards the body [35–38, 52, 60]. As a rule of thumb, the adhesive force is approximately half the shear force applied during detachment [Fig. 2. See 36, 38]. This empirical rule holds for large or small, ‘wet’, ‘dry’, ‘smooth’ or ‘hairy’ adhesive systems tested with various methods, suggesting the presence of a universal control mechanism that is independent of contact size, adhesive mechanism, pad morphology, and experimental method (see Fig. 2). Importantly, the increase of adhesion with shear force arises from an increase in adhesive strength, and not solely from changes in contact area [37, 52, 60, 70]. While this characteristic shear-sensitivity of biological adhesive pads is empirically well-established, the exact mechanism(s) through which shear forces increase contact strength are still unclear. Why is this relationship approximately linear, and why is the slope of this linear relationship 0.5? To the best of our knowledge, there is currently no theoretical model which predicts these peculiar features from first principles [36, 38].

The most successful theoretical attempts at explaining the shear-sensitivity of biological adhesive pads have been based on tape peeling theory, which likens the pads to thin strips of adhesive tape [37, 38, 71–73, See Fig. 3 A-C]. Based on peeling theory, the effect of shear forces may be under-

stood qualitatively as follows [for a quantitative discussion, see 38]: breaking adhesive contacts increases the system’s total energy, as it creates new surfaces. This energy per unit area, G , is ‘paid for’ by the work done when the point of force application moves by a distance δ whilst detaching a unit length L_0 of tape (see Fig. 3 D). In this framework, climbing animals can hence increase the adhesive force F_A by (i) increasing G ; or (ii) reducing δ . Actively applying a shear force makes good use of both options in at least three different ways:

First, as the shear component of the applied force is increased, the pads peel at lower angles ϕ . For a perpendicular pull-off, $\delta = L_0$, but for pull-offs at lower angles, the point of force application only moves by a fraction of the peeled tape length, $L_0(1 - \cos(\phi))$, so that $\delta \leq L_0$ [74, see Fig. 3 D]. Thus, a larger force F must be supplied to provide the same amount of work. To resist detachment, animals can hence reduce $\delta/L_0 = 1 - \cos(\phi)$ by decreasing ϕ , i. e. by actively pulling their pads inwards. This effect is based purely on geometry.

Unfortunately, there is a limit to this strategy: detached parts of the pads stretch, and this stretch increases δ [75, see Fig. 3 E]. As the amount of work done for stretching the pad is larger than the associated increase in elastic strain energy [75], stretching reduces the force required to peel off the pads. For soft and thin biological adhesive pads, this effect would severely limit the positive effect of applying a shear force.

It is here where the second effect comes in: large shear forces eventually result in pad sliding, which also strains *attached* parts of the pads prior to detachment [38, Fig. 3 F]. Upon detachment, these ‘pre-stretched’ pads then stretch less than unstretched pads, reducing the negative impact of stretching outlined above. This second effect is thus based on ‘energy dissipation’ [38, 65, 76]: The work done for pad stretching does not help to create new surfaces, but is instead balanced by the frictional work done when pads are stretched while still in contact with the surface [38, 76]. Here, shear-sensitive biological adhesives differ fundamentally from many commercial high-strength adhesives, as they dissipate energy at the interface (via friction) instead of the bulk (via cavitation, viscoelastic fingering etc) [38, 65, 77].

The effect of (i) a decrease in peel angle, and (ii) stretching attached parts of the tape have both been included in quantitative models [38, 73–76, 78], which show good agreement with experimental data on biological adhesive systems [37, 38]. However, data for stick insects showed that this agreement was limited to peel angles larger than approximately 30° . For smaller peel angles, adhesive forces systematically exceeded theoretical predictions [38]. There hence must be a third effect. In contrast to the first two effects, which reduce δ , this effect must reflect an increase

