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Optimized structures for vibration attenuation and sound control in nature: A review / Bosia, Federico; Dal Poggetto, Vinicius F.; Gliozzi, Antonio S.; Greco, Gabriele; Lott, Martin; Miniaci, Marco; Ongaro, Federica; Onorato, Miguel; Seyyedizadeh, Seyedeh F.; Tortello, Mauro; Pugno, Nicola M.. - In: MATTER. - ISSN 2590-2393. - ELETTRONICO. - 5:10(2022), pp. 3311-3340. [10.1016/j.matt.2022.07.023]

*Availability:*

This version is available at: 11583/2972465 since: 2022-10-20T07:06:41Z

*Publisher:*

Cell Press

*Published*

DOI:10.1016/j.matt.2022.07.023

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<http://dx.doi.org/10.1016/j.matt.2022.07.023>

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# Optimized structures for vibration attenuation and sound control in Nature: a review

Federico Bosia<sup>1</sup>, Vinicius F. Dal Poggetto<sup>2</sup>, Antonio S. Gliozzi<sup>1</sup>, Gabriele Greco<sup>2</sup>, Martin Lott<sup>1</sup>, Marco Miniaci<sup>3</sup>, Federica Ongaro<sup>2</sup>, Miguel Onorato<sup>4</sup>, Seyedeh F. Seyyedizadeh<sup>1</sup>, Mauro Tortello<sup>1</sup>, Nicola M. Pugno<sup>2,5\*</sup>

<sup>1</sup> Department of Applied Science and Technology, Politecnico di Torino, Torino, 10129, Italy

<sup>2</sup> Laboratory for Bioinspired, Bionic, Nano, Meta Materials and Mechanics, Department of Civil, Environmental and Mechanical Engineering, University of Trento, Trento, 38123, Italy

<sup>3</sup> CNRS, Univ. Lille, Ecole Centrale, ISEN, Univ. Valenciennes, IEMN - UMR 8520, Lille, F-59000, France

<sup>4</sup> Department of Physics, University of Torino, Torino, 10125, Italy

<sup>5</sup> School of Engineering and Materials Science, Queen Mary University of London, London, E1 4NS, UK

\* Corresponding author: nicola.pugno@unitn.it

## Summary:

Nature has engineered complex designs to achieve advanced properties and functionalities through millions of years of evolution. Many organisms have adapted to their living environment producing extremely efficient materials and structures exhibiting optimized mechanical, thermal, optical properties, which current technology is often unable to reproduce. These properties are often achieved using hierarchical structures spanning macro, meso, micro, and nanoscales, widely observed in many natural materials like wood, bone, spider silk and sponges. Thus far, bioinspired approaches have been successful in identifying optimized structures in terms of quasi-static mechanical properties, such as strength, toughness, adhesion, but comparatively little work has been done as far as dynamic ones are concerned (e.g. vibration damping, noise insulation, sound amplification, etc.). In particular, relatively limited

31 knowledge currently exists on how hierarchical structure can play a role in the optimization of  
32 natural structures, although concurrent length scales no doubt allow to address multiple  
33 frequency ranges. Here, we review the main work that has been done in the field of structural  
34 optimization for dynamic mechanical properties, highlighting some common traits and  
35 strategies in different biological systems. We also discuss the relevance to bioinspired  
36 materials, in particular in the field of phononic crystals and metamaterials, and the potential of  
37 exploiting natural designs for technological applications.

38

39

## 40        **1. Introduction**

41

42    It is well known that engineering materials such as metals or fibre-reinforced plastics are  
43    characterized by high stiffness at the expense of toughness. In particular, these materials do not  
44    efficiently dissipate energy via vibration damping. On the other hand, particularly compliant  
45    materials, such as rubbers and soft polymers, perform well as dampers, but lack in stiffness<sup>1,2</sup>.  
46    In this context, biological natural materials such as wood, bone, and seashells, to cite a few  
47    examples, represent excellent examples of composite materials possessing both high stiffness  
48    and high damping, and thus combine properties that are generally mutually exclusive. This  
49    exceptional behaviour derives from an evolutionary optimization process over millions of  
50    years, driven towards specific functionalities, where the natural rule of survival of the fittest  
51    has led to the continuous improvement of biological structure and organization. For instance,  
52    spider silk, bone, enamel, limpet teeth are examples of materials that combine high specific  
53    strength and stiffness with outstanding toughness and flaw resistance<sup>3-8</sup>. In these examples, a  
54    hierarchical architecture has often been proved to be the responsible for many energy  
55    dissipation and crack deflection mechanisms over various size scales, simultaneously  
56    contributing to exceptional toughness<sup>2</sup>. Given these numerous examples and the related  
57    interesting properties, the rich research field of biomimetics has emerged, with the aim of  
58    drawing inspiration from natural structures and implementing them in artificial systems, to  
59    bring progress to many technological domains.

60    Despite rapid progress in the field, studies in biomechanics and biomimetics linking material  
61    structure to function have mainly been limited to the quasistatic regime, while the dynamic  
62    properties of these materials have been somewhat less investigated, although notable examples  
63    of impact tolerance (e.g., the bombardier beetle's explosion chamber<sup>9</sup>) or vibration damping  
64    (e.g., the woodpecker skull<sup>10</sup>) have been studied. In fact, the first attempt to analyse biological

65 vibration isolation mechanisms in the woodpecker date as far back as 1959, when Sielmann<sup>11</sup>  
66 found, through dissection and observation, that the cartilage in sutures in its skull have the  
67 effect of buffering and absorbing vibration<sup>11</sup>. Furthermore, recent studies have shown that  
68 structural hierarchy, which is typical of biological materials, can enhance the performance of  
69 artificial metamaterials<sup>12,13</sup>

70 As confirmed by these examples, it is reasonable to assume that biological structures whose  
71 main function is vibration and impact damping, sound filtering and focusing, transmission of  
72 vibrations, etc., have also been optimized through evolution, and that it is possible to look for  
73 inspiration in Nature for technological applications based on these properties. Based on this  
74 assumption, a growing interest in the superior vibration attenuation properties of biological  
75 systems has emerged, and nowadays, applications such as bio-inspired dampers are beginning  
76 to be used in the protection of precision equipment and the improvement of product comfort<sup>14</sup>.  
77 Motivated by this emerging field of research, we provide here a review of some of the main  
78 biological systems of interest for their dynamic properties, focusing on the role of structural  
79 architecture for the achievement of superior performance.

80

## 81 **2. Impact resistant structures**

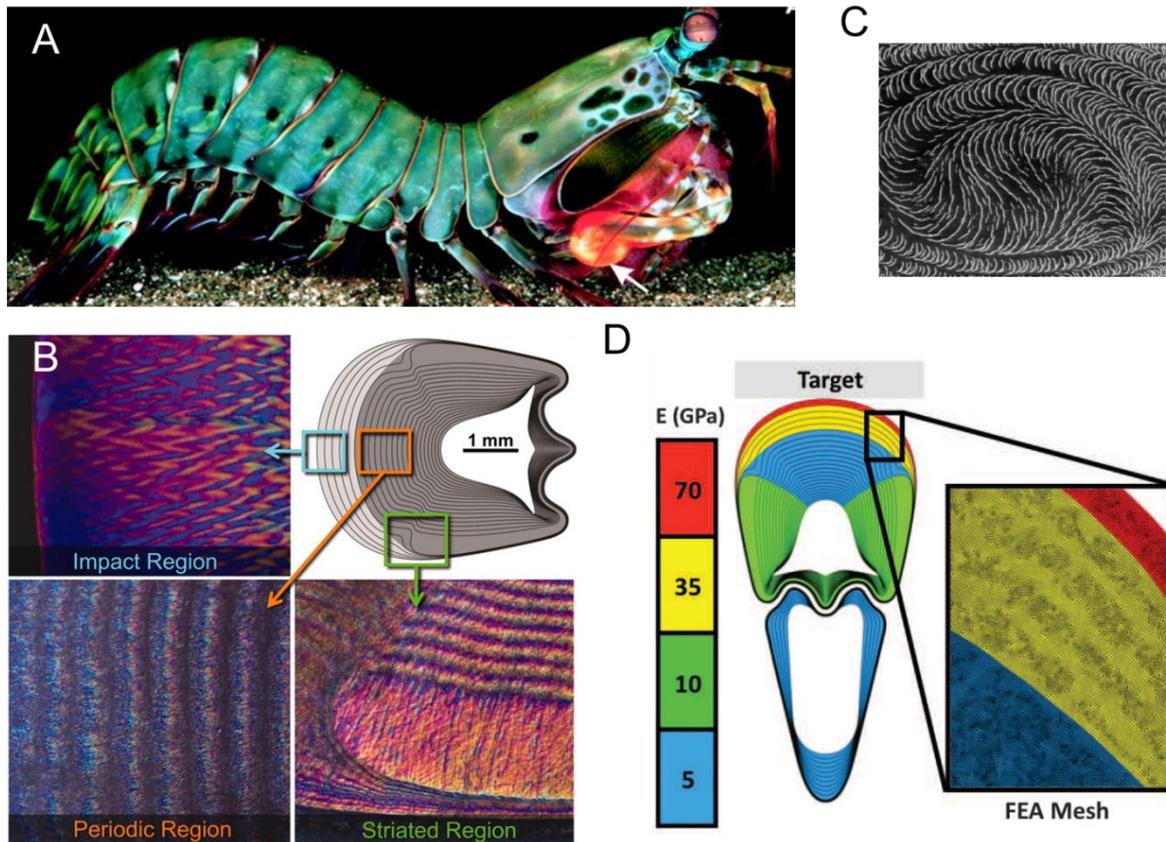
### 82 **2.1 Mantis shrimp**

83 Probably the most well-known example of impact resistant structure in Nature is the  
84 stomatopod dactyl club. The mantis shrimp (*Odontodactylus scyllarus*) is a crustacean with a  
85 hammer-like club that can smash prey (mainly shells) with very high velocity impacts<sup>15-17</sup>,  
86 reaching accelerations of up to 10000 g, and even generating cavitation in the water<sup>18</sup>. To  
87 sustain repeated impacts without failing, the claw requires extreme stiffness, toughness and

88 impact damping, and has emerged as one of the main biological systems that epitomizes  
89 biological optimization for impact damage tolerance <sup>19</sup>.

90 The exceptional impact tolerance is obtained thanks to the graded multiphase composition and  
91 structural organization of three different regions in the claw (Figure 1). The impact region, or  
92 striking surface, is dominated by oriented mineral crystals (hydroxyapatite), arranged so that  
93 they form pillars perpendicular to the striking surface. A second region called the “periodic  
94 region” backs up the impact zone and is mainly constituted by chitosan. This area, which lies  
95 just beneath the impact zone, is stacked at different (helical) orientations, generating crack  
96 stopping and deviation. Thus, the structure consists of a multiphase composite of oriented stiff  
97 (crystalline hydroxyapatite) and soft (amorphous calcium phosphate and carbonate), with a  
98 highly expanded helical organization of the fibrillar chitinous organic matrix, leading to  
99 effective damping of high-energy loading events <sup>19,20</sup>. The impact surface region of the dactyl  
100 club also exhibits a quasi-plastic contact response due to interfacial sliding and rotation of  
101 fluorapatite nanorods, leading to localized yielding and enhanced energy damping <sup>21</sup>.

102 Interestingly, it has been found that the mantis shrimp also displays another highly efficient  
103 impact damping structure, since it has evolved a specialized shield in its tail segment called a  
104 telson, which absorbs the blows from other shrimps during ritualized fighting<sup>22</sup>. The telson is  
105 a multiscale structure with a concave macromorphology, ridges on the outside and a well-  
106 defined pitch-graded helical fibrous micro-architecture on the inside, which also provides  
107 optimized damage tolerance <sup>23,24</sup>.



