

TOPICAL REVIEW

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## TOPICAL REVIEW

# Clarity of objectives and working principles enhances the success of biomimetic programs

Jonas O Wolff<sup>1</sup>, David Wells<sup>1</sup>, Chris R Reid<sup>1</sup> and Sean J Blamires<sup>2</sup>

<sup>1</sup> Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

<sup>2</sup> Evolution & Ecology Research Centre, School of Biological, Earth & Environmental Sciences, The University of New South Wales, Sydney, NSW 2052, Australia

E-mail: [s.blamires@unsw.edu.au](mailto:s.blamires@unsw.edu.au)

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## Abstract

Biomimetics, the transfer of functional principles from living systems into product designs, is increasingly being utilized by engineers. Nevertheless, recurring problems must be overcome if it is to avoid becoming a short-lived fad. Here we assess the efficiency and suitability of methods typically employed by examining three flagship examples of biomimetic design approaches from different disciplines: (1) the creation of gecko-inspired adhesives; (2) the synthesis of spider silk, and (3) the derivation of computer algorithms from natural self-organizing systems. We find that identification of the elemental working principles is the most crucial step in the biomimetic design process. It bears the highest risk of failure (e.g. losing the target function) due to false assumptions about the working principle. Common problems that hamper successful implementation are: (i) a discrepancy between biological functions and the desired properties of the product, (ii) uncertainty about objectives and applications, (iii) inherent limits in methodologies, and (iv) false assumptions about the biology of the models. Projects that aim for multi-functional products are particularly challenging to accomplish. We suggest a simplification, modularisation and specification of objectives, and a critical assessment of the suitability of the model. Comparative analyses, experimental manipulation, and numerical simulations followed by tests of artificial models have led to the successful extraction of working principles. A searchable database of biological systems would optimize the choice of a model system in top-down approaches that start at an engineering problem. Only when biomimetic projects become more predictable will there be wider acceptance of biomimetics as an innovative problem-solving tool among engineers and industry.

## Introduction

Design and engineering have a history of drawing from natural models [1]. Biomimetics, the transfer of functional principles from living systems into engineering applications, is an example that has been embraced recently across multiple disciplines [2–7]. When using biomimetics to find solutions to a design problem a designer or engineer observes how the problem is resolved by a living system and then attempts to mimic the relevant features. Biomimetics can be performed on a bottom-up (i.e. starting from a biological question) or top-down basis (i.e. starting from a technical problem) [8]. Both approaches require a clear identification and isolation of the working principles from the biological model, due to the fundamental differences between living and

engineered systems. *Mimicry*, however, appears to be a misleading term in this context as it suggests that the objective is to take on the external appearance of an organism when it is really to achieve the same function as a living system by replicating its attributes at a fundamental level. This objective is unlikely to be accomplished by the slavish copying of the living model since living models are self-repairing and capable of growth and reproduction, while the engineered product is synthetic and produced to a fixed standard. Although *analogy* or *equivalence* seem to be more accurate descriptions of the process deployed, *mimicry* is the conventional term and we will continue to use it here.

There are compelling reasons for modelling engineering solutions on natural processes. Since it lacks foresight, evolution by natural selection can arrive at

solutions unlikely to be devised by human ingenuity. Moreover, step-by-step modifications of traits over thousands or millions of generations allow for the assembly of complex hierarchical structures that comply with environmental demands [9]. The traits of an organism have redundancy, and hence robustness, because they must respond to multiple competing requirements. Organisms can also self-repair as a corollary of their ability to change plastically during development [10].

One could point out success stories, where basic biological research and biomimetics have had significant economic and scientific impacts. For example, the discovery of the Lotus-effect pushed the boundaries in water-repellent and self-cleaning surfaces and led to multiple commercially successful products [11]. Aircraft engineering has always drawn from the study of bird wings, while advances in biotechnology, bioengineering, biomedical engineering and pharmacy are founded on the mimicry of biological substances and processes. On the other hand for many ambitious and well-known long-term programs, such as the fabrication of a biomimetic spider silk, significant breakthroughs are still pending. With continuing advances building on several years of practical experience it is now the time for a critical assessment of the efficiency of biomimetics.

Here we broach the question: which factors and strategies have led to success or hampered the advancement of biomimetic programs? First, we briefly review the discrepancies between biological systems and engineering designs that researchers must acknowledge when using biomimetics. Then, we examine three long term biomimetic research programs from different disciplines in an attempt to identify common problems and pathways to success. Finally, we suggest some more directed and defined processes to enhance the success of biomimetic projects.