Figure 3: (A) Due to the sprawled-leg posture of most climbing animals, externally applied attachment forces result in the application of both a normal and a shear force at the level of individual pads (illustrated in (B); climbing animals can also apply shear forces actively). These shear forces make it harder to detach the pads, and this ‘shear-sensitivity’ can be partially understood through peeling models (C), which liken adhesive pads to thin strips of adhesive tape, with width w , peeled at an angle ϕ . (D) As a unit length L_0 of the tape is peeled, the point of force application moves by a fraction of this distance. Because this fraction decreases with decreasing peeling angle (or increasing shear force component), more force needs to be supplied to do the required work, leading to an apparent ‘strengthening’ of the contact. (E) Biological adhesive pads are thin and soft, and therefore likely stretch upon detachment (strain ε). This stretching increases the work done upon detachment, so reducing the effect outlined in (D). (F) The negative effect of pad stretching can be circumvented if the tape is stretched *prior* to detachment (‘pre-strain’ ε_0). Storing strain energy in attached parts of the tape can not only make involuntary detachment harder, but also aid rapid voluntary detachment. A more detailed discussion is provided in the text.

in G , which may be understood as follows: The positive effects of pad sliding are bound by the geometrical limit $\delta \leq L_0 - L_0 \cos \phi$, i. e. the distance moved for a unit length of tape which does *not stretch at all* upon detachment (a more formal proof is presented in the SI). While pad sliding can thus make even thin and soft pads behave as if they were effectively inextensible [38], the peeling model for such tapes only predicts a square-root dependency of adhesion on shear force [in the limit of large shear forces, see 38, 52]. As the observed relationship is linear, the only way to reconcile peeling theory with the experimental data is therefore a shear-induced increase in G .

In stick insects, the departure from peeling theory coincided with the onset of whole-pad sliding [70], so that it appears plausible that sliding results in an increase of G . Two hypothetical mechanisms could explain such an increase: first, sliding may result in triboelectric charging. However, the relationship between adhesion and friction remained unaltered on conducting surfaces [70], suggesting that triboelectric effects do not play an important role; second, sliding can rapidly deplete liquid films in the contact zone [79], and such changes in film thickness may cause an increase in G [38, 77]. Indeed, recent experiments suggested that the contact-mediating secretion found in all insects studied to date acts as a ‘release layer’, consistent with this hypothesis [77, 80]. However, fluid depletion should only occur in animals with wet adhesive systems, so that we would still be lacking an explanation for identical data on dry adhesive systems [36].

Clearly, more theoretical and experimental work is required to quantitatively explain the approximately linear relationship between adhesion and friction in biological adhesive systems. The sharp drop of adhesion for peel angles $> 30^\circ$ is biologically important, as it allows animals to use relatively small movements to switch from weak to strong adhesion. Clarifying the basis for this most fundamental adhesion control mechanism across climbing animals should therefore be a core area for future research.

Control of contact area

Changes in contact area occur by definition during attachment and detachment, but as any soft object increases its contact area when pressed against a substrate, and decreases it during pull-off, not all such changes correspond to an active control mechanism. In the following discussion, we will therefore focus on non-trivial contact area changes in two scenarios: in the context of *attachment*, we will describe active and passive adjustments of the contact area which occur rapidly as a direct result of increased

loading requirements. In the context of *voluntary detachment*, we will discuss strategies through which the contact can be broken by other means than the supply of a force normal to the surface.

