

A spider's vibration landscape: adaptations to promote vibrational information transfer in orb webs

B. Mortimer^{1*}

¹ Department of Zoology, University of Oxford, South Parks Road, OX1 3PS

* Corresponding author: +441865 271124, beth.mortimer@zoo.ox.ac.uk

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Abstract: Spider orb webs are used not only for catching prey, but also for transmitting vibrational information to the spider. Vibrational information propagates from biological sources, such as potential prey or mates, but also abiotic sources, such as wind. Like other animals, the spider must cope with physical constraints acting on the propagation of vibrational information along surfaces and through materials – including loss of energy, distortion and filtering. The spider mitigates these physical constraints by making its orb web from up to five different types of silks, closely controlling silk use and properties during web building. In particular, control of web geometry, silk tension and silk stiffness allows spiders to adjust how vibrations spread throughout the web, as well as their amplitude and speed of propagation, which directly influences energy loss, distortion and filtering. Turning to how spiders use this information, spiders use lyriform organs distributed across their eight legs as vibration sensors. Spiders can adjust coupling to the silk fibres and use posture to modify vibrational information as it moves from the web to the sensors. Spiders do not sense all vibrations equally – they are least sensitive to low frequencies (<30 Hz) and most sensitive to high frequencies (c. 1 kHz). This sensitivity pattern cannot be explained purely by the frequency range of biological inputs. The role of physical and evolutionary constraints are discussed to explain spider vibration sensitivity and a role of vibration sensors to detect objects on the web as a form of echolocation is also discussed.

1. Introduction

Vibrational information transfer involves the transmission of mechanical vibrations along surfaces or through materials (Hill and Wessel 2016; Mortimer 2017). It is an important sensory mode utilised by a wide variety of organisms from nematode worms to elephants (Hill 2008; 2009; Holbrook and Mortimer 2018; O'Connell-Rodwell and others 2000).

Vibrational information can be transferred via communication, where signals have evolved to transfer information within a variety of contexts, such as between conspecifics during courtship (Davranoglou and others 2019). Vibrational information can also propagate as cues, often generated incidentally by animals as they move, but used for information by receivers, such as during predator-prey interactions (Devetak and others 2007) or to coordinate hatching (Endo and others 2019). As well as biotic sources of vibrational information, abiotic sources also exist and can be used to inform receivers about the status of their environment (Snarr 2005).

Unlike other sensory modes, vibrational information transfer is particularly sensitive to physical constraints as vibrations propagate from a sender to a receiver via a heterogeneous physical environment (Mortimer 2017). These constraints include filtering of vibrational information, loss or dissipation of energy that reduces signal to noise ratio, and distortion of vibrational information. Whereas airborne and waterborne vibrations propagate via the bodies of air and water respectively, the substrate-borne vibrations of interest here tend to propagate along surfaces (e.g. plant leaf, water surface, sandy beach) or through the bodies of solid materials (e.g. subterranean vibrations). The geometry of the substrate – whether a body of solid material, a surface, a plate, rod or string – as well as the arrangement of types of heterogeneous materials will both influence information propagation (Mortimer 2017). The arrangement and type of substrates between sender and receiver is what I will term 'vibration landscape'.

Despite physical constraints acting within the physical environment, many animals have evolved to use substrate-borne vibrations as an information source. This is due to an array of mitigation mechanisms to overcome physical constraints. These include control of vibration generation and sensing in the sender and receiver respectively, incorporating a range of physiological adaptations, including behavioural, morphological, sensory and neuronal adaptations.

Here, I focus on a particular special case of how animals can mitigate physical constraints – by making their own substrate. This is the strategy of orb weaving spiders who effectively act as engineers to build their own vibration landscape (Mortimer and others 2018; Mortimer and others 2016). I will discuss how this strategy enables orb weavers to control vibration propagation in their web, with a focus on ecribellate orb weavers on which most vibration propagation research has been done. I will then move on to the evidence for sensory adaptations of spiders to use web vibration as an information source. Most research on vibration sensing in spiders has focussed on the wandering spider *Cupiennius salei*, but I will link these findings to what this tells us about orb weaver adaptations to promote vibrational information transfer. I will finish with an overview of the open questions still unanswered in this topic.