### Why biomimetic approaches to engineering designs may be suboptimal

In effect biomimetics assumes that evolution by natural selection is a series of natural experiments that have optimized a design and rendered any suboptimal alternatives extinct. Biologists question this assumption [10, 12–14], highlighting the difficulties that may arise because of systematic differences between evolution by natural selection and engineering procedures. In contrast to engineering, evolution by natural selection:

- (1) has a constrained starting-point, namely the traits of the organism as they exist at any moment in time, whereas engineers potentially arrive at a solution by choosing any convenient starting-point;
- (2) acts on organisms that draw on materials available in the local environment, whereas engineers

can utilize materials taken from any environment;

- (3) responds to contemporary rather than future requirements, and hence has no foresight. In contrast, engineering processes can assess alternative solutions based on criteria such as sustainability; and, most importantly,
- (4) responds to multiple competing requirements imposed by the environment. The traits of an organism therefore almost always represent some degree of trade-off between a multitude of functions, rather than being optimised for a single function [13].

The awareness of these limits is an important precondition for successful biomimetics and ignorance of these distinctions is a common pitfall in the process of working principle extraction.

In the following we take a closer look at three distinct cases and investigate how the process of identification of working principles and their transfer onto a technical model has been realized.

### Designing reversible adhesives based on gecko toe pads

Most physical and biological interactions between an organism and its environment take place on surfaces. Accordingly, biological surfaces perform a variety of tasks, and were the first biological system to capture the interest of physicists and engineers seeking new ways to push boundaries and create novel materials. One prominent example is the dry adhesive toe pad system of gecko lizards. Gecko toe pads are more strongly and reversibly adherent to most surfaces than synthetic adhesives. There is therefore immense interest in developing adhesives that mimic the properties of gecko toes.

#### The working principles of gecko toe pad adhesion

In order to design gecko-inspired adhesives from synthetic polymers it has been essential that engineers understand the basic physical mechanisms acting in gecko toe pad surfaces. Researchers have used techniques such as scanning electron microscopy to examine the microscopic hair-like keratinous protuberances called setae on the gecko toe [15, 16]. Geckoes lacking setae cannot climb smooth surfaces. At their tips the setae subdivide into finer nano-branches with flattened endings called spatulae [17]. It is believed that these structures are so pliable that they can get exceptionally close to a naturally irregular substrate. Adhesion tests on synthetic surfaces have shown that the toe pads stick to surfaces via van-der-Waals forces between the spatulae and the substrate [18, 19]. The scale of the interaction is so small that even tiny dust particles can impede the adhesive mechanism. The gecko system is nevertheless efficient at self-cleaning, and full adhesive capacity is recovered

after just a few attachment-detachment cycles [20]. Rapid switchability between high and low adhesion was attributed to the anisotropy of the setae, which cyclically align, misalign and re-align with the surface by shear forces [21]. These principles have duly been identified for the development of gecko-inspired adhesives.

### Designs of gecko-inspired adhesives

Projects aimed at developing gecko-inspired adhesives have almost without exception focussed on the setae as the primary structure providing the desired functionality. As there were initially no fabrication methods that could produce such fine scaled structures, simplified derivatives were used. Some of these emphasized the fibrillary character of the setae [22–25], others the spatula-shaped contact elements [26, 27], while others emphasized a tilting of the fibrous arrays [28–31], structural anisotropy [32], or the multiple hierarchy (i.e. ‘hairs on hairs’) of the structures [33–35] (figure 1).

Choice of the key feature appears to have been most commonly determined by the fabrication methods available and the properties of the usable materials. For instance, fibrillary characters were apparently chosen not on the basis of functional analysis but because fibre arrays are considerably easier to produce than complex spatulate structures. It has also emerged that competing properties in any fibrous adhesive must be balanced to function adequately [36–38]. For example, if the fibres are too stiff and thick they are not flexible enough for effective adhesion, but when they are too soft and thin they break under load or stick to each other rather than to the substrate [36]. Arguably, excessive branching and minute spatula-shaped contacts are important features that facilitate the high efficacy of the gecko adhesive system because they enable extreme compliance with a relatively stiff building material (keratin), which is simultaneously durable and wear-resistant under excessive loads. This highlights the danger of focusing too much on a single feature of a living system in a biomimetic approach where multifunctionality is key to the design goal.

Some studies have circumvented this problem by applying a broader view of natural model systems. Instead of focusing exclusively on the gecko model, broad comparative studies of insects and spiders have revealed a diversity of functional structures for adhesion. Some of these might be easier to transfer into manufactured products, or might more closely match a particular designer’s goal [39, 40]. Notably, spatulate structures such as those found on gecko toe pads, are highly beneficial for rapid attachment-detachment cycles but the design goal of most gecko-inspired adhesives is longer term attachment. Surface features that have evolved for strong but not dynamic attachment exhibit contact elements with entirely different shapes [27, 41, 42]. This principle was used in the development of one of the few commercially devel-

oped dry adhesive tapes derived from biomimetic procedures (Gecko® Nanoplast®, Gottlieb Binder GmbH & CoKG, Holzgerlingen, Germany) [43, 44]. A comparative study of gecko toe pads proposed that focussing on setae as the fundamental feature might be ineffectual because their properties cannot be scaled up [45]. These authors emphasized the mechanical properties of the underlying material and developed a fabric-polymer blend (Geckskin™, University of Massachusetts, Amherst, MA, USA) which mimics the anisotropic compliancy of a gecko toe but does not mimic any of the fibrillary features [45, 46].