108

109 *Figure 1: A) Peacock mantis shrimp, with highlighted raptorial dactyl clubs to strike hard*  
 110 *objects (adapted from <sup>18</sup>); B) Morphological features of the clubs, in cross-section view,*  
 111 *divided in an impact region, a periodic region and a striated region; C) Scanning electron*  
 112 *micrograph of the coronal cross-section, showing reinforcing fibre helicoidal arrangement;*  
 113 *D) schematic of a Finite Element model accounting for graded material properties (adapted*  
 114 *from <sup>19</sup>).*

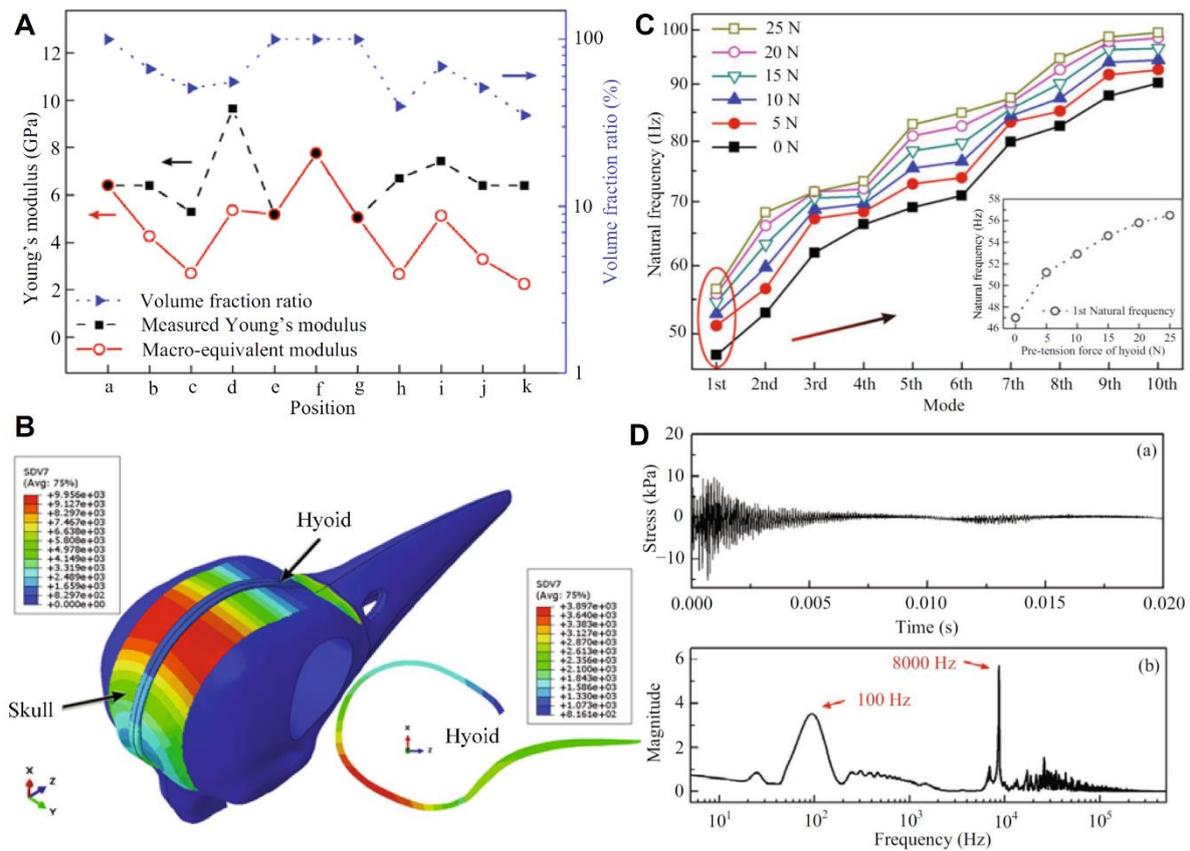
115

## 116 2.2 Woodpecker skull

117 Another well-known example in Nature of a highly impact-resistant system is that of the  
 118 woodpecker skull and beak, which repeatedly strikes wooden surfaces in trees at a frequency  
 119 of about 20 Hz, a speed of up to 7 m/s, and can reach accelerations of the order of 1200 g, while  
 120 avoiding brain injury <sup>10,25</sup>. This structure has been widely studied to draw inspiration for

121 impact-attenuation and shock-absorbing applications and biomimetic isolation <sup>14</sup>. Limiting our  
122 observations to the head, and neglecting the body, feathers, and feet (which could also play a  
123 role), the woodpecker emerges as a very complex and rich system, from the mechanical and  
124 structural point of view at different spatial scales: macro-, micro- and nanoscale. The head is  
125 mainly formed by the beak, hyoid bone, skull, muscles, ligaments, and brain <sup>26</sup>.

126 Several groups have investigated the mechanical behaviour of the woodpecker using finite  
127 element analysis <sup>26-32</sup>. Generally, the models are based on the images obtained by X-ray  
128 computed tomography (CT) scans. The stress distribution due to the impacts due to pecking is  
129 investigated. In some of these studies, the results are also compared with *in vivo* experiments,  
130 where the pecking force is measured by using force sensors and compared with that in other  
131 birds <sup>27</sup>. Zhu et al. <sup>31</sup> measured the Young’s modulus of the skull, finding a periodic spatial  
132 variation, as reported in Figure 2A. Moreover, they performed a modal analysis on the skull by  
133 using a finite element model (Figure 2B), based on CT scan images, and determining the first  
134 ten natural frequencies, as shown in Figure 2C. The largest amplitude frequency components  
135 appear at 100 Hz and 8 kHz, which are well separated from the working frequency (around 20  
136 Hz) and the natural frequencies (as derived in simulations), thus ensuring protection of the  
137 brain from injury.



138

139 *Figure 2 : Vibration attenuation in the woodpecker skull (adapted from <sup>31</sup>). A): Volume fraction*  
 140 *ratio of skull bone, local measured modulus, and macro-equivalent modulus around the skull.*  
 141 *B): 3D finite-element model of the skull and hyoid bone, with spatial variation of the Young's*  
 142 *modulus in the skull. C): first ten modes of the skull under a pre-tension on the hyoid in the*  
 143 *range 0-25 N. D), upper panel: stress wave at a brain location under impact direction; lower*  
 144 *panel: stress spectrum in the frequency domain obtained by FFT.*

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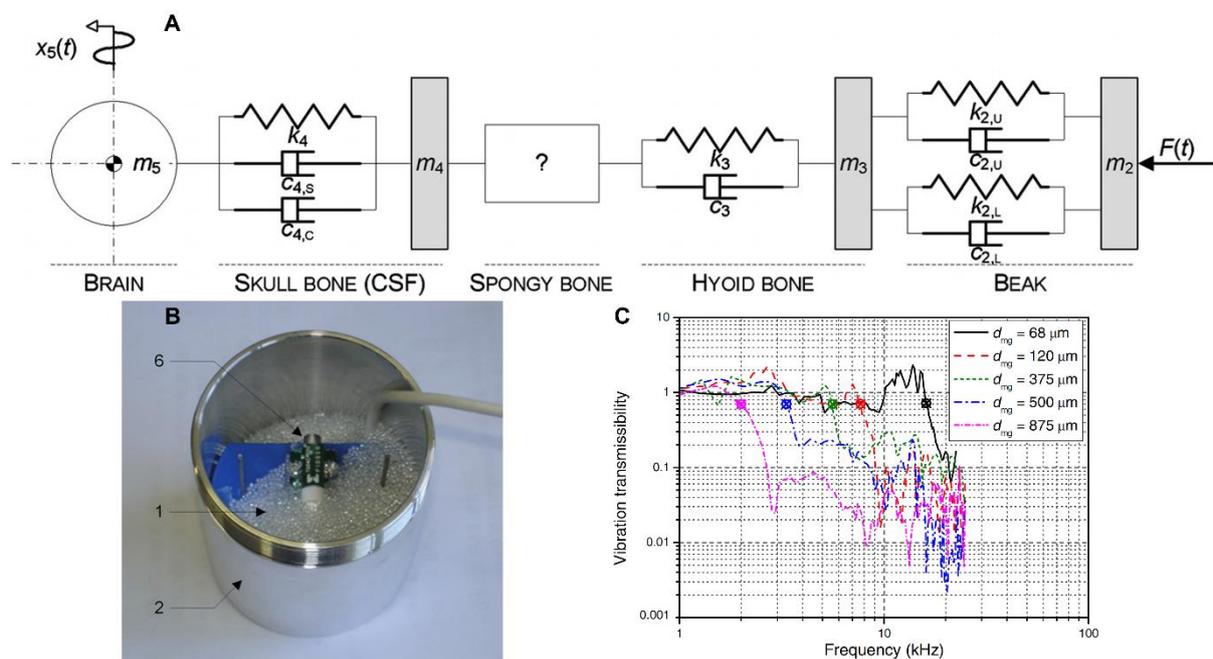
146 Although the results from different groups are not always in agreement, most researchers  
 147 conclude that the shape of the skull, its microstructure and material composition are all relevant  
 148 for the exceptional impact-attenuation properties in woodpeckers <sup>10</sup>. In particular, a grading in  
 149 the bone porosity and mechanical properties is particularly important in damping high  
 150 frequency vibrations, which can be particularly harmful <sup>33</sup>. Many papers also point out the

151 importance of the hyoid bone, very peculiar in woodpeckers, in the shock-absorption  
152 capability<sup>34</sup>. The hyoid is much longer than in other birds and wraps the skull until the eye  
153 sockets, forming a sort of safety belt around the skull. A specific study of the hyoid bone has  
154 been carried out by Jung et al. <sup>34</sup>, who performed a macro- and micro-structural analysis of the  
155 hyoid apparatus and hyoid bones. The authors developed a 3D model of the hyoid which they  
156 showed it to be formed by four main parts connected by three joints. Interestingly, by  
157 performing nanoindentation measurements, they also showed that it features a stiffer, internal  
158 region surrounded by a softer, porous outer region which could play an important role in  
159 dissipating the energy during pecking. Another important issue is the relative contribution of  
160 the upper and lower beaks in the stress wave attenuation <sup>27,35</sup> which is most probably dissipated  
161 through the body <sup>32</sup>.

162 Yoon and Park <sup>10</sup> showed that simple allometric scaling is not sufficient to explain the shock-  
163 absorbing properties of the woodpecker. Furthermore, they investigated its behaviour by using  
164 a lumped element model including masses, springs, and dampers, as shown in Figure 3A. Given  
165 the difficulty in modelling the complexity of the sponge-like bone within the skull with lumped  
166 elements, the authors characterized its behaviour by using an empirical method consisting of  
167 close-packed SiO<sub>2</sub> microglasses of different diameter (Figure 3B). The vibration  
168 transmissibility shows that the porous structure absorbs excitations with a higher frequency  
169 than a cut-off frequency which is determined by the diameter of the glass microspheres, as  
170 reported in Figure 3C.

171 Lee et al. <sup>33</sup> reported a detailed analysis on the mechanical properties of the beak, showing that  
172 the keratin scales are more elongated than in other birds and the waviness of the sutures  
173 between them is also higher than for other birds (1 for woodpecker, 0.3 for chicken and 0.05  
174 for toucan), most probably to favour energy dissipation due to the impact. Raut et al. <sup>36</sup> designed  
175 flexural waveguides with a sinusoidal depth variation inspired by the suture geometry of the

176 woodpecker beak which were tested by finite element analysis. The suture geometry helps  
 177 reducing the group speeds of the elastic wave propagation whereas the presence of a  
 178 viscoelastic material, as is the case for collagen in the beak sutures, significantly attenuates the  
 179 wave amplitudes, suggesting a promising structure for applications in impact mitigation.  
 180 Garland et al.<sup>37</sup> took inspiration from the same mechanism of the sliding keratin scales in the  
 181 beak to design friction metamaterials for energy adsorption.



182

183 *Figure 3 : Modelling of vibration attenuation in the woodpecker skull (adapted from<sup>10</sup>). A):*  
 184 *lumped-elements model of the head of a woodpecker. B): empirical model of the spongy bone*  
 185 *by means of an aluminium enclosure filled with glass microspheres. C): vibration*  
 186 *transmissibility as a function of frequency for different diameters of the SiO<sub>2</sub> microspheres.*

187

### 188 2.3 Seashells

189 Seashells are rigid biological structures that are considered to be ideally designed for  
 190 mechanical protection, and they are now viewed as a source of inspiration in biomimetics<sup>38,39</sup>.

191 A seashell is essentially a hard ceramic layer that covers the delicate tissues of molluscs. Many  
192 gastropod and bivalve shells have two layers: a calcite outer layer and an iridescent nacre inner  
193 layer. Calcite is a prismatic ceramic material composed of strong yet brittle calcium carbonate  
194 ( $\text{CaCO}_3$ ). Nacre, on the other hand, is a tough and pliable substance that deforms significantly  
195 before collapsing <sup>40</sup>. It is considered that a protective structure that combines a hard layer on  
196 the surface with a tougher, more ductile layer on the interior optimizes the impact damping  
197 properties <sup>39-41</sup>. When a seashell is exposed to a concentrated stress, such as a predator's bite,  
198 the hard ceramic covering resists penetration while the interior layer absorbs mechanical  
199 deformation energy. Overloading can cause the brittle calcite layer to fracture, causing cracks  
200 to spread into the soft tissue of the mollusc. Experiments have demonstrated that the thick  
201 nacreous layer can slow and eventually halt such fractures, delaying ultimate shell collapse.  
202 Although a significant amount of research has been performed on the structure and  
203 characteristics of nacre and calcite, there has been little research done on how these two  
204 materials interact in real shells. While there is evidence that nacre is tuned for toughness and  
205 energy absorption, little is known about how the shell structure fully utilizes its basic  
206 constituents, calcite, and nacre.

