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Form, structure, and function: How plants *vs.* animals solve physical problems

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Abstract

Plants and animals have evolved solutions for a wide range of mechanical problems, such as adhesion and dispersal. Several of these solutions have been sources for bio-inspiration, like the Lotus Effect for self-cleaning surfaces or Velcro for adhesion. This symposium brought together plant and animal biomechanics researchers who tackle similar problems in different systems under the unifying theme of structure-function relations with relevance to bio-inspiration. For both communities it holds true that the structural systems, which have evolved in the respective organisms to address the mechanical challenges mentioned above, are often highly complex. This requires interdisciplinary research involving "classical" experimental biology approaches in combination with advanced imaging methods and computational modeling. The transfer of such systems into biomimetic technical materials and structures comes with even more challenges, like scalability issues and applicability. Having brought all these topics under one umbrella, this symposium presented the forefront of biophysical basic and application-oriented international research with the goal of facilitation knowledge transfer across systems and disciplines.

Introduction

Plants and animals have unique solutions for mechanical problems, such as adhesion (Wolff, van der Meijden et al. 2017, Stark, Arstingstall et al. 2018), folding (Edwards, Spriggs et al. 2016, Faber, Arrieta et al. 2018), dispersal (Cooper, Mosher et al. 2018), cleaning (Barthlott and Neinhuis 1997), and mechanical loading (Clair, Ghislain et al. 2019), amongst many more (Moulia 2013). By looking at these solutions across species, including across kingdoms, we can gain a deeper understanding of underlying physical mechanisms, of principles for effective bio-inspired designs, and of the role of physics in biological processes such as growth and development (Fournier, Stokes et al. 2006, Whitenack, Simkins Jr et al. 2011, Derr, Bastien et al. 2018, Geitmann, Niklas et al. 2019). The systems that animals and plants have evolved to address mechanical challenges are often highly complex. Studying these systems requires interdisciplinary research involving "classical" experimental biology approaches in combination with advanced imaging methods and computational modeling. The transfer of such systems into biomimetic technical materials and structures comes with even more challenges, like scalability issues and applicability (Schleicher, Lienhard et al. 2015). Both science and science education benefit when biology inspires technology and technology inspires biology.

How organisms solve physical problems

Mechanical function shapes organismal structure and motion. When different organisms perform the same mechanical function, the structures and motions that serve this function are shaped by shared physical principles underlying this function. To deduce these underlying principles, functional morphologists and biomechanists examine those structures and motions across species (Chin and Lentink 2016, Hu, Nelson-Maney et al. 2017). When a mechanism is discovered in one organism, researchers quickly find additional examples. Three such mechanisms are the leading edge vortex, gyroscopic backspin, and linkages. The role of the leading edge vortex in organismal flight was discovered when scientists were looking for a mechanism that could provide sufficient lift for insect fliers (Ellington, Van Den Berg et al. 1996, Van Den Berg and Ellington 1997, Birch and Dickinson 2001). Leading-edge-vortices were consequently found in many organisms and for a range of tasks, including bats and birds for flight (Videler, Stamhuis et al. 2004, Warrick, Tobalske et al. 2005, Muijres, Johansson et al. 2008), grebes and fish for swimming (Johansson and Norberg 2003, Borazjani and Daghooghi 2013), and samara seeds for dispersal (Lentink, Dickson et al. 2009). Leading edge vortices form on swept wings and on rotating wings and they enhance lift by forming a vortex attached to the wing's leading edge (Lentink and Dickinson 2009). The second mechanism, gyroscopic backspin, was first discovered in one plant species with explosive seed dispersal (*Ruellia ciliatiflora*) (Cooper, Mosher et al. 2018), which led to the re-evaluation of a previous study on a different plant, the Jabillo or Sandbox tree (*Hura crepitans*) (Swaine and Beer 1977, Ribera, Desai et al. 2020). The third example are linkages, such as four-bar linkages, Watt's linkages, and Peaucellier linkages, which have been found in animal skulls, legs, and wings (Muller 1987, Westneat 1990, Wissa, Han et al. 2015, Hu, Nelson-Maney et al. 2017, Usherwood 2020). Linkages are used in engineering and biology to convert one type of motion into another, they help reduce mechanical work or inertia, and provide leverage to manage the force or speed of a movement. Engineering and physics provide many useful tools and theories for studying organismal structure and motion that allow researchers to quantitatively describe and understand the function of observed organismal behaviors and structures.