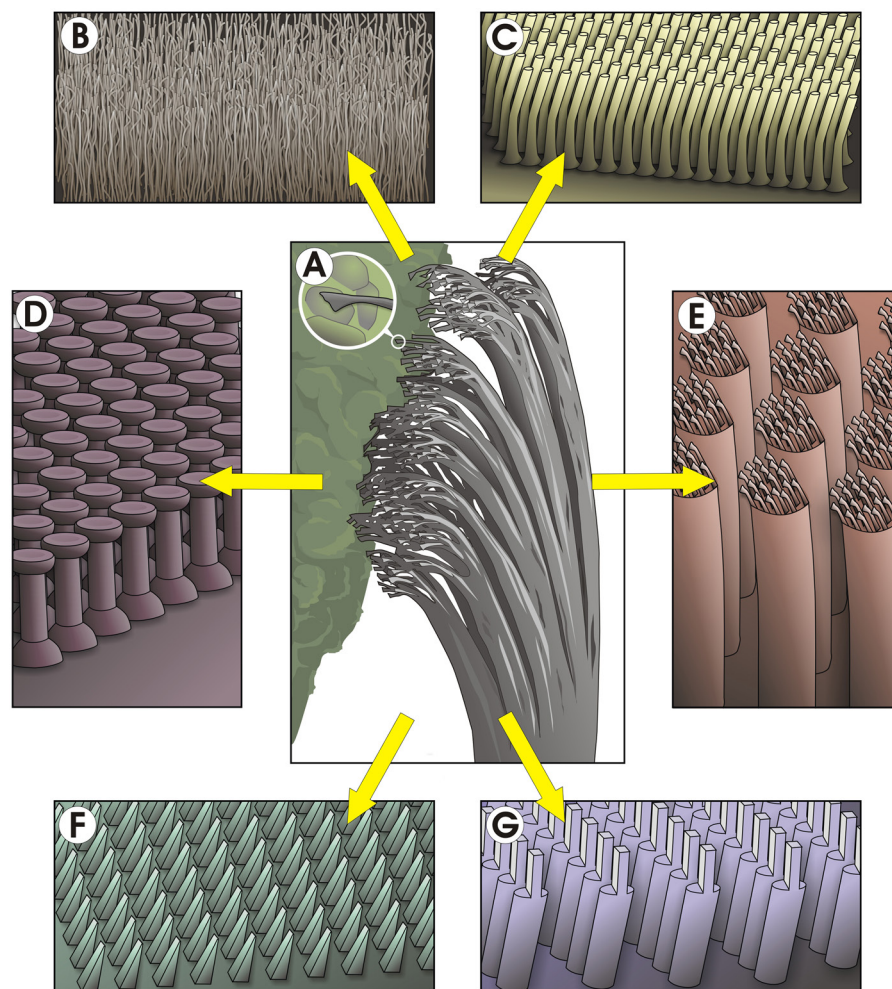
### Evaluation

The difficulties associated with developing adhesives inspired by gecko toe pads highlight several problems with biomimetic design approaches. One is an apparent discrepancy between the biological function and the intended, often not clearly defined, application. Gecko-inspired adhesives ought to stick instantly on various surfaces and should be removable without leaving marks. Many authors claim that their developments would perform as well as or even better than the natural model [24, 26, 47, 48]. However, such claims are usually made upon evaluation of only a single characteristic (e.g. perpendicular pull-off strength, dynamic friction, or self-cleaning capacity) and/or by using a particular testing method, substrate surface, or sample type. Rigorous testing of performance relative to conventional synthetic adhesives is rare. The efficacy of gecko-inspired adhesives is particularly difficult to evaluate since the pull-off forces are usually measured with reference to the direct contact between the micro-hair tips with a substrate rather than the effective adhesive area. This means that it is often unclear whether a non-structured flat sample of the same material produces similar adhesive and friction forces as the bio-inspired one. A further problem is the restrictive and highly unnatural functional analyses performed for the gecko adhesive system [49]. For instance, although geckos stick to any surface regardless of how smooth, rough, dirty, or wet, a feat which cannot be matched by any synthetic adhesive tapes [49–51], most tests are performed on smooth polar artificial surfaces. Overall, it appears that poor understanding of the natural model has been the main reason for the long-term trial-and-error process observed in the development of gecko-inspired adhesives [49].

### Development of high performance materials based on spider dragline silk

Spider dragline silk is an exceptional material with a unique combination of high tensile strength and extensibility. Its toughness exceeds that of most natural and synthetic materials, including Kevlar® [52]. Moreover, it is produced within an aqueous solution at room temperature and is highly biocompatible.