Active and passive control of attachment

In technical adhesives, contact formation is typically achieved via the application of a force perpendicular to the interface. In sharp contrast, the contact area of dynamic biological adhesive systems can be controlled via shear forces. An increase of contact area in response to shear forces towards the body has been found across most dynamic adhesive systems of climbing animals studied to date, despite the striking diversity of adhesive pad morphologies. For example, the smooth footpads of ants and bees can unfold passively (without any muscular action) when the retracted pad in surface contact is dragged towards the body [55, 67]. The adhesive footpad of stick insects is not foldable, but possesses an internal fibrillar ultrastructure, which hydraulically translates longitudinal pulls into a lateral expansion of the adhesive contact zone [81]. The hairy adhesive pads of lizards, many arachnids and diverse insects, in turn, possess spatula-shaped tips with a non-adhesive ‘default’ (non-contact) position, i. e. they are not parallel to the substrate. Only when setae are sheared towards the body, do the tips bend and come into full contact [36, 49, 82, 83]. Importantly, these increases in contact area with shear forces are not an all-or-nothing reaction. Stronger shear forces generally lead to larger contact areas, until the contact zone has reached its maximum size [55, 68], allowing a gradual adjustment to external loads. Such gradual contact area adjustments can be made actively, i. e. via the contraction of muscles pulling feet inwards (or pushing them outwards), but they can also arise passively. Because of the sprawled posture of climbing arthropods and vertebrates, legs are pulled inward automatically by the animal’s body weight during inverted climbing (or pushed outward during horizontal locomotion); during vertical climbing, legs above the body centre of gravity (CoG) will be pulled automatically, whereas those below will be pushed. External forces resulting from wind, rain, or from carrying load, further add to the shear force arising from the animal’s own body weight.

Because shear forces arise passively in situations where strong attachment is required, shear-sensitivity ensures an ‘automatic’ engagement and activation of the adhesive organs. Indeed, it is no coincidence that adhesion control is both active and passive. Neuromuscular control of attachment and detachment is essential for climbing, and for

377 adjusting to different environmental conditions, substrate
378 geometries and textures [84, 85]. However, passive mecha-
379 nisms simplify the complexity of the active feedback con-
380 trol that needs to be mastered for successful climbing [86],
381 and a purely mechanical response triggered by shear forces
382 can result in extremely rapid increases in adhesive contact
383 area. For example, the pad contact area of the smooth
384 adhesive pads of weaver ants and stick insects can dou-
385 ble within less than a millisecond of a perturbation [37].
386 Even for small animals such as insects, any control via ac-
387 tive neuromuscular ‘reflexes’ would take at least an order
388 of magnitude longer. The virtually instantaneous ‘preflex’
389 is hence essential for preventing detachment during rapid
390 and unpredictable perturbations (such as raindrops or wind
391 gusts), and avoids the need to use large contact areas and
392 therefore high detachment forces during locomotion. In
393 practice, contact area is thus likely controlled by a combi-
394 nation of passive and active loads. Indeed, in cockroaches
395 walking upside-down, loading triggers the activation of the
396 tibial flexor muscle which mediates an inward pull of the
397 legs [87], suggesting a coupling between active and passive
398 control mechanisms.

399 While likely the dominant mechanism, shear forces are
400 not the only way in which the adhesive contact area can
401 be controlled. Some climbing animals are also capable of
402 directly influencing the adhesive contact zone by muscular
403 control. For example, contraction of the claw flexor muscle
404 in insects and spiders can not only bring adhesive pads
405 into surface contact, but also induce local deformations of
406 the cuticle which increase the size of the contact zone; its
407 relaxation in turn can drive the pad’s detachment [6, 55,
408 62, 67, 86, 88, 89, and see next section]. Recent findings
409 show that adhesive pads of tree frogs contain bundles of
410 smooth muscle fibres which may be involved in the direct
411 control of adhesion [90].

412 **Rapid detachment via release of elastic energy**

413 Voluntary detachment during climbing locomotion has to
414 occur rapidly, and should consume minimal amounts of en-
415 ergy. Both needs are at least partly met through an inbuilt
416 release mechanism which arises as a direct consequence of
417 pad *engagement*: Due to the shear-sensitivity of their pads,
418 climbing animals need to pull their legs inwards in order
419 to resist detachment. As outlined above, the resulting
420 shear forces cause deformations of the attachment struc-
421 tures which typically increase the adhesive contact area.
422 For example, shear forces straighten curved adhesive setae
423 or the tarsus as a whole [49, 65, 67, 86], bend adhesive
424 hair tips or internal rod-like structures [49, 64, 81], unfold
425 smooth pads or expand their cuticle along the transverse
426 axis [55, 81], and likely stretch pads and adhesive hair tips
427 along the longitudinal axis [38, 81, 91–93]. All these de-
428 formations bring with them the storage of elastic energy,
429 which, upon removal of the shear force, can help breaking
430 the contact, and even result in spontaneous detachment of
431 the pads in the absence of external forces [65, 73, 93].