207 One method employed to analyse the geometry of the shell at the macroscale, while accounting  
208 for the micromechanics of the nacreous layer, is to adopt multiscale modelling and optimization  
209 <sup>39</sup>. Different failure modes are possible depending on the geometry of the shell. On the other  
210 hand, according to optimization procedures, when two failure modes in different layers  
211 coincide, the shell performs best in avoiding sharp penetration. To reduce stress concentrations,  
212 the shell construction fully leverages the material's capabilities and distributes stress over two  
213 different zones. Furthermore, instead of converging to a single point, all parameters converge  
214 to a restricted range inside the design space.

215 According to the experiments done on the two red abalone shells <sup>39,42</sup> the actual seashell  
216 arranges its microstructure design to fully utilize its materials and delay failure, a result that is  
217 also obtained through optimization. The crack propagates over the thickness of the shell in  
218 three different failure situations. Furthermore, the seashell, which is constructed of standard  
219 ceramic material, can resist up to 1900 N when loaded with a sharp indenter, which is an  
220 impressive load level given its size and structure.

221

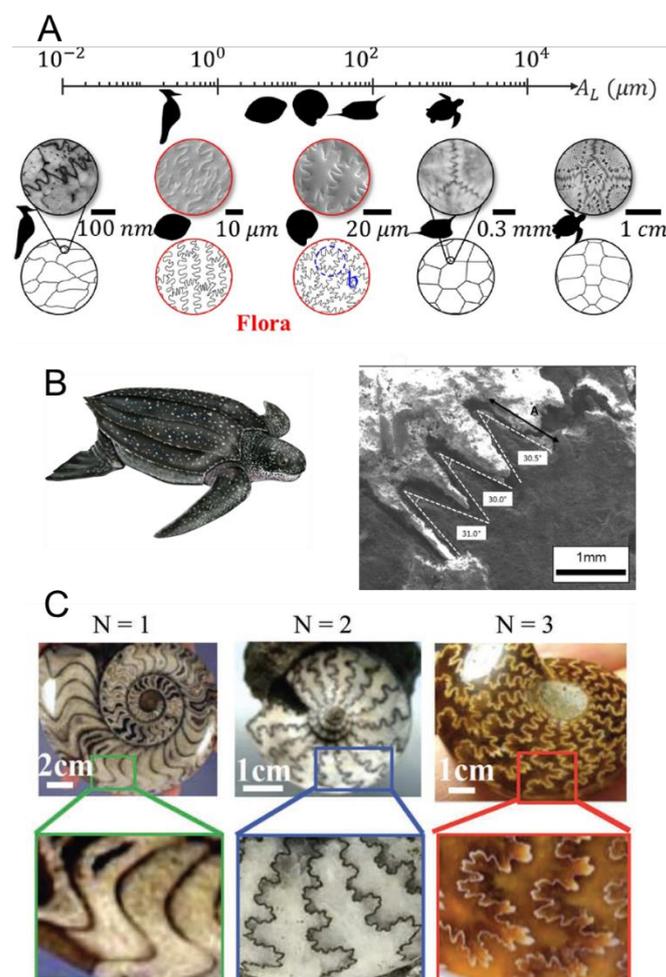
## 222       **2.4 Suture joints**

223 Suture joints with different geometries are commonly found in biology from micro to macro  
224 length scales (Figure 4A) <sup>43</sup>. Examples include the carapace of the turtle <sup>44,45</sup>, the woodpecker  
225 beak <sup>33</sup>, the armoured carapace of the box fish <sup>8,46</sup>, the cranium <sup>47</sup>, the seedcoat of the *Portulaca*  
226 *oleracea* <sup>48</sup> and *Panicum miliaceum* <sup>49</sup>, the diatom *Ellerbeckia arenaria* <sup>50</sup> and the ammonite  
227 fossil shells <sup>51</sup>, among others.

228 In the aforementioned systems, the suture joint architecture, where different interdigitating stiff  
229 components, i.e., the teeth, are joined by a thin compliant seam, i.e., the interface layer, allows  
230 a high level of flexibility and is the key factor for the accomplishment of biological vital  
231 functions such as respiration, growth, locomotion and predatory protection <sup>52-54</sup>. Also, from a  
232 mechanical point of view, it has been demonstrated computationally and/or experimentally that  
233 this particular configuration allows an excellent balance of stiffness, strength, toughness,  
234 energy dissipation and a more efficient way to bear and transmit loads <sup>54-58</sup>.

235 Several existing studies confirm this aspect. Among others <sup>53,59</sup>, where, in the case of cranial  
236 sutures, it emerges that an increased level of interdigitation, found among different mammalian  
237 species, leads to an increase in the suture's bending strength and energy storage. Emblematic  
238 is the case of the leatherback sea turtle (Figure 4B), a unique specie of sea turtle having the  
239 capacity to dive to a depth of 1200 m <sup>60</sup>. This is due to the particular design of the turtle's

240 carapace, where an assemblage of bony plates interconnected with collagen fibres in a suture-  
 241 like arrangement is covered by a soft and stretchable skin. As reported in <sup>60</sup>, the combination  
 242 of these two elements provides a significant amount of flexibility under high hydrostatic  
 243 pressure as well as exceptional mechanical functionality in terms of stiffness, strength and  
 244 toughness, the collagenous interfaces being an efficient crack arrester. In addition, the study in  
 245 <sup>61</sup> explained not only how the high sinuosity and complexity of the suture lines in ammonites  
 246 (Figure 4C) are the result of an evolutionary response to the hydrostatic pressure, but also that  
 247 the stress, displacements and deformations significantly decrease with the level of complexity.  
 248 A similar result is also obtained in <sup>62</sup>, which seeks to clarify the functional significance of the  
 249 complex suture pattern in ammonites.



251 *Figure 4: Biological systems with suture tessellation: A) examples from Flora and Fauna*  
252 *(adapted from <sup>58</sup>); B) the leatherback turtle shell (adapted from <sup>60</sup>); C) Hierarchical sutures of*  
253 *increasing complexity found in ammonites (adapted from <sup>63</sup>).*

254

## 255 **2.5 Bone**

256 Bone has an extremely complex structure, encompassing seven levels of hierarchical  
257 organization, from nanocomposite mineralized collagen fibril upwards <sup>64</sup>. Based on this  
258 building block, varying mineral contents and microstructure allow to construct various types  
259 of tissue for different functionalities, e.g. withstanding tension, resisting impacts, supporting  
260 bending and compression. Human cortical bone consists of cylindrical Haversian canals, each  
261 surrounded by multilayers of bone lamellae  $\sim 10\ \mu\text{m}$  thick, which have a rotated plywood  
262 structure in which mineralized collagen fibrils ( $\sim 100\ \text{nm}$  in diameter) rotate from the transverse  
263 direction to the longitudinal direction across five sublayers. The fibrils are cemented together  
264 by extrafibrillar minerals and noncollagenous proteins <sup>6</sup>. Hierarchical structure plays a  
265 fundamental role in bone’s exceptional mechanical properties. Bone’s trabecular structure and  
266 hierarchy is responsible for its unmatched tensile strength, anisotropy, self-healing and  
267 lightweight properties <sup>64,65</sup>, but also dynamic properties like impact damping <sup>66,67</sup>. Bio-  
268 inspiration from bone structures has been exploited to seek enhanced static properties, strength  
269 and toughness <sup>68</sup>, but relatively limited works have investigated it for dynamic applications.  
270 Ultrasonic wave measurements in bone to measure propagating velocity and attenuation have  
271 been performed for many years in various settings <sup>69</sup>, including “wet” bone <sup>70</sup>, showing that  
272 hydration is fundamental in defining dynamic properties. Studies in ultrasonics have typically  
273 focused on non-destructive evaluation of the bone structure <sup>71,72</sup>. It has also been shown that  
274 modal damping can be useful to detect bone integrity and osteoporosis <sup>73</sup>, also supported by  
275 ultrasonic wave propagation simulations in cancellous bone <sup>74</sup>. Dynamic measurement methods

276 assessing modal damping have also been used to validate bone models <sup>75</sup>. In terms of  
277 bioinspiration, the porous structure of trabecular (rod or truss-like structure) or velar bone (sail-  
278 like structure) is of particular interest, due to its lightweight and impact damping  
279 characteristics. Most of the work on such 3D frame structures <sup>76</sup> has addressed static properties  
280 <sup>77</sup>. However, recent articles have also addressed wave propagation <sup>78,79</sup> and impact loading <sup>80</sup>.  
281 Frame structures offer a convenient way to approximate trabecula using truss-like structures,  
282 inspired by the well-known Bravais lattices <sup>81</sup>. The implementation of such lattices could pave  
283 the way to a simplified model of the bone structure, where the joints can be collapsed to point-  
284 like connections and the number of degrees of freedom can be drastically reduced.

285

## 286 **2.6 Attenuation of surface gravity waves by aquatic plants**

287 If one considers damping of low frequency vibrations over long timescales, one can look to  
288 natural barriers that allow to prevent or delay coastal erosion, and the destruction of the  
289 corresponding habitats. One such example is the *Posidonia Oceanica*, a flowering aquatic plant  
290 endemic of the Mediterranean Sea, which aggregates in large meadows forming a  
291 Mediterranean habitat. This macrophyte has evolved by angiosperms typical of the intertidal  
292 zone and displays features similar to that of terrestrial plants: it has roots and very flexible thin  
293 leaves of about 1 mm thickness and 1 cm width, without significant shape variations along the  
294 leaf length. The anchoring to sandy bottoms is provided by the horizontal growth of the  
295 rhizomes, which also grow in vertical. The leaf length varies throughout a year due to the  
296 seasonal cycle and the marine climatic conditions and can vary as much as 0.3 m in winter and  
297 1 m in summer.

298 The effects of seagrasses on unidirectional flows are well studied at different scales in the field  
299 and in laboratory flumes and in numerical studies, while much less is known about the  
300 interaction between seagrass and waves. Wave attenuation due to *Posidonia* and flow

301 conditions over and within vegetation fields have been investigated experimentally <sup>82</sup> and  
302 numerically <sup>83</sup>. It was found that the *Posidonia* is a good natural candidate for dissipating  
303 surface gravity waves in coastal regions. The study assessed quantitatively the physical value  
304 of the seagrass ecosystem restoration in this area, also opening new routes of action towards a  
305 resilient, efficient, and sustainable solution to coastal erosion. Other natural barriers to water  
306 wave propagation, other than vegetation such as the *Posidonia*, exist and are fundamental. For  
307 example, ice covering the surface of the ocean around Antarctica and the Arctic Sea represents  
308 an important wave attenuation medium for slowing down the disintegration of the polar ice  
309 shelves. Quantitative measurements of such attenuation have been recently obtained through  
310 stereoscopic measurements <sup>84</sup>.

311

## 312 **2.7 Attenuation of surface seismic waves by trees**

313 Further recent evidence of natural barriers for large scale vibrations is the attenuation of seismic  
314 surface waves achieved by trees <sup>85</sup>. The vibrations are transmitted to the trees through two  
315 coupling mechanisms, associated with two distinct vibrational modes. At high frequency  
316 (around 50 Hz), the longitudinal motion of the trees perpendicular to the soil surface is  
317 responsible for a high scattering effect on the surface wave and a hybridization to bulk shear  
318 waves. This means that the soil surface is mechanically blocked by the trees around those  
319 frequencies. In the low frequency range, below 1 Hz, the flexural motion of the trees induces  
320 different coupling effects on surface wave propagation. The flexural motion creates a bending  
321 moment at the soil/tree interface with can create long range coupling phenomena. Flexural  
322 resonances for the trees generally fall in the same frequency band as the micro-seismic noise  
323 produced by the ocean (between 0.3 and 0.8 Hz, detectable all over the world), which suggest  
324 a potential use of these frequencies to monitor the growth process of the trees and the evolution  
325 of their surrounding environment <sup>86</sup>.