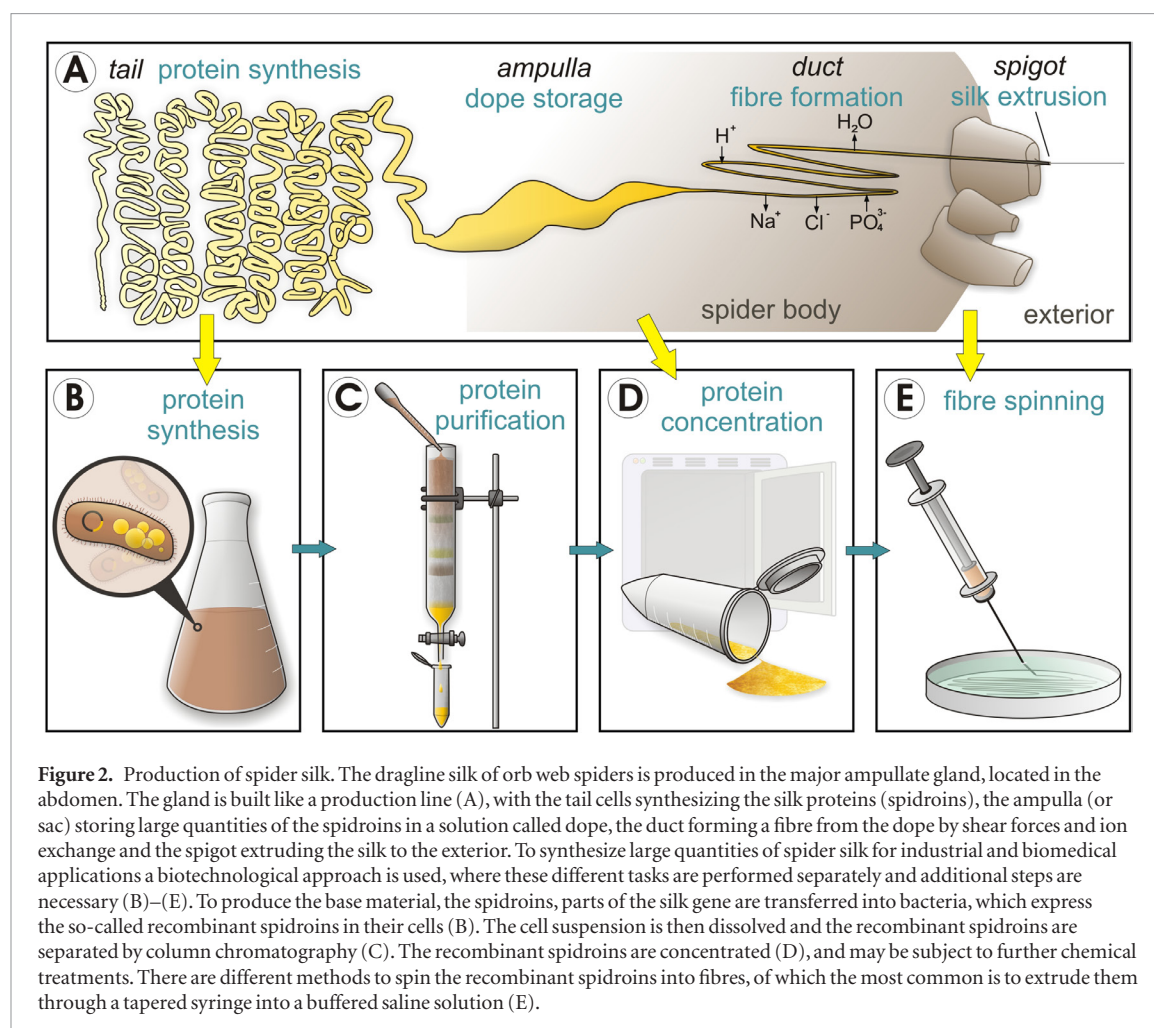
**Figure 1.** Pathways of extracting the essential feature(s) in gecko-inspired adhesives. The adhesive hairs (setae) of geckoes ((A) schematic view of a single seta tip in contact with a plant surface) split into numerous branches with nano-scale flattened tips, so-called *spatulae* ((A) inset). This structure combines stability with a high degree of conformability, such that spatulae can closely contact the substrate surface so short range inter-molecular forces can be utilized. Material engineers attempt to divide this complicated structure into simplified models to mimic the working principles. Thereby single structural features are often used in isolation: e.g. high aspect ratio nano-fibres ((B), adapted from [103], with permission from AAAS); tilted micro-columns ((C), adapted with permission from [25]. © 2007 American Chemical Society); micro-columns with discoidal tips ((D), adapted from [26], with the permission of AIP Publishing); bi-hierarchical fibres with flattened tips ((E), adapted with permission from [104]); wedge-shaped elements with shear-sensitive adhesion ((F), adapted from [32], with permission of the Royal Society); tilted micro-columns with flexible tips ((G), adapted with permission from [31]. © 2012 American Chemical Society). Notably, none of these materials exhibits adhesive properties similar to gecko toes.

The production of artificial fibres that mimic the properties of dragline silk is therefore sought-after. Potential applications include novel light-weight, high-performance materials (e.g. ropes, protective clothing) and functional bio-composites for tissue engineering [53]. Harvesting silk from spiders, as opposed to silkworms, is commercially unviable as spiders require vast amounts of space for their webs, tend to cannibalize each other, and do not readily produce large quantities of silk. Genetic engineering procedures utilizing biomimetic spinning methods appear the best option for the large scale production of high performance spider silks.