432 An intuitive way to understand how storing elastic en-
433 ergy can result in spontaneous detachment is to think of a
434 pad as a thin strip of adhesive tape, which is stretched to a
435 ‘pre-strain’ ε_0 prior to or during surface attachment. If the
436 elastic energy stored in the stretched tape exceeds the de-

Figure 4: ‘Stability envelopes’ for tape peeling at varying tape
pre-strains and peel angles ϕ . If the strain exceeds a minimum
strain ε_{\min} (dashed blue line), stable attachment requires the
application of the minimum force to stabilise the contact (red
line). In this regime, spontaneous detachment occurs whenever
the applied force drops below this lower bound, providing a
rapid and efficient detachment mechanism.

crease in surface energy associated with contact formation,
the contact is unstable, because a detached but relaxed
tape corresponds to a more favourable energetic state. In
the SI, we show that spontaneous detachment of a tape re-
quires a minimum pre-strain $\varepsilon_{\min} = \frac{1}{\zeta} (1 + \sqrt{1 + 2\zeta})$ (here,
 $\zeta = Eh/G$ is a characteristic dimensionless number repre-
senting the ratio between elastic and adhesive work done
during detachment; h is the thickness of the tape, and
 E its Young’s modulus). If this strain is exceeded, the
tape can only adhere if *an external force is applied* [see
also 73]. The somewhat complex relationship between con-
tact stability and pre-strain can be visualised in ‘stability
envelopes’, encompassing combinations of pre-strain and
applied force for which stable attachment is possible (see
Fig. 4). For $\varepsilon_0 < \varepsilon_{\min}$, these plots only have an upper
bound, corresponding to the critical peel force. In this
regime, detaching the tape always requires the application
of a force. If $\varepsilon_0 > \varepsilon_{\min}$, however, the envelopes also have
a lower bound, corresponding to the force required to sta-
bilise the tape against spontaneous detachment [see SI and
ref. 73]. In this regime, voluntary detachment can simply
be triggered by *reducing* the applied force below this lower
bound, causing the tape to peel spontaneously. Remark-
ably, pre-stretching hence not only enhances the resistance
against forced detachment, but also provides a mechanism
for fast and effortless voluntary detachment [73]. Storage
of elastic energy during attachment to recover it for de-
tachment helps to balance the contradictory demands of a
strong yet easy-to-detach adhesive system, and may there-
fore be a key principle enabling controllable adhesion.

As compelling as these arguments may be, the extent to
which climbing animals use ‘pre-strain’ to ease detachment
remains largely unclear. Benefiting from the release mech-
anism described above requires $\varepsilon_0 > \varepsilon_{\min}$. For biological
adhesive pads, the required strain levels are probably un-
realistically large (for an estimated range of $1 < \zeta < 100$,
 $15\% < \varepsilon_{\min} < 273\%$). We provide a more detailed discus-
sion of the limits of this model in the SI). Thus, longitu-
dinally stretched pads are unlikely to be the sole provider of
the elastic energy which drives detachment, but other de-
formations in pads and legs may be involved (see above).
The compliance of the pads or such external structures
needs to be fine-tuned to the system’s demands, so as to
enable sufficient elastic energy storage without requiring
excessive stresses or strains [80]. More generally, adhesive
pads may be designed so that unloading does not cause
complete detachment but only facilitates it, as maintain-
ing some active control over detachment may be adaptive
to protect against unwanted detachment by perturbations.
An example of an actively controlled detachment that does
not appear to rely on the release of elastic energy is the de-
tachment of gecko toes by digital hyperextension [94].