Comparisons across species or even across kingdoms not only help reveal underlying physics of organisms performing the same function, but they can also reveal differences in what organisms prioritize within this function. Both samara seeds and swifts use leading edge vortices in their flight, yet they differ in which performance parameter they prioritize: whereas swifts minimize cost, samara seeds maximize the time spent in the air (Lentink, Müller et al. 2007, Lentink, Dickson et al. 2009). Furthermore, the same function can be achieved by a variety of mechanisms. Organisms that disperse by flight can use inertia (ballistic mechanisms), drag (ballooning, parachuting), and lift forces (gliding) (Money 2016, Cho, Neubauer et al. 2018, Cooper, Mosher et al. 2018, Seale and Nakayama 2020). Ballistic mechanisms require elastic energy storage in specialized tissues (Hofhuis and Hay 2017) and can be supplemented by secondary strategies to reach longer distances, including the exploitation of vortices generated during the explosion (Hayashi, Feilich et al. 2009, Whitaker and Edwards 2010). Organisms can generate aerodynamic forces by spinning, rocking, or tumbling (Minami and Azuma 2003, Lentink, Dickson et al. 2009) or they can rely on wind or fluid resistance alone (Tackenberg, Poschlod et al. 2003, Cho, Neubauer et al. 2018, Cho and Koref 2020).

Interspecific comparisons are particularly powerful when they include many species, span a wide range of body sizes, and compare functions that likely share underlying physical principles, such as swimming and flying. In such cases, physics and engineering concepts can provide a lens to understand not only how organisms solve mechanical problems, but also how the physical world sets limits to organismal structures and their movements. Take the effect of body size; the effectiveness of many mechanisms depends on physical size, in which case such mechanisms impose limits on organisms' dimensions (Vogel 1988, Vogel 1994). For example, large organisms cannot depend on diffusion alone for transport (Kranenbarg, Muller et al. 2000), while small organisms struggle to exploit fluid-dynamic mechanisms that require them to operate in the inertial flow regime (Müller and Videler 1996, Fuiman and Batty 1997, China, Levy et al. 2017, Deban, Holzman et al. 2020). Other mechanisms' usefulness is context-dependent, hindering in one context yet aiding in another. For example, surface tension allows water striders living on the water surface to walk on water (Hu, Chan et al. 2003, Thorp and Covich 2010); but tadpoles living underwater struggle against surface tension when trying to breathe air (Schwenk and Phillips 2020). Some organisms, such as trees, carefully manage surface tension to ensure water transport and avoid cavitation (Domec 2011). A case that exemplifies how comparing across body size and across functional contexts advances our understanding is Strouhal number as an indicator of power efficiency in swimming and flying (Taylor, Nudds et al. 2003, Gazzola, Argentina et al. 2014). Other informative comparisons across species, size, and functional context concern the role of elastic-energy versus muscle-powered motion (Ilton, Bhamla et al. 2018) and adhesion (Gilman, Imburgia et al. 2015, Labonte, Clemente et al. 2016, Stark 2020).

Functional context matters

If we want to understand the function of organismal structures and motion, we must study them in their ecological context. A case in point is our growing appreciation for environmental factors affecting adhesion (Bauer, Poppinga et al. 2020, O'Donnell and Deban 2020, Stark and Yanoviak 2020). Surface roughness, orientation, wetness, and temperatures have all been shown to affect adhesion strategy and performance (Bauer and Federle 2009, Stark, Arstingstall et al. 2018, Bauer, Poppinga et al. 2020, O'Donnell and Deban 2020, Stark 2020, Stark and Yanoviak 2020). As surfaces get smoother, salamanders and insects rely more on adhesion than gripping (O'Donnell and Deban 2020), and in ants this switch in strategy is elicited by the substrate without neural control (Endlein and Federle 2008). Insects change gait and running speed as incline increases (Ramdya, Thandiackal et al. 2017, Stark and Yanoviak 2020). Although theoretical studies and laboratory experiments can help us formulate predictions about an organism's performance as a function of its environmental conditions (Ramdya, Thandiackal et al. 2017), a true test of those predictions are observations in the field, as apparent in a case shared by Bauer (Bauer, Poppinga et al. 2020): ants that performed well walking on the very slippery surfaces of the *Macaranga* plants (Federle, Maschwitz et al. 1997) did not necessarily perform well in lab experiments intended to document the ants' ability to generate high friction forces (Federle, Rohrseitz et al. 2000). Observing organisms in their natural context is vital to understanding (physical) function and performance.

From biology to bioinspiration

Understanding the solutions that organisms have evolved can serve as inspiration not only to other biologists but can also lead to bio-inspired technical solutions. Two iconic examples are the Lotus Effect® and Velcro® (Spaeth and Barthlott 2008). Effective bioinspired design often requires thorough understanding of the underlying physics and incomplete understanding of underlying mechanisms risks sub-optimal performance in biomimetic and bio-inspired designs (Casas, Krijnen et al. 2020, Langowski, Dodou et al. 2020), as evident in the mismatch between biological studies emphasizing their potential for bio-inspired design and the actual number of bio-inspired technologies that have crossed the so-called valley of death for innovation (Chirazi, Wanieck et al. 2019). But as the term bioinspiration suggests, biology often serves even better as a concept generator than as a direct provider of technical solutions (Poppinga, Correa et al. 2020). And as such a concept generator for technical solutions, it can serve also a powerful educational tool (Full, Dudley et al. 2015, Hansen, Langdon et al. 2020).

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Conflict of interest statement

The authors declare no conflicts of interest.

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