#### Structure-property relationship in natural spider silk

Detailed studies have established the links between the expression of certain spider silk genes and the proteins

(spidroins) produced [54–60]. The properties of the silks are described across species, so we know that: (i) the spidroins form crystalline and non-crystalline nanostructures that respectively contribute to the silk's strength and extensibility [54–57], and; (ii) the amino acid composition of the spidroins correlates well with certain nanostructures [54, 59–62]. Dragline silk is manufactured in the major ampullate gland, which consists of three subsections that serve spidroin production, storage of the liquid precursor (dope) and fibre formation respectively (figure 2(a)). Prior to extrusion the dope flows through a funnel-shaped aperture [63], and the decreased lumen width generates shear stress on the dope, inducing a thinning and solidification of the fibre [64]. Despite a good working knowledge of silk genetic structures and an understanding of the influences of genetic expression on the proteins produced and the functional properties



of the proteins, commercial-scale engineering of a material that performs as well as natural spider silk has proved elusive [65–67].

### Biomimetic approaches to spinning synthetic spider silk

The development of synthetic spider silk involves the creation of spinning dope and a biomimetic spinning process (figures 2(b)–(e)). The biomimetic spinning process includes chemical and physical treatments of the proteins under specific conditions to promote aggregation and folding of the proteins at precise moments as well as controlled drawing of the solid fibre. There are limitations to the effectiveness at each stage.

#### Creating the proteins and their treatment

Three alternative sources of spinning dope have been utilised: native, recombinant and genetically modified [65–68]. Native dope contains the desired proteins in the desired ratio so is considered the ‘gold standard’ used to test the efficiency of the treatments and spinning methods [68]. Native dope is obtained directly from the glands of sacrificed spiders or from spun fibres dissolved in caustic solvents.

Recombinant dope is derived by transferring the silk genes to bacteria which express the proteins. The problem with deriving dope proteins via recombinant expression is that few full-length spidroin-encoding

gene sequences are known, and clones of those that are known have not produced high quality silk [69, 70]. Moreover, attaining full length recombinant spider silk proteins is difficult because the length and size of the proteins render them difficult for bacterial hosts to synthesize and secrete, and for researchers to isolate and purify [69, 71]. Accordingly, a limited range of recombinant spidroins have ever been effectively produced. Moreover, non-spidroin encoding genes can influence the structure and function of spider silks [55, 72]. We clearly do not know enough about the function of the spidroin and non-spidroin coding genes and how they interact to fully exploit recombinant technologies for the creation of spinning dopes [65, 66, 73].

An alternative to the creation of dope by recombination is development by genetic modification of the proteins secreted by bacteria (e.g. *Escherichia coli*), plants (e.g. tobacco), yeasts, or animals (e.g. goats) [71, 74, 75]. This approach produces dopes that contain silk-like proteins but of significantly reduced molecular weight. These proteins accordingly require further chemical treatment to produce silk threads [76].

#### Biomimetic spinning

A combination of changes in water content, salt concentration, pH and shear stresses act on the dope as it flows from the sac to the duct during natural silk spinning and these induce the proteins to rearrange

into nanostructures that give dragline silk its properties [62, 77]. Accordingly, immersion in a combination of saline and acidic solutions is utilized prior to and during biomimetic spinning. An inability to precisely co-ordinate the actions of salts, pH and shear stresses has generally led to the synthesis of inferior artificial silks [64, 68].

The methods used for spinning artificial silk fibres currently include the pulling of fibres through microfluidic, electrospinning and mechano-spinning devices at draw speeds as close as possible to natural spinning speeds. During spinning the crystalline and non-crystalline nanostructures self-align to varying degrees depending on draw speed and frictional forces at the spinning valve [52]. The faster the draw the greater the nanostructural alignment and the greater the stiffness of the silk [54, 59, 61]. Researchers have, however, so far only spun silk fibres with strengths and extensibilities about half the value of native dragline silk using recombinant proteins spun into a water solvent [78, 79].

### Evaluation

As indicated, each step in the production process of synthetic silk fibres exhibits problems that are still challenging despite a relatively good understanding of the natural silk secretion process. It is apparent that we cannot simply copy the elaborate synthesis and secretion process of a gland into a biotechnological process. Recombinant protein expression and artificial spinning are an inevitable necessity to produce fibres with properties that mimic those of spider silk. When developing a synthetic spider silk we should also ask: what are the properties we desire and why? If, for instance, the desired properties do not match those of dragline silk, then some refinements of the current spinning methods might suffice. Ultimately not all properties of dragline silk will be desirable in commercial materials. For instance, dragline silk shrinks and becomes rubbery when exposed to water [62]. While this property might be useful in some contexts [80], clearly a rigid structural material should not have this property and the proteins or spinning processes might need to be further modified to remove it.