489 **Contact mechanics affect organismal-level locomotion,**
490 **and vice versa**

491 Locomotion constrains how adhesive pads can be attached
492 and detached, but surface attachment also influences lo-
493 comotion. Comparisons of animals climbing on vertical,
494 horizontal and inverted surfaces, as well as on non-slippery
495 versus slippery substrates have revealed clear differences.
496 Flies walking upside down showed a higher duty factor
497 (average proportion of legs in surface contact) than when
498 walking horizontally. While flies mainly used a tripod gait
499 for horizontal walking, they switched to gaits with four or
500 more legs in surface contact when climbing [95, 96]. Sim-
501 ilar kinematic adjustments are seen in insects climbing on
502 slippery substrates [e.g. waxy plant stems; see ref. 97], or
503 following pad contamination [98]. In both cases, insects
504 showed an increase in the duty factor, accompanied by a
505 decrease in step frequency and walking speed. The detailed
506 causes triggering these kinematic changes are still unclear;
507 they may include both direct physical effects of gravity or
508 slipping on locomotion, and sensory detection of substrate
509 orientation, substrate texture or leg slip, followed by ac-
510 tive adjustment of locomotion. Indeed, numerous sensors
511 have been identified on the legs and tarsi of insects, which
512 can detect substrate engagement and leg slip, and trigger
513 the activation of the grip-enhancing claw flexor and tibial
514 flexor muscles [85, 99, 100]. Sensory feedback is doubtlessly
515 essential for adapting locomotion to changes in load and
516 environmental conditions [87, 101].

517 The higher number of legs in surface contact during in-
518 verted climbing may simply provide insects with a propor-
519 tional increase in adhesive capacity, but it may also be
520 critical for attaching and detaching their shear-sensitive
521 adhesive pads. A simple geometric rule that may always
522 hold during slow inverted walking is that the projection
523 of the body CoG onto the surface must be located within
524 the polygon formed by the feet in contact. If this con-
525 dition is met, all the legs in stance can be under tension
526 and sheared inward simultaneously. This ‘inverted stabil-
527 ity’ rule is equivalent to the rule for static stability during
528 upright walking, which demands that the CoG has to fall
529 within the polygon of support in order to avoid toppling
530 [102]. In contrast to the rule of static stability, the mini-
531 mum number of legs in surface contact for achieving stable
532 inward shear is two [103]. However, under quasi-static
533 conditions (and assuming that small insect pads can only
534 produce negligible torques around their contact zones), at
535 least four legs must be in surface contact to allow detach-
536 ment of one leg by unloading or pushing. Hence, the higher
537 number of legs in contact during inverted walking may not
538 only increase adhesion, but also enable controlled detach-
539 ment, and as such may arise as a direct consequence of the
540 control mechanisms on the level of single adhesive contacts.

541 Pad detachment can be driven by the controlled release
542 of elastic energy, but it can also be achieved by an increase
543 of the peel angle, which strongly reduces adhesion as pre-
544 dicted by tape peeling models. As joint torques in running
545 animals are typically minimized by keeping force vectors
546 approximately aligned along the legs [104, 105], changing
547 from a low to a high peel angle for detachment would re-
548 quire a corresponding movement of the leg. Such a ‘rolling’
549 motion (lifting the tarsus from the proximal side) is a ‘nor-

mal’ part of walking and running for the forward-oriented
front legs of lizards and insects, but would be less natural
for middle and hind legs, as it would require the animals
to walk sideways or backward, respectively. Indeed, obser-
vations on ants and flies suggest that rolling is commonly
used only by the front legs, whereas middle and hind legs
mostly detach without such an angle change [40, 106].

While the shear sensitivity of adhesion allows animals to
efficiently switch adhesion on and off during locomotion, it
also leads to constraints. As adhesive pads detach easily
when pushed, they are not suitable for transmitting forces
in this direction. Both during horizontal running and ver-
tical climbing, however, at least some of the legs have to
produce pushing forces. Vertically climbing tree frogs and
geckos can solve this problem by adjusting the orientation
of their limbs and digits for head-up, head-down or lateral
climbing, so that for each leg some toes are pointing up-
ward, in the correct orientation to support the body weight
by pulling [107–109]. Climbing arthropods, however, pos-
sess only one tarsus per leg. Similar to geckos and frogs,
vertically climbing insects can re-orient their legs to some
extent so that a larger proportion of their body weight is
supported by legs above the body centre of gravity, where
the adhesive pads are in the correct pulling orientation
[110, 111]. However, using only the legs above the body
CoG for climbing would impose a severe constraint on lo-
comotion.