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## 2.8 Conclusions on impact resistant structures

From the examples seen in the previous Sections, it emerges that impact-resistant biological structures have a number of common features. The first is related to a complex hierarchical architecture spanning from the nano- to the macro-scale, as in the case of the woodpecker skull or suture joints. Hierarchy, in particular, allows the system to be multifunctional and to accomplish both biological and mechanical functions in an optimized fashion. Additionally, in terms of dynamical behaviour, hierarchical structure allows to simultaneously address various size scales and therefore frequency ranges. The second characteristic is heterogeneity, enabling natural materials to combine the desirable properties of their building blocks, which are typically light, widely occurring materials: polymeric and ceramic for mineralized systems or crystalline and amorphous phases for non-mineralized ones. Heterogeneity allows Nature to create hierarchical composites that perform significantly better than the sum of their parts. Typically, the stiffer phase provides rigidity and strength while the soft phase increases ductility. This distinctive quality leads, for example, to the exceptional impact damping properties of the seashells described above. Another common trait of impact-resistant biological structures is porosity, which plays an important role in dissipating impact energy and, at the same time, allows to decrease the overall weight of the system. Finally, the occurrence of complex geometrical features is a characteristic commonly found in impact-resistant structures in biology. The high sinuosity of the suture lines in ammonites or the helicoidal organization of the mantis shrimp’s dactyl clubs are examples of this, and direct evidence of their continually optimized nature, deriving from adaptation to the form that best achieves the required function.

### 351        **3. Sensing and predation**

#### 352        **3.1 Spider webs**

353        Of all the natural structures that inspire and fascinate humankind, spider orb webs play a  
354        particularly central role and have been a source of interest and inspiration since ancient times.  
355        Spiders are able to make an extraordinary use of different types of silks to build webs which  
356        are the result of evolutionary adaptation and can deliver a compromise between many distinct  
357        requirements <sup>87</sup>, such as enabling trapping and localizing prey, detecting the presence of  
358        potential predators, and serving as channels for intraspecific communication <sup>88</sup>. The variety of  
359        structures, compositions, and functions has led to the development of a large amount of  
360        literature on spider silks and webs <sup>88-90</sup> and their possible bio-inspired artificial counterparts  
361        <sup>91,92</sup>.

362        The overall mechanical properties of spider orb webs emerge from the interaction between at  
363        least five types of silk <sup>3,93</sup>, each with a distinct function in the web. The most important  
364        vibration-transmitting elements are made from the strong radial silk <sup>94</sup>, which also absorbs the  
365        kinetic energy of prey <sup>95,96</sup> while sticky spiral threads, covered with glue, are used to provide  
366        adhesion to retain the prey <sup>97,98</sup>. Moreover, junctions within the webs can be composed of two  
367        different types of silk <sup>93</sup>: the strong and stiff piriform silk that provides strength to the  
368        anchorages <sup>99,100</sup> (Figure 5A-B), and the aggregate silk that minimizes damage after impacts  
369        <sup>5,93</sup> (Figure 5C). The mechanical synergy of such systems is therefore due to the mechanical  
370        response of the junctions <sup>101</sup>, the constitutive laws of different types of silks, and the geometry  
371        of the webs <sup>5</sup>. The richness of these features, which are still the subject of many studies, have  
372        already inspired technologies with different goals in various scientific fields <sup>102-104</sup>.

373        Spider orb webs are able to stop prey while minimizing the damage after impacts, thus  
374        maintaining their functionality <sup>5</sup>, partially exploiting the coupling with aerodynamic damping

375 that follows prey impacts <sup>96</sup>. This makes orb webs efficient structures for capturing fast-moving  
376 prey <sup>105</sup>, whose location can then be detected due to the vibrational properties of the orb web.  
377 Efficiency in detecting prey by the spider is mediated by the transmission of signals in the  
378 webs, which needs to carry sufficient information for the prey to be located <sup>106</sup>. Using laser  
379 vibrometry, it has been demonstrated that the radial threads are less prone to attenuating the  
380 propagation of the vibrations compared to the spirals <sup>87</sup>, due to their stiffer nature <sup>107</sup>, allowing  
381 them to efficiently transmit the entire frequency range from 1 to 10 kHz.

382 Spiral threads can undergo several types of motion, including: (i) transverse (perpendicular to  
383 both the thread and the plane of the web) (ii) lateral (perpendicular to the thread but in the plane  
384 of the web), and (iii) longitudinal (along with the thread axis), thus yielding complex frequency  
385 response characteristics <sup>108–110</sup>. Distinct wave speeds are also associated with each type of  
386 vibration, i.e., transverse wave speed is determined by string tension and mass density, while  
387 longitudinal wave speed is linked to mass density and stiffness <sup>111</sup>. With the addition of more  
388 reinforcing threads due to the multiple lifeline addition by the spider, the orb webs appears to  
389 maintain signal transmission fidelity <sup>112</sup>. This provides further evidence of the impressive  
390 optimization achieved in these natural structures, which balance the trade-offs between  
391 structural and sensory functions.

392 The sonic properties of spider orb webs can also be significantly influenced by pre-stressing,  
393 as demonstrated in the study conducted by Mortimer et al. <sup>113</sup>. Wirth and Barth <sup>114</sup> have shown  
394 that silk thread pre-stress increases with the mass of the spider, considering both inter and intra-  
395 specific variations, and may be used to facilitate the sensing of smaller prey <sup>115</sup>. The pre-tension  
396 in webs can also be strongly influenced by large amplitude vibrations, as demonstrated by  
397 numerical analysis <sup>116</sup>. This dependence has been shown to be stronger if the structure is  
398 damaged, especially in the radial threads <sup>117</sup>.

399 Investigations on the vibration transmission properties of silk have been conducted by  
400 accessing its high-rate stress-strain behaviour using ballistic impacts on *Bombyx mori* silk  
401 (which can be partially compared to spider silk)<sup>118</sup>. Some studies indicated that the capability  
402 of transmitting vibrations is relatively independent of environmental conditions such as  
403 humidity<sup>119,120</sup>, but in general it is expected that they affect the silk Young’s modulus and the  
404 pre-stress level on the fibres, and therefore the speed of sound (i.e., wave propagation speed)  
405 in the material<sup>121–123</sup>. This dependence is one of the reasons why the measurement of the speed  
406 of sound in silk has not produced homogeneous data<sup>109,124,125</sup>, and could provide a possible  
407 degree of freedom for spiders in tuning the vibrational properties of their webs<sup>113,124</sup>.

408 Spider orb webs have proven to be one of the most inspiring systems to design structures able  
409 to manipulate elastic waves. Although many types of webs can be extremely efficient in  
410 detecting and stopping prey<sup>126</sup>, plane structures tend to be preferred when it comes to bio-  
411 inspired systems, due to their simplicity. Metamaterials can be designed exploiting the rich  
412 dynamic response and wave attenuation mechanism of orb webs<sup>127</sup>, based on locally resonant  
413 mechanisms to achieve band gaps in desired frequency ranges<sup>128</sup>, and further optimized to  
414 achieve advanced functionalities<sup>129</sup>. The possibility of designing low-frequency sound  
415 attenuators is also regarded as a common objective in metamaterials design, and spider web-  
416 inspired structures seem to be able to provide lightweight solutions to achieve this goal<sup>130,131</sup>.

### 417 **3.2 Spider sensing**

418 Although many spiders have poor sight, remarkable sensors that make them capable of  
419 interacting with their surroundings have evolved<sup>132</sup>, including hair-shaped air movement  
420 detectors, tactile sensors, and thousands of extremely efficient strain detectors (lyriform organs  
421 such as slit sensilla) capable of transducing mechanical loads into nervous signals embedded  
422 in their exoskeleton<sup>133–135</sup>. Air flow sensors, named trichobothria (Figure 5D), seem to be

423 specifically designed to perceive small air fluctuations induced by flying prey, which are  
424 detectable at a distance of several centimetres <sup>136</sup>. Spiders can process these signals in  
425 milliseconds and jump to catch the prey using only the information about air flow <sup>137</sup>. Although  
426 this could be sufficient to guide the detection of the prey using trichobothria, it could be that  
427 different hair-like structures undergo viscosity-mediated coupling that affects the perception  
428 efficiency. Interestingly, in the range of biologically relevant frequencies (30–300 Hz), viscous  
429 coupling of such hair-like structures is very small <sup>138</sup>. It seems, in particular, that the distance  
430 at which two structures do not interact is about 20 to 50 hair diameters, which is commonly  
431 found in Nature <sup>138,139</sup>. Spiders are also equipped with strain sensors (lyriform organs), which  
432 are slits that occur isolated or in groups (Figure 5E) with a remarkable sensory threshold in  
433 terms of displacement (from 1.4 nm to 30 nm) and corresponding force stimulus (0.01 mN).  
434 Moreover, many of such organs have an exponential stiffening response to stimuli, which  
435 makes them suitable to detect a wide range of vibration amplitudes and frequencies. These  
436 organs act as filters with a typical high-pass behaviour <sup>140</sup> to screen the environmental noise  
437 found in Nature. Despite their remarkable capability in detecting vibration patterns (in  
438 frequencies between 0.1 Hz and several kHz), it is not yet clear how low-frequency signals are  
439 transmitted <sup>141</sup>. In any case, spider impact sensing on orb webs has been shown to be an intricate  
440 mechanism determined by both material properties and web structure <sup>142</sup>.

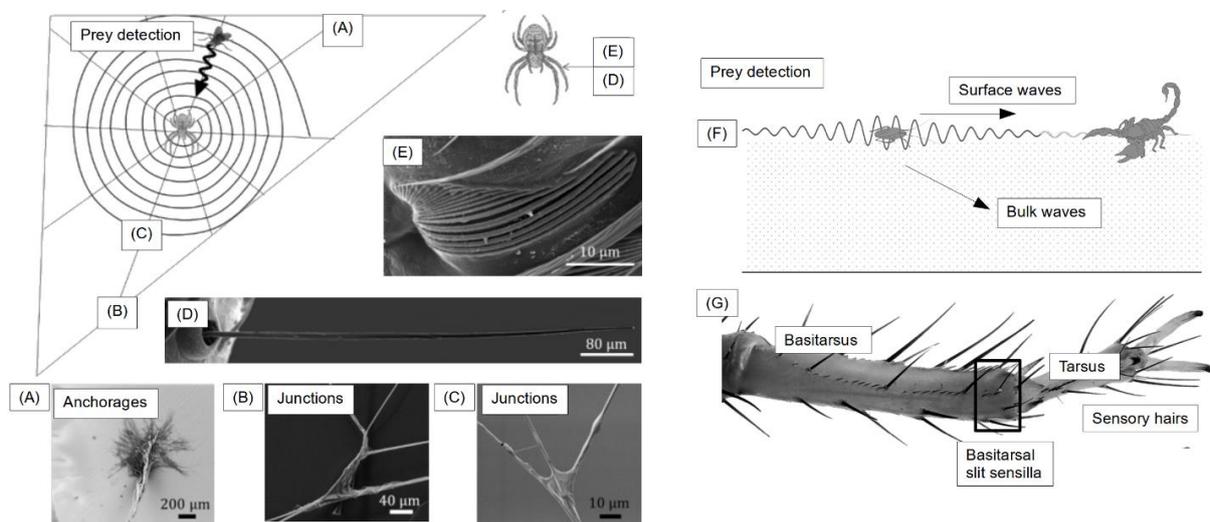
441 The sensing capabilities of spiders have driven the design of bio-inspired solutions in terms of  
442 sensor technology. Materials scientists have designed bio-inspired hair sensors realized to work  
443 both in air <sup>143,144</sup> and water <sup>145</sup>. Furthermore, the lyriform organs have inspired crack-based  
444 strain sensors <sup>146,147</sup>, eventually coupled with the mechanical robustness of spider silk <sup>146</sup>.  
445 Interestingly, these two types of structures (crack and hair sensors) may be combined in a multi-  
446 functional sensor. Results for such a spider-inspired ultrasensitive flexible vibration sensor  
447 demonstrated a sensitivity that outperforms many commercial counterparts <sup>147</sup>.

448 Spider silk threads are also capable of detecting airflows by means of their fluctuation <sup>148</sup>,  
449 providing an incredibly wide range of detectable frequencies, from 1 Hz to 50 kHz. Thus, by  
450 modifying these materials (e.g., making them conductive) it may be possible to produce devices  
451 able to expand the range of human hearing. It is clear, however, that many difficulties remain  
452 to be resolved to scale and fully optimize such bio-inspired solutions. Firstly, the reduction of  
453 the exposed surface can be large due to the need to integrate a sensor in the electronics.  
454 Secondly, wearing and application of the device could mechanically deteriorate its efficiency  
455 during its lifetime. Lastly, an engineering approach is in stark contrast with biological ones. In  
456 this context, a profound breakthrough is needed to achieve high efficiency in the self-assembly  
457 materials at the submicron scale.