### Engineering systems modelled on swarm intelligence

Self-organisation occurs when patterns and structures arise entirely from internal mechanisms and local interactions and not according to a pre-conceived blueprint or the directions of a central controller [81]. Local interactions may modify the behaviour of the interacting individual units either directly, e.g. when units physically collide, or indirectly, e.g. through environmental changes [82]. From simple interactions at an individual level we see sophisticated 'emergent' properties at the group level, where the whole becomes not only greater than but very different from the sum of its component parts [83].

The biomimetics of self-organization has been adopted in many fields but we focus here on a subset of these known as 'swarm intelligence', the collective intelligence that emerges at a group level from the interactions between individuals acting to collectively solve problems that they cannot solve alone [84, 85]. We discuss how the complex behaviour of colonies of social insects (ants, bees, wasps and termites) has inspired biomimetic designs for computer algorithms that optimise network routing or control coordinated behaviour in groups of robots. In all cases the design objective is to gain benefits in efficiency and capability by moving away from a centralised approach where a single, complicated, unit processes all of the information and performs all actions to a decentralised system of many simple (and therefore cheap) units with only local information processing and action.

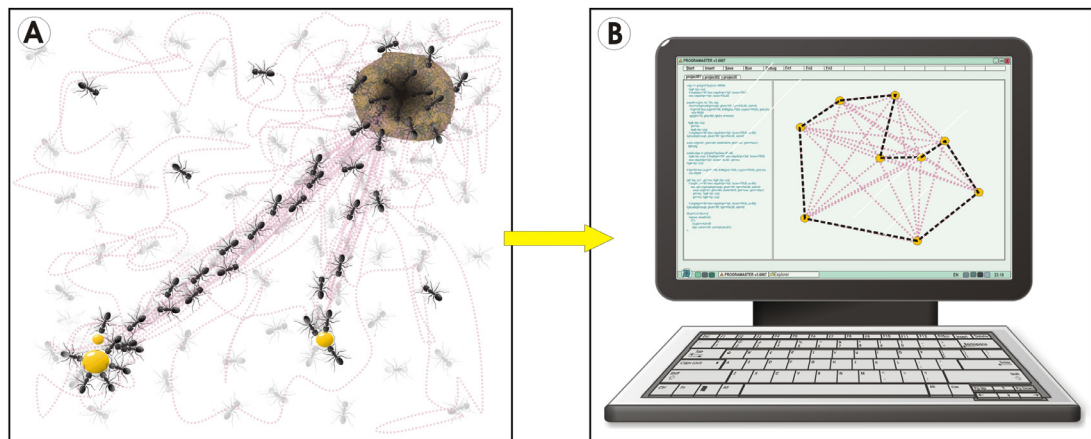
### Working principles and biomimetic approaches

Perhaps the most useful applications of swarm intelligence have been the ant colony optimisation (ACO) algorithms [86]. These algorithms are primarily designed to find the most efficient path through a network, and are used for such diverse applications as routing telephone calls and internet data through busy, dynamic networks, scheduling assembly lines to construct complex machinery at the lowest possible cost and construction time, and calculating the most efficient pick-up and set-down routes for delivery vehicles. ACO is inspired by the pheromone trail laying and following behaviour of mass-recruiting ant species as they forage for food, and is primarily driven by a positive feedback reinforcement of 'good' solutions essentially found at random (figure 3).

Designing decentralised control algorithms capable of reproducing social insect swarm intelligence in robot swarms has been a major focus of this field over the past decade. In the classic group retrieval task inspired by the cooperative transport of large prey items by teams of foraging ants a group of robots must manipulate a payload to a target destination, where the payload is too heavy for a single robot to move and the robots possess no *a priori* information about the payload or the environment. A model of collective transport that could be used to define novel control algorithms for multi-robot systems was developed by Berman *et al* [87], based on experimental observations of cooperative prey retrieval by *Aphaenogaster cockerelli* ants. With process refinement over millions of years of natural selection, the ants have evolved decentralised solutions to the group retrieval task, including assembling a team at the prey discovery site, distributing the carriers around the payload, coordinating physical forces so as not to inhibit each other, negotiating obstacles along the route, and dynamically allocating the various subtasks involved in retrieval [87]. This work has led to effective biomimetic control algorithms for group retrieval by multi-robot swarms.