Many arthropods have therefore evolved distinct types
of attachment devices on their tarsus, which allow them to
push (see Fig. 5). For example, vertically climbing cock-
roaches engage the tarsal pads (euplantulae) in legs be-
low the body CoG, but use the distal adhesive pad in legs
above the CoG [58]. Similar observations have been made
in beetles, stick insects, and crickets [60, 112, 113]. The
ability to produce large pushing forces is particularly es-
sential for insects performing explosive jumps by rapidly
extending their hind limbs [68]. As pushing is typically
coupled with positive normal forces, the proximal tarsal
pads do not need to produce adhesion, but only high trac-
tion forces; they have therefore been termed *friction pads*
(see Fig. 5). Single-pad force measurements in stick insects
demonstrate that the biomechanical properties of friction
pads can differ fundamentally from those of adhesive pads
[60, 114]: while adhesive pads produce high adhesion when
activated by shear forces, friction pads produce little ad-
hesion, but high friction when activated by normal forces
[60]. Because of the sprawled posture of arthropods, adhe-
sive pads therefore automatically increase adhesion when
exposed to pull-off forces, whereas friction pads automati-
cally increase friction when exposed to shear during natural
locomotion. Therefore, both types of pad may be thought
of as ‘self-stabilising’. Their mechanisms of attachment
and detachment are also analogous: both store elastic en-
ergy during contact formation, the release of which then
drives detachment.

The different functional adaptations of proximal fric-
tion pads and distal adhesive pads are also reflected in
their anatomical position, which can be explained by the
chain-like flexibility of the arthropod tarsus. As the tar-
sus buckles easily, the tibia can transmit large pushing
forces only to the friction pads on the proximal tarsus,
but not to the distal adhesive pads. However, the tarsus

Figure 5: Comparison of adhesive pads and friction pads in insects. Both pad types are specialised for resisting forces in different directions, and thereby serve fundamentally different functions. Adhesive pads are located distally on the foot, and produce high adhesion when activated by shear (pulling) forces, whereas friction pads are located proximally on the foot, and produce high friction when pressed against the substrate.

is a tensile structure, and can easily transmit a strong pull to the distal adhesive pads. As a result, pulling legs towards the body increases contact area for (distal) adhesive pads, but decreases the contact area of (proximal) friction pads; the opposite holds when legs are pushed [57, 58]. Because this anisotropy is at least partly based on the structure of the insect leg, it can be reduced by immobilising the tarsus and pre-tarsus. Such experimental manipulation strongly reduces or even reverses anisotropy in insects with smooth adhesive pads [tested in cockroaches and stick insects, 57, 58, 115], but in some cases, directionality is retained, likely due to anisotropic surface sculptures or the complex fibrous ultrastructure characteristic of smooth pads [64, 81, 116, and see Fig. 5]. In hairy pads, in contrast, the reduction is much weaker because of the direction-dependence at the level of individual setae, which is based on their angled orientation and non-parallel tips [12, 57].

Conclusions

The ability of many animals to climb on vertical and even inverted surfaces has struck scientists with awe for centuries, and is a hallmark of dynamic biological adhesive systems. Strong adhesion is achieved by maximising the amount of energy needed for the creation of new surfaces; rapid detachment, in turn, requires the exact opposite. Controlling adhesion on short timescales hence requires combining two opposing demands. The shear-sensitivity of dynamic biological adhesive systems is an ingenious strategy to solve this conundrum, as it effectively uses the same mechanism to achieve both: during attachment, elastic energy is stored in the attachment systems, but cannot drive detachment, as the active application of a stabilising force renders continued pad attachment energetically favourable. During voluntary detachment, climbing animals can actively use the stored strain energy to trigger pad detachment, and thus effortlessly detach their feet. Further research will uncover more of the fundamental physical principles underlying this core property, which will enable the rationale design of strong yet highly dynamic bio-inspired adhesives.

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