### 458       **3.3 Scorpion sensing**

459 Scorpions are arachnids belonging to the *Subphylum Chelicerata* family of the arthropods  
460 (which includes spiders), which have evolved sensory mechanisms specially adapted to  
461 desertic environments <sup>149</sup>. Once structure-borne vibrations are produced in the ground, they  
462 propagate through bulk and surface waves: while the former propagate into the soil at large  
463 speeds and cannot be perceived by surface-dwelling animals, the latter can provide a useful  
464 information propagation channel for various species <sup>150,151</sup>. Sand offers an especially interesting  
465 medium in this regard, since its wave speed and damping are significantly lower than in other  
466 soils, favouring time-domain discrimination and processing <sup>152</sup>. Brownell <sup>153</sup> has shown that  
467 two types of mechanoreceptors can be observed in the *Paruroctonus Mesaensis* desert scorpion  
468 species: (i) sensory hairs on the tarsus, which sense compressional waves, and (ii)  
469 mechanoreceptors located at the slit sensilla, which sense surface waves, thus serving as the  
470 basis for the scorpion's perception of the target direction, performing a role of mechano-  
471 transduction similar to that observed in spiders <sup>154</sup>. Thus, these structures appear to be those  
472 responsible for vibration sensing in scorpions, even though some controversy exists regarding

473 the use of other scorpion appendages for the same purpose <sup>155</sup>. Brownell and Farley have shown  
 474 that this scorpion species can discriminate the vibration source direction by resolving the time  
 475 difference in the activation of the slit sensilla mechano-receptors even for time intervals as  
 476 small as 0.2 ms <sup>156</sup>. The same authors have also shown that for short distances (down to 15  
 477 cm), scorpions can discriminate not only direction but also distance and vibration signal  
 478 intensities, which are means to distinguish between potential prey from potential predators <sup>157</sup>.  
 479 Such underlying phenomena have been used to construct a computer theory that simulates prey-  
 480 localizing behaviour in scorpions <sup>158</sup>, further motivating the development of artificial  
 481 mechanisms based on this approach. Microstructural investigations as the ones performed by  
 482 Wang et al. <sup>159</sup> have demonstrated that the slit sensilla owe their micro-vibration sensing  
 483 properties to their tessellated crack-shaped slits microstructure <sup>160</sup>, further indicating that this  
 484 type of microstructure can serve as a bioinspiration for the design of new mechano-sensing  
 485 devices <sup>146,161</sup>.



486  
 487 *Figure 5: Prey sensing similarities in spiders and scorpions. A) web structure: a typical orb*  
 488 *web of a spider Nuctenea umbratica. The web is built by means of junctions between threads*  
 489 *and surfaces, B) junctions between radial threads, C) and junctions between radial and spiral*  
 490 *threads. A flying prey can be eventually detected by air flow sensors, D) the trichobothria. If the*

491 *prey impacts the web, the vibrational signal will be transmitted mainly by radial threads and*  
492 *be perceived by E) lyriform organs of the spider. Figure adapted from*<sup>93,132</sup>. *F) schematic of*  
493 *scorpion prey detection using surface waves; G) sensory hairs and mechanoreceptors located*  
494 *at the slit sensilla sense surface waves. Adapted from*<sup>159,162</sup>

495

### 496 **3.4 Control of ground-borne sound by mammals**

497 Vibration control in mammals is not restricted to air-borne signals. Many use impacts by  
498 “drumming” parts of their bodies to generate vibrations that propagate in the soil. For example,  
499 foot-drumming patterns may be found in rabbits or elephant to communicate with other  
500 individuals. Unlike in the Cochlea, where the signal is split, and thus analysed, according to its  
501 frequency content, foot-drumming is based on the generation and analysis of complex transient  
502 vibrational patterns. One of the first species identified to use foot-drumming to communicate  
503 is the blind rat<sup>163</sup>. More recent studies have identified the social and environmental monitoring  
504 purposes associated with this communication channel in elephants<sup>164–166</sup>.

505

### 506 **3.5 Anti-predatory structures and strategies**

507 It is thought that the origin of many distinctive morphological and/or behavioural traits of living  
508 organisms is related to the selective pressure exerted by predators<sup>167,168</sup>. Generally, various  
509 defensive strategies can be adopted by organisms to reduce the probability of being attacked  
510 or, if attacked, to increase the chances of survival. The first consists in avoiding detection (i.e.,  
511 *crypsis*), through camouflage, masquerade, *apostatic* selection, subterranean lifestyle or  
512 nocturnality, and deterring predators from attacking (i.e., *aposematism*) by advertising the  
513 presence of strong defences or by signalling their unpalatability by means of warning  
514 coloration, sounds or odours<sup>169</sup>. The second are based on overpowering, outrunning and

515 diverting the assailants’ strikes by creating sensory illusions to manipulate the predator’s  
516 perception<sup>170–172</sup>.

517 Despite being extremely fascinating from an engineering point of view, the effectiveness of the  
518 first type of defensive strategies is restricted mainly to visual phenomena and none of them  
519 work on non-visually oriented predators. However, although rare, several acoustic based  
520 deflection strategies exist in Nature. Most of them are related to one of the most famous  
521 examples of non-visually oriented predators, i.e., echolocating bats (Figure 6A) that rely on  
522 echoes from their sonar cries to determine the position, size and shape of moving objects in  
523 order to avoid obstacles and intercept prey in the environment<sup>168,173–175</sup>.

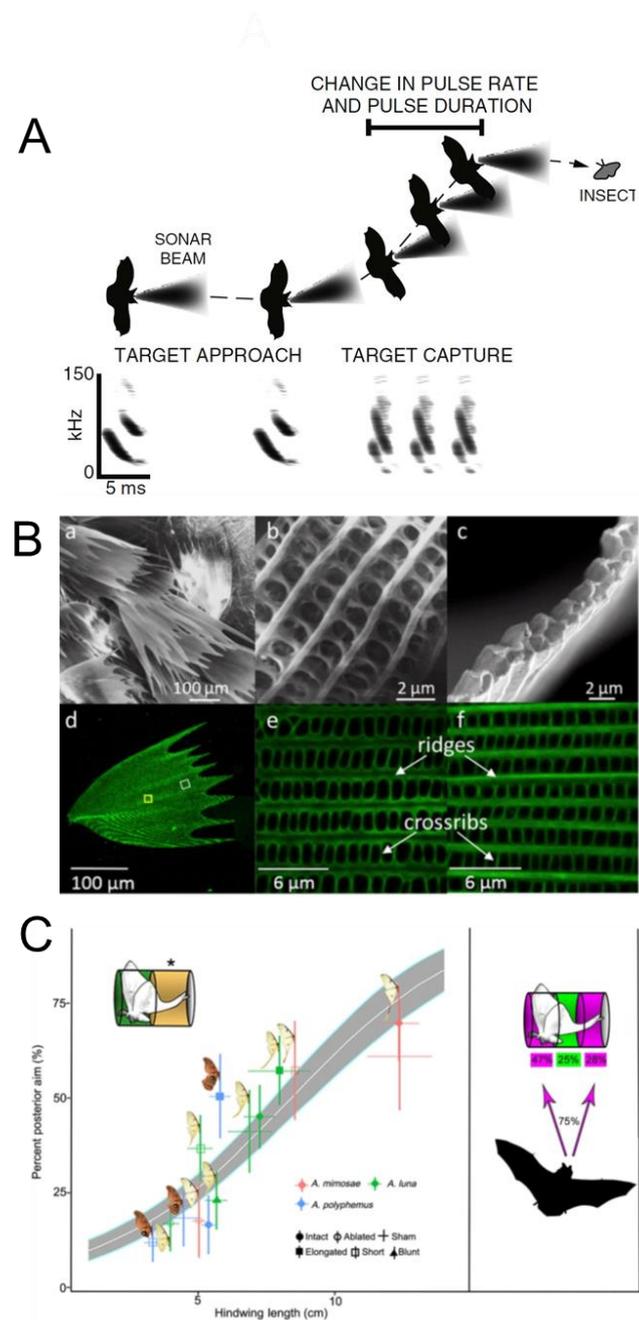
524 The first strategy to avoid detection by bats can be seen in some species of earless moth that,  
525 as a result of millions of years of evolution, developed a passive acoustic camouflage relying  
526 on a particular configuration of both the thorax and the wings. In particular, differently from  
527 the other species of moth which evolved ears to detect the ultrasonic frequencies of  
528 approaching bats or produce, when under attack, ultrasound clicks to startle bats and alert them  
529 to the moth’s toxicity<sup>176–178</sup>, the wings of earless moths are covered with an intricate layer of  
530 scales (Figure 6B) that serve as acoustic camouflage against bat echolocation<sup>177,179</sup>. According  
531 to<sup>177</sup>, each leaf-like shaped scale shows a hierarchical design, from the micro-to the nanoscale,  
532 consisting, at the larger scale, of two highly perforated laminae made of longitudinal ridges of  
533 nanometer size connected by a network of trabeculae pillars. This configuration leads to a  
534 highly porous structure which is able, because of the large proportion of interstitial honeycomb-  
535 like hollows, to absorb the ultrasound frequencies emitted by bats and thus reduce the amount  
536 of sound reflected back as echoes<sup>180</sup>. As a result, the moth partially disappears from the bat’s  
537 biosonar and the distance at which the bat can detect the moth is reduced by 5-6%<sup>179</sup>,  
538 representing a significant survival advantage. In addition, by exploring the vibrational  
539 behaviour of a wing of a *Brunoa alcinoe* moth, researchers discovered that each scale not only

540 behaves like a resonant ultra-sound absorber having the first three resonances in the typical  
541 echolocation frequency range of bats <sup>177</sup>, but also that each one has a different morphology and  
542 resonates at a particular frequency, creating a synergistically broadband absorption <sup>180</sup>. As  
543 reported in <sup>180</sup>, it can be thus said that the complex pattern of scales on moth wings exhibit the  
544 key features of a technological acoustic metamaterial.

545 Another example of an acoustic-based strategy to confuse predators is the long hindwing tail  
546 (Figure 6C) commonly found on luna moths (*Actias luna*). Such tail presents a twist toward the  
547 end and this distinguishing feature, as suggested in <sup>181</sup>, is the key for how the tail creates a sort  
548 of acoustic camouflage against echolocating bats. The tail, in particular, because of its length  
549 and twisted morphology, in reflecting the bat’s sonar calls produces two types of echoic sensory  
550 illusions <sup>181</sup>. The first consists in deflecting the bat’s attacks from the vital parts of the body,  
551 i.e., head and thorax, to this inessential appendage. By using high-speed infrared videography  
552 to analyse the bat-moth interactions, according to the authors, in over half of the interactions,  
553 bats directed the attack at the moth’s tail as the latter created an alternative target distracting  
554 from the principal one, i.e., the moth’s body. Also, by comparing moths with the tail and moths  
555 with the tail ablated, it emerged a survival advantage of about 47%.

556 The second sensory illusion provided by the twisted tail consists in inducing a misleading  
557 echoic target localization that confuses the hunting bats <sup>170,181</sup>. As reported in <sup>181</sup>, the origin of  
558 this effect is the twist located at the end of the tail that creates a sequence of surfaces having  
559 different orientations so that, independently of the inclination of both the incident sound waves  
560 and the fluttering moth, the tail is able to return an echo, complicating and spatially spreading  
561 the overall echoic response of the moth. In addition, the analysis of the overall acoustic return  
562 generated by the wings, body and tail of a Luna moth, revealed an additional survival  
563 contribution of the twisted tail, consisting in a shift of the echoic target centre, i.e., the centre

564 of the echo profile used by the bat to estimate the prey location, away from the moth’s thorax  
 565 181.