Using swarms of simple robots that mimic the swarm intelligence of social insect colonies has several





**Figure 3.** Collective behaviour in ants and ant colony optimisation algorithms (ACO). Groups of ants efficiently and rapidly find the shortest way between their nest and valuable food sources (A). In the initial phase scouts will randomly search the environment for food (symbolized by pale ants and tracks). If a food source is found, scouts walk back to the nest, depositing a trail of scent signals (the pheromone trail, symbolized by pale pink lines). Other ants will follow the pheromones, depositing their own pheromone in turn. The shortest trail selected by the scouts will receive the highest rate of ant flow and hence a rapid increase in pheromone deposition, making it the most attractive route for future ant traffic. ACO algorithms mimic this behaviour to calculate the shortest route between different nodes in a given network (travelling salesman problem), using a swarm of virtual ‘ant’ agents that walk randomly between nodes and deposit a fixed amount of virtual ‘pheromone’ (B). The amount of pheromone is inversely proportional to the length of the tour, such that shorter tours receive more pheromone. Ants in subsequent cycles preferentially follow the strongest pheromone trail, as well as contributing their own pheromone to the trail. This positive feedback focuses the virtual colony’s traffic on the shortest ant-trail through the network, thereby finding the optimal solution to the problem (or one close to it—the ants do not sample the entire solution space, and so cannot guarantee that they find the globally optimal solution). Just as in real ant colonies where the volatile pheromone evaporates at a constant rate, the colony is allowed to ‘forget’ sub-optimal paths through the network.

advantages over the traditional approach to robotics, including: (1) scalability—the same control architecture will apply to group sizes of two to two thousand; (2) increased flexibility and robustness to damage—the individual units can be added or removed without altering the organisation of the group, allowing the system to operate in dangerous and dynamic situations such as natural disaster zones; (3) the emergence of behaviours and properties beyond the abilities of single units, such as self-assembly, collective construction, collective sensing, collective retrieval and group exploration [87–91]. Some of these attributes result in an economy of scale that ensures robot swarms are cheaper than single, specialised units. Recent advances in the cost-efficient miniaturisation of processors, sensors and actuators [92, 93] have made the swarm robotic approach more feasible.

### Evaluation

The ACO approach has been successful for solving two kinds of problem: computationally complex problems, and dynamic problems. In many important optimisation problems the time required to solve the problem increases exponentially with the number of components in the system. There is no known algorithm for solving instances of these problems within a feasible time frame, so we use ‘heuristic’ algorithms such as ACO, which finds near-optimal solutions in a reasonable time. The dynamic nature of real-life problems, where the solution space or network parameters are in a state of continual change, also makes real-time optimisation difficult. The

probabilistic choice of routes through the virtual maze of the network means that ACO algorithms often maintain several short paths in addition to the best one. Hence, if the parameters of the network change, virtual ants will quickly switch to the next shortest path, whereas other algorithms would have to compute the shortest path again from scratch [94].

Swarm robotic control provides a crucial test-case for the transfer of biomimetic algorithms from the purely *in silico* domain into the physical world. The comparatively rapid success of the biomimetic approach in designing new algorithms, as opposed to adhesive tapes or silk-like fibres, could derive mainly from the fact that the latter are physical products that must interact with the physical world, while computer algorithms generally do not. Robot swarms, however, may be composed of actual as opposed to merely virtual robots. In the former case, they must interact with the physical world, and there is usually an associated loss of performance. This loss of performance is attributed to unexpected interactions and behaviours of the individual units themselves, e.g. several robots may differ slightly from others in the turning rate of their wheels, and this may lead to unpredictable group-level behaviour.

Biomimetic designs based on self-organisation and swarm intelligence generally perform well in scenarios where it is vital to maintain dynamic adaptation to changing internal or external parameters. Where the problem to be solved is static, swarm intelligence approaches are usually outperformed by more specialised approaches. For instance, ACO algorithms are



outperformed by an order of magnitude by specialised computer science and operations research algorithms when solving static versions of the Travelling Salesman Problem or classical shortest path problems [95]. Similarly, the distributed sensing capabilities of swarms of robots give them an advantage in dynamic environments, where up-to-date global information is not available. If information on the global state of a static environment is available, a single robot capable of planning its actions into the future may be more efficient than a swarm of locally-reactive units. There appear to be two main factors at work here: firstly, enhanced performance through dynamic adaptation to a changing environment is a benefit that comes at a cost which can be ignored by more directed and specialised, albeit less flexible, approaches, and secondly static scenarios are typically not natural.

## Pathway to enhanced outcomes

### Specification of the target function(s)

- (i) *Defining the objective:* The starting point of any biomimetic approach is a key question. This may be an unresolved technical problem (top-down approach) or the aim to understand a biological function (bottom-up approach). In both cases the problem should be clearly defined. For example it might be asked how can we achieve enhanced toughness in a certain material to prevent fracture under defined load? Or how does an aquatic insect retain the air bubble around its abdomen when underwater? However, in many cases the problem may be more complex. For instance when asking how can we enhance the toughness of 3D-printed components or how do geckoes reversibly stick to various surfaces?
- (ii) *Defining elemental functions:* If the aim is multi-functionality as in gecko-inspired adhesives and synthetic spider silks, then a more directed approach is to break down the problem into single, clearly defined sub-topics. Sub-topics represent single functions that are, at first, studied separately, and later jointly implemented into the product. Such a modularisation of the core problem may facilitate the identification of elemental working principles and guide the subsequent design process. For instance, in spider silk it was found that extensibility and strength are caused by specific motifs within the amino acid sequences [54, 61]. Such motifs can be used as 'building blocks' to design tough silks that are much simpler than the natural model and can be tailored for the intended application [96, 97].
- (iii) *Defining the intended application:* In the above examples the final applications are only vaguely defined, possibly because much of the work is purely exploratory. In the case of gecko toe biomimetics a universal reversible adhesive will be difficult to achieve and will always involve a compromise between conflicting functions.

Instead, clearly defining the specified strength of adhesion required and to what specified substrate or surface it is to be applied will assist the development of more directed biomimetic procedures.

### Choice of model

If the target function is clearly defined, the outcomes may depend on the suitability of the model. This requires a basic understanding of the biological role of the target function within the model system. For instance, the adhesive system of the gecko toe is adapted to rapid movements, rather than strong attachment, and most applications may require durable, strong adhesion. Accordingly, the design features of one of the few commercially successful structural adhesive tapes were found in the adhesive system of male leaf beetles that durably attach to the smooth wings of their female partners [39, 43]. Since engineers, and even biologists, will not know the vast biodiversity and biological literature, a beneficial tool would be a central searchable database that gathers biological model systems and working principles in a uniform style.

### Extraction of working principles

Understanding the working principles and their isolation from the biological model (in some literature this process is called '*abstraction*') is a crucial and risky step because it is unpredictable. As we illustrated at the outset multi-functional trade-offs and evolutionary history can obscure structure-function relationships and make it difficult to identify the basic unit that is responsible for the function of interest. Furthermore, the function of interest may be caused by a set of features, some of which might not be apparent. For example, it has been largely overlooked that the properties of the underlying soft tissue have a major effect on the functions performed by the surface features of gecko toes and shark skin, which has led to some false assumptions [45, 98].

For the identification and extraction of working principles, the following approaches have proved useful and led to success in exemplary cases.

- (i) *Experimental manipulation:* Descriptive performance assessments are typically used to identify copy-worthy features. However, such assessments will not uncover working principles. Where possible, the most efficient way to identify working principles is to experimentally deactivate features that are putatively involved in the target function and to observe the effects on the target function. However, it is not always possible to disable single features. For instance, in geckoes, setae could be removed or sealed, but it is not possible to manipulate the stiffness gradient or chemical composition of the setae.
- (ii) *Computational models:* Computer models provide an alternative method for identifying the functional relevance of traits when the exper-

imental testing of functionality is difficult. For instance, simulations using finite elements and similar models have been used to test the effect of different features of adhesive setae on their adhesive properties, like stiffness gradients [19], or contact geometry [99].

- (iii) *Use of comparative methods*: One of the most reliable ways to identify the functionally relevant aspects of a trait is to reconstruct the trait's evolutionary history using comparative methods [100]. For example, where a trait evolved once in a common ancestor of a species group and was lost by members of the group which do not perform a function of interest but retained by other members of the group which do, we have evidence that the trait evolved, at least in part, to perform the relevant function [100]. Even more informative are cases where a similar trait and function has evolved multiple times independently among species, thus helping to decouple the effect of a function from the effect of ancestry [40, 100].
- (iv) *Artificial models*: Simplified, designed models are useful tools to test hypothetical working principles, because they permit considerable freedom in altering various parameters. This has repeatedly been applied in studies on gecko-inspired adhesives [27]. In functional materials, recent advances in 3D-printing technology have opened new doors to test hypotheses on working principles with physical models from nano- to macroscales. However, this approach risks a costly and time-consuming cycle of trial-and-error. Therefore, this method is ideally deployed once there is a basic understanding of the factors involved. Frølich *et al* [101] and Hsiung *et al* [102] demonstrated a time-effective workflow for structural biomimetic materials, where the results of basic morphometric and mechanical measurements of the biological model are fed into a computer model that is used to find the optimal parameters. These are used as a blueprint for 3D-printed physical models to test the proposed working principle.

### Designing prototypes

The process of prototype design should consider the final application and scale of use. The main limitation in this step is the availability of fabrication methods. Biomimetics is especially constrained by the fact that biological systems are built additively at a nano-scale, and analogous technologies are still premature. This is one of the main obstacles for the successful implementation of synthetic spider silk production and gecko-like adhesives.

### Testing prototypes

The testing of prototypes against the previously defined target function and the comparison of their performance with the biological model and existing products is, regrettably, often neglected. This may be because scientists are under pressure to produce

success stories. As discussed in the example of gecko-inspired adhesives, tests need to be standardized to objectively evaluate the performance of the prototype. If the prototype meets the objective, next steps will involve its implementation into a commercial product.

## Conclusion

Biomimetics has been repeatedly shown to be an innovative process for resolving engineering predicaments. Nevertheless, the prevailing view of living systems as fixed and essentially mechanical is a common pitfall that leads to misconceptions about working principles. The success of biomimetic approaches is unpredictable. Clear and simple objectives and the choice of the right model are critical for a rapid progress in biomimetic projects. An increase of the efficiency, success rate and a reduction of the risk of biomimetic projects is clearly demanded to advance and maintain the acceptance of biomimetics as an innovative tool in engineering and applied biosciences.

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