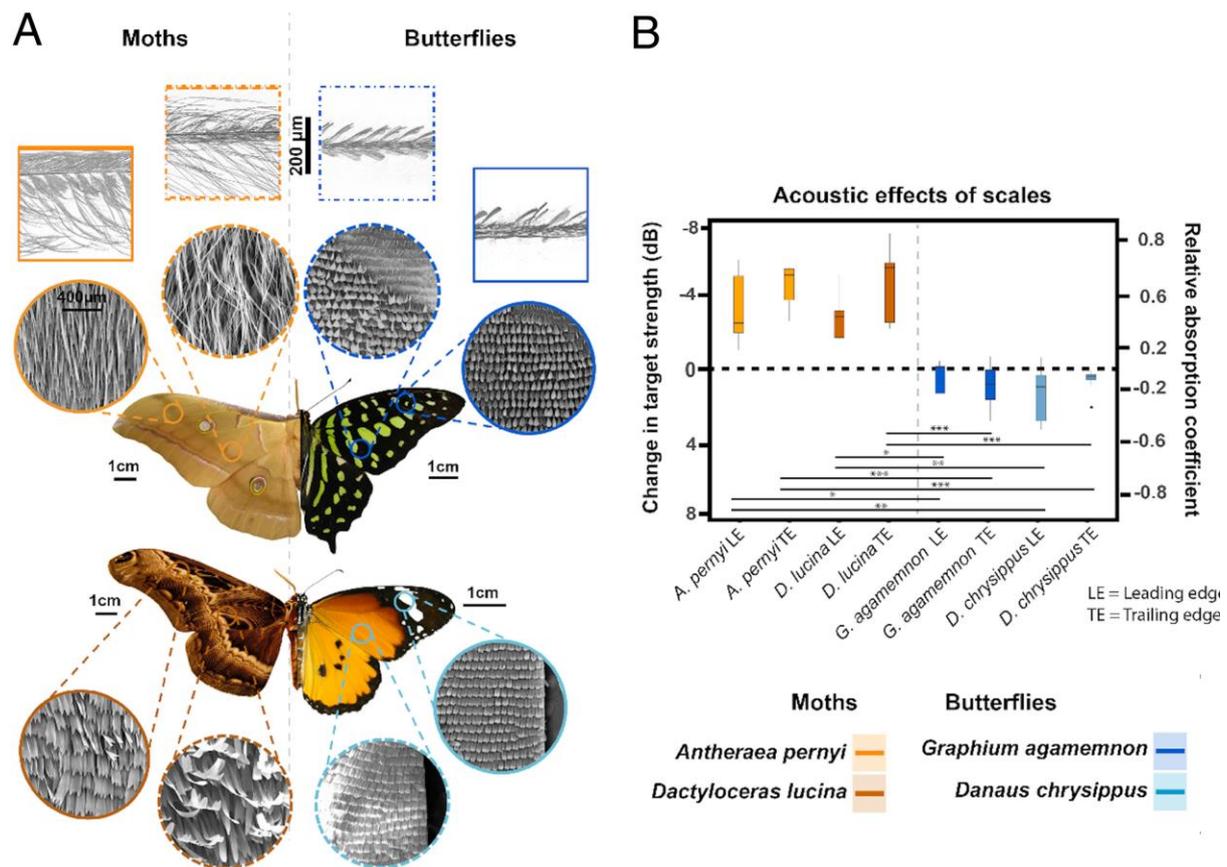
566  
 567 *Figure 6: Anti-predatory strategies. A) The high-resolution 3D acoustic imaging system evolved by*  
 568 *the echolocating bats (adapted from <sup>182</sup>) and the moth’s strategies to avoid being detected: B)*  
 569 *appropriate scale arrangement and structure (adapted from<sup>176</sup>). and C) hindwing tails. Behavioural*  
 570 *analyses reveal that (A) bats aim an increasing proportion of their attacks at the posterior half of the*  
 571 *moth (indicated by yellow cylinder with asterisk) and that (B) bats attacked the first and third sections*

572 *of tailed moths 75% of the time, providing support for the multiple-target illusion. An enlarged echo*  
573 *illusion would likely lead bats to target the hindwing just behind the abdomen of the moth, at the*  
574 *perceived echo centre (highlighted in green); however, bats targeted this region only 25% of the time*  
575 *(adapted from <sup>170</sup>).*

576

577 As previously mentioned, the second type of passive acoustic camouflage developed by earless  
578 moths consists in having much of the thorax covered by hair-like scales (Figure 7A) acting as  
579 a stealth coating against bat biosonar<sup>183–185</sup>. As suggested by<sup>185,186</sup> such thoracic scales create  
580 a dense layer of elongated piliform elements, resembling the lightweight fibrous materials used  
581 in engineering as sound insulators. Their potential as ultrasound absorbers was explored in <sup>185</sup>  
582 by means of tomographic echo images and an average of 67% absorption of the impinging  
583 ultrasound energy emerged. Also, to provide a more in-depth investigation, the authors  
584 employed acoustic tomography to quantify the echo strength of diurnal butterflies that are,  
585 contrary to moths, not a target for bat predation. The results were then used to establish a  
586 comparison with those derived for moths (Figure 7B). Interestingly, the analysis revealed that  
587 the absorptive performance is highly influenced by the scale thickness and density, with the  
588 very thin and less dense scales typical of butterflies that can absorb just a maximum of 20% of  
589 the impinging sound energy. Conversely, the denser and thicker moth’s thorax scales possess  
590 ideal thickness values that allow the absorption of large amounts of bat ultrasonic calls. These  
591 findings are confirmed by <sup>183</sup> where an extended list of references is also provided.

592



593

594 *Figure 7: Tiling patterns and acoustic effects of lepidopteran scales: A) SEM images of butterflies*  
 595 *Graphium agagemnon and Danaus chrysisippus and moths Dactyloceras lucina and Antheraea pernyi,*  
 596 *B) Change in target strength caused by presence of scales, and equivalent intensity absorption*  
 597 *coefficient (Adapted from<sup>179</sup>).*

598

599 Finally, airborne sound and vibration signals play an important role in bee communication and  
 600 defence mechanisms<sup>187</sup>. The thorax of the bee contains a powerful musculature that is used to  
 601 fly but also to produce vibratory impulses. For a long time, communication between bees  
 602 seemed to be almost exclusively regulated by chemical signals, i.e. pheromones. In recent  
 603 decades, it has become increasingly clear that bees live and interact in a world of sound and  
 604 vibration<sup>187,188</sup>. One particular species, the Japanese bee *Vespa mandarinia japonica*, uses  
 605 sounds to coordinate and attack predators *en masse*. In particular, the defence mechanism  
 606 developed by *Vespa mandarinia* relies on the control of dorso-ventral and longitudinal muscles

607 that do not contract alternately, as in flight, but tense simultaneously while the bee remains  
608 motionless. After a few minutes, the temperature of its thorax increases and can reach 43°  
609 (maximum temperature). If a foraging hornet tries to enter the hive, more than 500 workers  
610 quickly engulf it in a ball to rapidly raise the temperature to 47°C, which is lethal for the hornet  
611 but not to the bees<sup>188</sup>. This behaviour is also associated with high neural activity, underlying  
612 the bees' computation for the use and production of sounds and vibrations<sup>189</sup>.

### 613 **3.6 Conclusions on structures for sensing and predation**

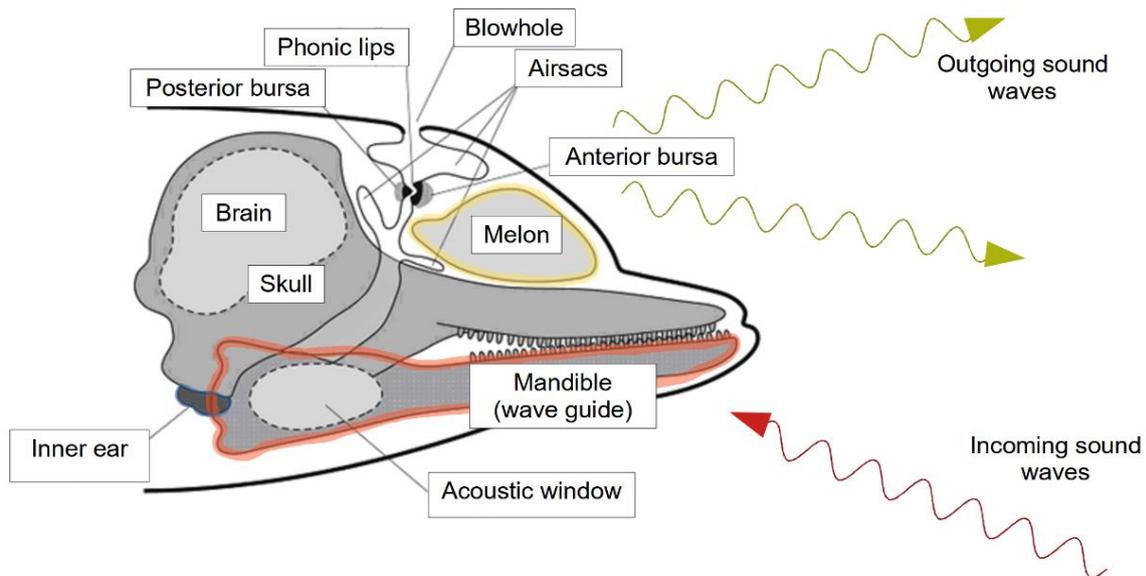
614 We have seen that structures that perform sensory functions are generally related with  
615 localization, allowing a certain species to either perceive its surroundings, localize prey, or  
616 escape from predators. Some common and recurring features can be found. In all cases, the  
617 sensory capability of an organism benefits from specialized transducers used to detect  
618 vibrations (e.g., cuticles for insects and arachnids, silk for spiders). Interestingly, these  
619 transducers are often associated with nonlinear constitutive behaviour, e.g., both cuticle<sup>190</sup> and  
620 silk<sup>191</sup> present a high stiffening behaviour with an exponential constitutive law. Moreover, this  
621 relationship is strongly mediated by water content, which influences the properties of both the  
622 cuticle<sup>140,192</sup> and silk<sup>193</sup>. Thus, natural structures often present a strong relationship with a fluid  
623 or viscous medium, as an agent capable to confer specific mechanical properties. Generally  
624 speaking, the sensing capability is also strongly mediated by the interaction with the substrate  
625 (e.g., trees, and leaves for spiders; sand and rocks for scorpions). Another common feature is  
626 that the interaction with the environment is also often mediated by air flows sensors, with a  
627 common hair-like shape that is present in spiders<sup>136</sup>, scorpions<sup>194</sup>, crickets<sup>195</sup>, and fish<sup>196</sup>.

628

## 629 **4. Sound/vibration control, focusing and amplification**

### 630 **4.1 Echolocation in Odontocetes**

631 Apart from communication purposes, toothed whales and dolphins (Odontocetes) use clicks,  
632 sounds and ultrasounds for sensing the surrounding environment, navigating, and locating prey  
633 <sup>197</sup>. This process is similar to that adopted by terrestrial animals like bats and is called  
634 echolocation <sup>198–200</sup>. The sounds are generated in special air cavities or sinuses in the head, can  
635 be emitted in a directional manner <sup>201,202</sup>, and their reflections from objects are received through  
636 the lower jaw and directed to the middle ear of the animal (Figure 8)<sup>203,204</sup>. A number of studies  
637 have adopted CT scans and FEM to simulate sound generation and propagation in the head of  
638 dolphins or whales, demonstrating how convergent sound beams can be generated and used to  
639 direct sound energy in a controlled manner, and also how sound reception can be directed  
640 through the lower jaw to the hearing organs <sup>205,206</sup>. Dible et al. have even suggested that the  
641 teeth in the lower jaw can act as a periodic array of scattering elements generating angular  
642 dependent band gaps that can enhance the directional performance of the sensing process <sup>207</sup>.  
643 The emitted frequencies of the sounds used for echolocation are typically in the kHz range,  
644 e.g., bottlenose dolphins can produce directional, broadband clicks lasting less than a  
645 millisecond, centred between 40 to 130 kHz. Some studies have suggested that high intensity  
646 focussed sounds can even be used to disorient prey, although this remains to be confirmed  
647 <sup>208,209</sup>. The process of echolocation is extremely sensitive <sup>210,211</sup> and can provide odontocetes  
648 with a “3D view” of their surrounding environment world. This is confirmed by the fact that  
649 sonar signals employed by military vessels can confuse and distress whales and dolphins, and  
650 even lead to mass strandings <sup>212</sup>. Reinwald and coworkers <sup>213</sup> envisaged that the capability,  
651 which is still poorly-understood, of dolphins to accurately locate targets over the whole solid  
652 angle might be due to the correspondence between the reverberated coda of the signal  
653 transmitted along the bone to the ear and the location of the target that generated the signal.



654

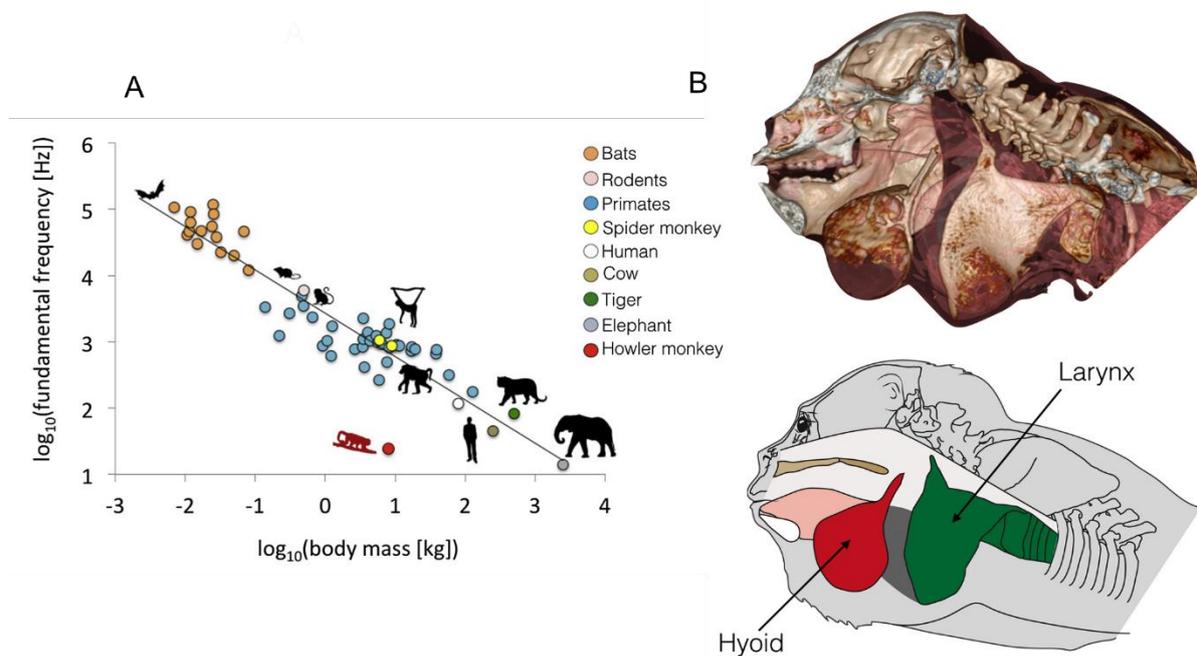
655 *Figure 8: Structures for sound production and detection in Dolphins. Modified and adapted*  
656 *from*<sup>214</sup>.

657

#### 658 **4.2 High amplitude sound generation in mammals**

659 An interesting mechanism exploited in Nature to produce sounds is to develop specific  
660 resonating structures attached to the sound-producing organs of animals with the role to  
661 selectively filter out some frequencies and amplify others<sup>215</sup>. There are several examples of  
662 anatomical adaptations to increase sound radiation efficiency, such as air sacs in frogs<sup>216</sup>, birds  
663<sup>217</sup>, and mammals (Riede et al., 2008), or enlarged larynges in howler monkeys<sup>218</sup> and  
664 hammerhead bats<sup>219</sup>. Some animals even change their environment by constructing horns or  
665 baffles that aid in radiating the sound<sup>220</sup>. The case of howler monkeys (*Alouatta*) is particularly  
666 interesting: these are widely considered to be the loudest land animals, since their vocalizations  
667 can be heard clearly at a distance of 4.8 km. They emit sound at a sound level of 88dB, which  
668 means 11 dB per kg - almost 10.000 times louder per unit mass compared to other animals  
669 (Figure 9A). The function of howling is thought to relate to intergroup spacing, territory  
670 protection and social behaviour, as well as possibly mate-guarding<sup>221</sup>. The extraordinary

671 capability of these monkeys to produce low frequencies and loud vocalizations has been largely  
 672 studied and the exact mechanism exploited is still debated <sup>222</sup>. However, two main elements  
 673 are considered essential in this mechanism: expansion of the hyoid bone into a large shell-like  
 674 organ in the throat and large hollow air sacs located on either side of the bone (Figure 9B).  
 675 When the glottis produces low frequency sounds, the hyoid and air sacs function as resonators  
 676 and the constrictions in the post-glottal structures (a narrow and curved supraglottal vocal tract)  
 677 reduce the velocity of the air flow, elevating its pressure and, consequently, raising its volume  
 678 <sup>223</sup>. The harshness of the roars is a result of the forced passage of air, resulting in irregular noisy  
 679 vibrations. The acoustic function of the air sacs, however, is unclear and not all authors agree  
 680 on their function as resonators, proposing as an alternative an impedance matching purpose <sup>224</sup>  
 681 or potentially to suppress resonances <sup>225</sup>.



682

683 *Figure 9: A) The exceptionally low frequency of Howler Monkey vocalizations; B) Howler*  
 684 *Monkey vocal apparatus. Adapted from <sup>218</sup>.*

685

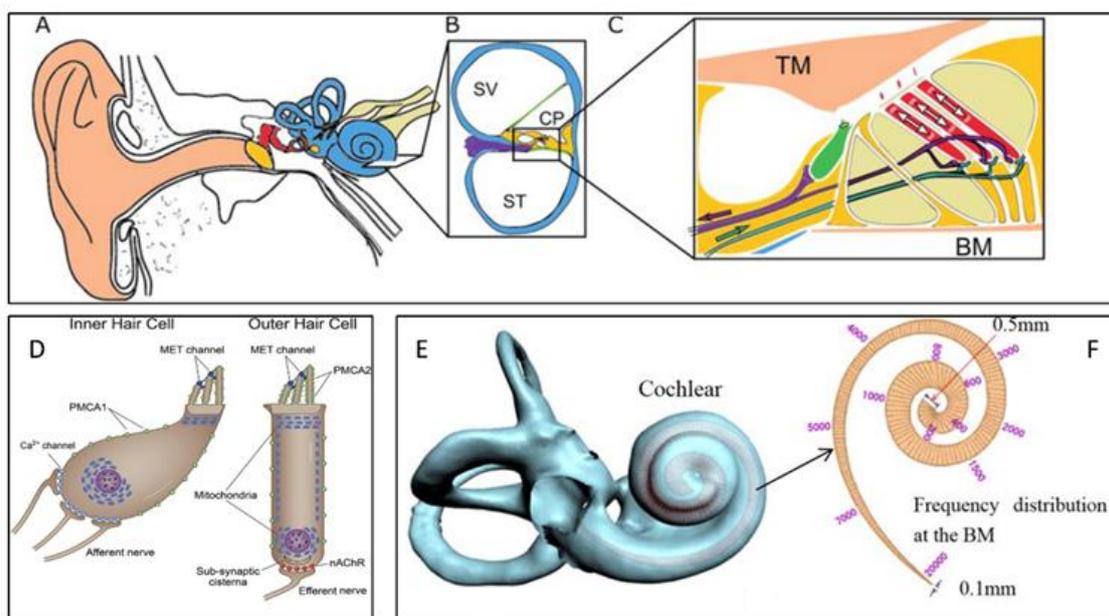
### 686 4.3 Cochlea in mammals

687 The hearing organ in mammals has developed extraordinary capabilities from the point of view  
688 of the extension of audible frequencies and perceived intensities. The human ear (Figure 10A-  
689 C), for example, is sensitive to 8 octaves of frequencies (20Hz-20kHz) and is capable of  
690 distinguishing sounds within 12 orders of magnitude of intensity (120 dB). The evolutionary  
691 complexity of this organ has represented an obstacle to the deep understanding of all the  
692 mechanisms involved and, even today, some aspects remain unexplained (for a review on the  
693 mechanical mechanisms involved see <sup>226,227</sup>). The *cochlea* (Figure 10E) is the core organ of the  
694 inner ear (in blue in Figure 10A), coiled in the form of a snail (hence its name) and enclosed  
695 by a bony shell. The cochlea is composed of two ducts (*scala vestibuli* (SV) and *scala tympani*  
696 (ST), see Figure 10B) filled with a liquid (perilymph) which is compressed by a membrane, hit  
697 by three miniscule bones of the middle ear (in red in Figure 10A). The pressure difference  
698 between the two ducts put in vibration the basilar membrane, which separates them, and which  
699 conducts a largely independent traveling wave for each frequency component of the input (this  
700 mechanism was proposed for the first time in <sup>228</sup> and then largely developed). Because the  
701 basilar membrane is graded in mass and stiffness along its length <sup>229</sup>, however, each traveling  
702 wave grows in magnitude and decreases in wavelength until it peaks at a specific frequency-  
703 dependent position (see Figure 10F), thus allowing a spatial coding of the frequency contents.  
704 This is referred to as the tonotopic organization of the cochlea <sup>230</sup>. The mechanical vibration of  
705 the basilar membrane is then collected and translated into an electrical impulse from the hair  
706 cells (see Figure 10D) and sent to the brain for the signal decoding.

707 One of the most relevant and studied characteristics of the basilar membrane is that its response  
708 to an external stimulus is highly nonlinear (i.e., not proportional to the input amplitude) and  
709 this nonlinear response is also frequency specific. Moreover, each point of the cochlea has a  
710 different nonlinear response depending on the characteristic frequency pertaining to this

711 specific point <sup>231,232</sup>. These features are especially evident in *in vivo* measurements, also  
 712 underling the existence of an active mechanism (otoacoustic emission) added to the merely  
 713 mechanical ones (see e.g., <sup>233–235</sup>).

714 The mechanisms at play are complex and often more than a possible explanation can be found  
 715 in literature, but different simplified models have tried to capture the basic features of the  
 716 cochlea and reproduce its incredible capacity of sensing, its tonotopic and amplification  
 717 behaviours (for a review see e.g., <sup>236,237</sup>). One of the aspects that can be relevant for bioinspired  
 718 applications in the propagation of elastic waves in solids, is the influence of the geometry  
 719 (spiral) on the frequency attenuation/loss and on the tonotopic property of the sample, as also  
 720 pointed out by some works (see <sup>238,239</sup>).



721  
 722 *Figure 10 : Cochlea structure. A) the outer (beige), middle (red) and inner (blue) parts of the*  
 723 *human ear. B) Cross-section of the cochlea showing the scala vestibuli (SV) and the scala*  
 724 *tympani (ST), separated by the cochlear partition (CP) which contains the basilar membrane*  
 725 *(BM) and the sensory hair cells (adapted from <sup>240</sup>). These cells are represented in panel C in*  
 726 *green (inner hair cells) and red (outer hair cells) and are also reported with more details in*

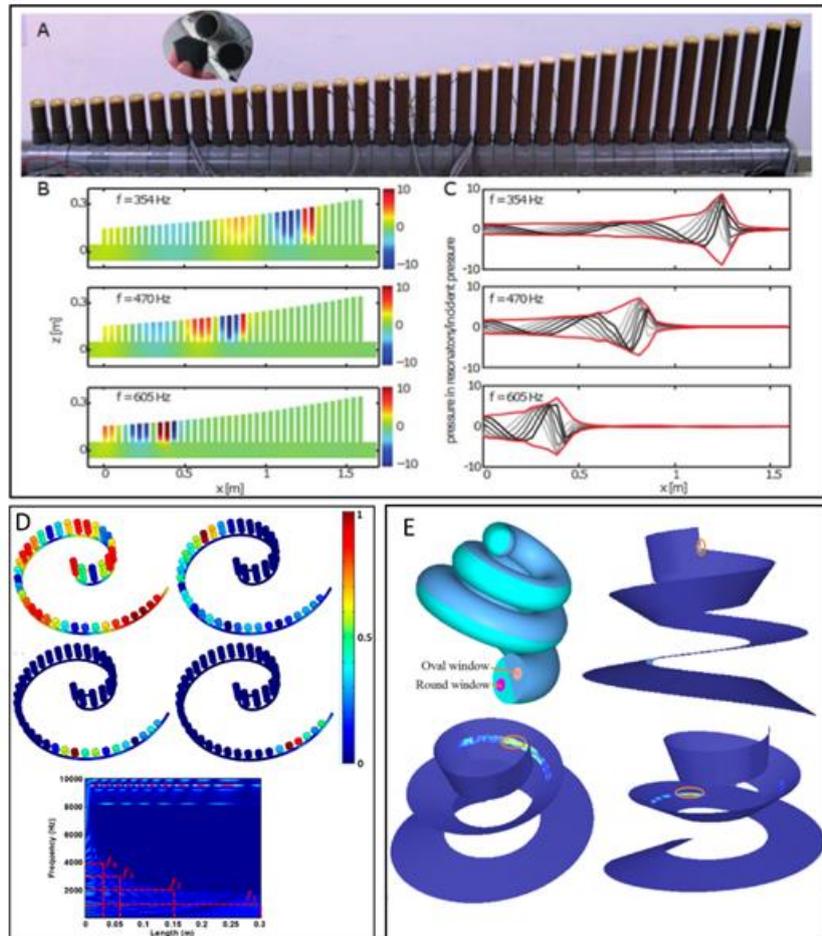
727 subplot D (adapted from <sup>241</sup>). In panel E a 3D representation of the cochlea is reported and a  
728 schematic map of the tonotopic property of the basilar membrane reported in panel F (adapted  
729 from <sup>242</sup>).

730

731 All these features attracted the interest of researchers working on mechanical and elastic waves  
732 manipulation devices, e.g., in the field of structural health monitoring, sensor development,  
733 guided waves, etc. There are specific works in the literature that explicitly refer to the cochlea  
734 as a bio-inspiration for metamaterial realizations and that propose acoustic rainbow sensors,  
735 where the aim is to separate different frequency components into different physical locations  
736 along the sensor (see Figure 11 and Refs. <sup>240,242–244</sup>). In particular, the tonotopy and the low  
737 amplitude amplifier is reproduced with a set of subwavelength active acoustic graded  
738 resonators, coupled to a main propagating waveguide in <sup>240</sup>. Similarly, based on a set of  
739 Helmholtz resonators arranged at sub-wavelength intervals along a cochlear-inspired spiral  
740 tube in <sup>243</sup>, the authors realize an acoustic rainbow trapper, that exploits the frequency selective  
741 property of the structure to filter mechanical waves spectrally and spatially to reduce noise and  
742 interference in receivers. The tonotopy can be also obtained in a 3D model of the cochlea <sup>242</sup>  
743 by grading the mechanical parameters of an helicoidal membrane: in this case the overall  
744 cochlear is a local resonant system with the negative dynamic effective mass and stiffness.

745 Some of the examples of cochlea-inspiration for the design of metamaterials are shown in  
746 Figure 11. In particular, in panels A, B, C a gradient-index metamaterial for airborne sounds,  
747 made from 38 quarter-wavelength acoustic resonators of different heights is reproduced (from  
748 <sup>240</sup>). In panel D a rainbow trapper based on a set of Helmholtz resonators is described (from  
749 <sup>243</sup>). In panel E a modal analysis of a helix model of cochlea is reported, showing the different  
750 responses to different frequency excitations (in particular, at the top circle, the minimum

751 natural frequency is 89.3 Hz; (c) at the medial circle is 5000.5 Hz; and at the base circle is  
 752 10097.2 Hz).



753  
 754 *Figure 11 : Metamaterial inspired by the cochlea. Some of the examples of cochlea-inspiration*  
 755 *for the design of metamaterials. In particular, in panels A,B,C, a gradient-index metamaterial*  
 756 *for airborne sounds, made from 38 quarter-wavelength acoustic resonators of different heights*  
 757 *is reproduced (adapted from <sup>240</sup>). In panel D, a rainbow trapper based on a set of Helmholtz*  
 758 *resonators is described (adapted from <sup>243</sup>). In panel E, a modal analysis of a helix model of*  
 759 *cochlea is reported, showing a different response to different frequency excitations.*

760

761 **5. Natural structural evolution vs. optimization through artificial algorithms**

762 The structures discussed in this review are the result of optimization processes due to natural  
763 evolution spanning millions of years. Their common features are summarized in Sections 2.8  
764 and 3.6. These evolutionary processes have however been constrained by the availability of  
765 material resources and their fabrication conditions. At the other end of the scale, there are fast  
766 developing computational algorithms used in current technology that can be used to optimize  
767 artificial materials (often bioinspired) for similar goals, where these boundary conditions can  
768 be relaxed or eliminated altogether. In artificial materials, the possibilities of design with  
769 different material combinations and distributions are virtually unbounded, and numerical  
770 algorithms can be used to optimize specific properties of nature-based architected structures  
771 <sup>245</sup>. The use of optimization techniques for the design of periodic structures able to attenuate  
772 vibrations, for instance phononic crystals, aims to systematically achieve objectives such as  
773 maximizing absolute band gap widths <sup>246</sup>, normalized band gap width with respect to their  
774 central frequency <sup>247,248</sup>, or maximized attenuation per unit length <sup>249</sup>. For each given  
775 combination of materials, the objective function must be evaluated through the computation of  
776 the band structure of a given unit cell configuration, using various numerical methods <sup>250–252</sup>.  
777 A wide variety of optimization techniques to pursue the chosen objective is available in the  
778 literature. Among these, topology optimization is one of the most employed and well-  
779 developed <sup>253</sup>, in combination with algorithms such as Bidirectional Evolutionary Structural  
780 Optimization <sup>254</sup>. Another common approach is the use of genetic algorithms, an optimization  
781 scheme which is a type of evolutionary algorithm <sup>255</sup> and is well suited for the design of  
782 phononic crystals <sup>256</sup>. Another possibility is the use of machine learning tools to design  
783 structures which present desirable characteristics, i.e., using an inverse approach <sup>257</sup>. Many of  
784 these approaches are being more and more applied in the field of phononics <sup>258</sup>. The types of  
785 optimized structures emerging from these algorithms have some common traits with naturally  
786 evolved structures, and some distinctive differences. On the one hand, recurring features are

787 many of those cited in Section 2.8: heterogeneity, porosity, hierarchical organization, efficient  
788 resonating structure, graded properties, in some cases chirality <sup>259,260</sup>. In this case, artificial  
789 optimization techniques can improve existing bioinspired design for specific objectives. On the  
790 other hand, implementing unconstrained numerical optimization can enable a wider  
791 exploration of the phase space, potentially leading to exotic designs with little resemblance to  
792 existing biological structures. However, this is not surprising, since optimization based on  
793 natural evolution is in most cases a multi-objective process, where different properties are  
794 simultaneously addressed (e.g., quasistatic strength/toughness and dynamic attenuation).

795

## 796 **6. Conclusions**

797 In conclusion, we have presented a review of some notable examples of biological materials  
798 exhibiting optimized non-trivial structural architectures to achieve improved vibration control  
799 or elastic wave manipulation, for many different purposes. The fields in which these features  
800 appear are mainly impact and vibration damping and control, communication, prey detection  
801 or mimesis, and sound amplification/focusing. From the documented cases, some recurrent  
802 strategies and structural designs emerge. Among them, an important feature is hierarchical  
803 structure, which appears to be essential to enable effects at multiple scale levels, and therefore  
804 in multiple frequency ranges. Moreover, these recurrent structural features appear at very  
805 different size scales (from microns to meters), in disparate environments (terrestrial or marine)  
806 and for different functions. This is an indication that the designs are particularly resilient and  
807 effective in their purposes, which encourages the adoption of a biomimetic approach to obtain  
808 the comparable types of optimized dynamic mechanical properties in artificial structures. This  
809 is a particularly attractive proposition in the field of phononic crystals and acoustic  
810 metamaterials, which have recently emerged as innovative solutions for wave manipulation  
811 and control, and where a biomimetic approach to design has thus far been limited to a few

812 cases, especially considering that biological materials derive from self-assembly, so that are  
813 inherently periodic or hierarchical in structure. In general, further investigations in the natural  
814 world will no doubt continue to reveal original architectures, designs, and advanced  
815 functionalities to be exploited for metamaterials and other vibration-control technologies,  
816 where function (or multiple functions) is/are achieved through form and structure.

817

### 818 **Acknowledgments**

819 All authors are supported by the European Commission H2020 FET Open “Boheme” grant no.  
820 863179.

### 821 **Author contributions**

822 Conceptualization, F.B and N.M.P. All authors contributed to the writing of the manuscript.

### 823 **Declaration of interests**

824 The authors declare no competing interests.

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1507 **Figure titles and legends**

1508

1509 ***Figure 1: Mantis shrimp***

1510 *a) Peacock mantis shrimp, with highlighted raptorial dactyl clubs to strike hard objects*  
1511 *(adapted from <sup>18</sup>); b) Morphological features of the clubs, in cross-section view, divided in an*  
1512 *impact region, a periodic region and a striated region; c) Scanning electron micrograph of the*  
1513 *coronal cross-section, showing reinforcing fibre helicoidal arrangement; d) schematic of a*  
1514 *Finite Element Analysis model accounting for graded material properties (adapted from <sup>19</sup>).*

1515 ***Figure 2: Vibration attenuation in the woodpecker skull (adapted from <sup>31</sup>)***

1516 *(A): Volume fraction ratio of skull bone, local measured modulus, and macro-equivalent*  
1517 *modulus around the skull. (B): 3D finite-element model of the skull and hyoid bone. Note that*  
1518 *the Young's modulus on the skull is not uniform. (C): first ten modes of the skull under a pre-*  
1519 *tension on the hyoid in the range 0-25 N. (D), upper panel: stress wave at a brain location*  
1520 *under impact direction. (d), lower panel: stress spectrum in the frequency domain obtained by*  
1521 *FFT.*

1522 ***Figure 3: Modelling of vibration attenuation in the woodpecker skull (adapted from <sup>10</sup>)***

1523 *(A): lumped-elements model of the head of a woodpecker. (B): empirical model of the spongy*  
1524 *bone by means of an aluminium enclosure filled with glass microspheres. (C): vibration*  
1525 *transmissibility as a function of frequency for different diameters of the SiO<sub>2</sub> microspheres.*

1526 ***Figure 4: Biological systems with suture tessellation***

1527 *(a) examples from Flora and Fauna (adapted from <sup>58</sup>); (b) the leatherback turtle shell (adapted*  
1528 *from <sup>60</sup>)*

1529

1530 **Figure 5: Prey sensing similarities in spiders and scorpions**

1531 *a) web structure: a typical orb web of a spider *Nuctenea umbratica*. The web is built by means*  
1532 *of junctions between threads and surfaces, b) junctions between radial threads, c) and*  
1533 *junctions between radial and spiral threads. A flying prey can be eventually detected by air*  
1534 *flow sensors, d) the tricothoria. If the prey impacts the web, the vibrational signal will be*  
1535 *transmitted mainly by radial threads and be perceived by e) lyriform organs of the spider.*  
1536 *Figure adapted from <sup>93,132</sup>. f) schematic of scorpion prey detection using surface waves; g)*  
1537 *sensory hairs and mechanoreceptors located at the slit sensilla sense surface waves. Adapted*  
1538 *from <sup>162159</sup>*

1539 **Figure 6: Anti-predatory strategies**

1540 *(a) The high-resolution 3D acoustic imaging system evolved by the echolocating bats (adapted*  
1541 *from <sup>174</sup>) and the moth's strategies to avoid being detected: (b) appropriate scale arrangement*  
1542 *and structure (adapted from <sup>178</sup>). and (c) hindwing tails. Behavioural analyses reveal that (A)*  
1543 *bats aim an increasing proportion of their attacks at the posterior half of the moth (indicated*  
1544 *by yellow cylinder with asterisk) and that (B) bats attacked the first and third sections of tailed*  
1545 *moths 75% of the time, providing support for the multiple-target illusion. An enlarged echo*  
1546 *illusion would likely lead bats to target the hindwing just behind the abdomen of the moth, at*  
1547 *the perceived echo center (highlighted in green); however, bats targeted this region only 25%*  
1548 *of the time (adapted from <sup>261</sup>).*

1549 **Figure 7: Tiling patterns and acoustic effects of lepidopteran scales**

1550 *(a) SEM images of butterflies *Graphium agamemnon* and *Danaus chrysippus* and moths*  
1551 **Dactyloceras lucina* and *Antheraea pernyi*, (b) Change in target strength caused by presence*  
1552 *of scales, and equivalent intensity absorption coefficient, (c) Change in target strength caused*

1553 *by presence of scales, and equivalent absorption coefficient as a function of wing*  
1554 *thickness/wavelength. (Adapted from<sup>185</sup>)*

1555 ***Figure 8: Sound generation in Howler monkeys***

1556 *a) The exceptionally low frequency of Howler Monkey vocalizations; b) Howler Monkey vocal*  
1557 *apparatus. Adapted from<sup>218</sup>.*

1558 ***Figure 9 : Metamaterial inspired by the cochlea***

1559 *Some of the examples of cochlea-inspiration for the design of metamaterials. In particular, in*  
1560 *panels A,B,C, a gradient-index metamaterial for airborne sounds, made from 38 quarter-*  
1561 *wavelength acoustic resonators of different heights is reproduced (adapted from<sup>240</sup>). In panel*  
1562 *D, a rainbow trapper based on a set of Helmholtz resonators is described (adapted from<sup>243</sup>).*  
1563 *In panel E, a modal analysis of a helix model of cochlea is reported, showing a different*  
1564 *response to different frequency excitations.*

1565