2. Orb weaver control over vibration propagation

Orb webs are snares made by specialised spiders that act to capture flying prey and transmit vibrational information to the spider. To put into context, many spiders make webs, although not all do, and webs vary widely in geometry (e.g. 3D, degree of silk use, connections between silk fibres), material properties (e.g. due to silk types employed, coupling to the environment, Araneomorph versus Mygalomorph silks), web decorations (use of stabilimenta) and likely their ability to transmit vibrations. A few studies have quantified vibration propagation through funnel, sheet and cob webs (Naftilan 1999; Singer and others 2000; Vibert and others 2016), although no systematic study exists to allow comparisons of

vibration transmission across different spider species, controlling for phylogeny. In theory, all Araneomorph web building spiders have equal control over vibration transmission in their webs, as they can alter web geometry, silk tension and silk properties using the suite of mechanisms outlined for orb weavers below. Research attention on vibration transmission in webs has focussed on orb weavers, and this review focusses on summarising how these spiders are adapted to promote vibrational information transfer through their web.

The orb web is made from up to five types of silks made by the spider (Figure 1): major ampullate (MA), or dragline, silk forms the converging radial threads, as well as the bridging and mooring threads outside the capture area (Zschokke and Vollrath 1995a); minor ampullate (MiA) silk is used as an auxiliary (stiff) spiral during orb web building, which is removed in some species, but maintained in others (e.g. *Araneus* versus *Nephila* spiders) (Zschokke and Vollrath 1995b); the viscid capture spiral of ecribellate spiders is a composite of flagelliform and aggregate (FL, AG) silk, forming a core fibre and sticky coating respectively (Elettro and others 2016); and finally piriform (PI) adhesive disks keep the web structure and allow the silks to be attached to the external environment (Wirth and others 2019).

Orb webs transmit three types of vibrational wave (Masters 1984a; Mortimer and others 2019). Longitudinal waves have their main axis of displacement within the fibre axis, whereas transverse and lateral waves have the main axis of displacement perpendicular to the fibre axis. Whereas lateral waves have their displacement axis within the major plane of the web, transverse wave displacement is perpendicular to the major web plane. Each type of vibrational wave differs in its propagation speed, how it spreads during propagation and how it loses energy over time and distance (Mortimer 2017).

Orb weavers are able to influence vibration propagation through their web by altering: i) the geometrical arrangement of the silks within the web, ii) the tensioning of the silk strands and iii) the silk properties within their web (Figure 2). In combination, these mechanisms allow

orb weavers to adjust the speed of waves propagating through their web, which affects frequency filtering during propagation and the propagation time from prey to spider; they can adjust the amplitude of waves propagating through the web, allowing them to reduce vibration amplitude under noisy conditions or increase amplitude when necessary; and finally it can influence the patterns of wave propagation over the web, which influences how they can determine prey location by comparing sensory inputs across their spatially separated vibration sensors on their legs (Mortimer 2017; Mortimer and others 2019). Combined, these control mechanisms represent adaptations of the orb weaver to promote vibrational information transfer using their extended phenotype of the web.

2.1 Adjusting web geometry

In terms of web geometry, orb weavers control which silks are used during web building and the architectural arrangement within the structure, using innate mechanisms to integrate a range of positional cues (Eberhard 2019; Krink and Vollrath 1997). Whereas stereotypical differences in web geometry can be seen between species (Zschokke and Vollrath 1995b), differences between individuals and plasticity within an individual is also known (Eberhard 2019; Nakata 2012). For example, wind causes specific changes in web architecture, including reduced capture area and increase in mesh height (Vollrath and others 1997).

Web geometry affects the tensioning of silk fibres in the web, as supported through experimental measurement and computer models (Mortimer and others 2016), which influences wave propagation as outlined below (Section 2.2). For example, model webs without a capture spiral show lower transverse wave amplitudes than those with, as the capture spiral creates a tensioning gradient on the radial threads (Mortimer and others 2016). Web geometry also affects how vibrations propagate over the web structure, known as geometric dispersion, which influences transverse and longitudinal wave amplitude due to dilution of vibrational energy as it is spread over the mesh structure. The effect is much greater for transverse waves, which show significant spreading of amplitude through the

capture, mooring and auxiliary (when present) threads of the web (Landolfi and Barth 1996; Masters 1984a; Mortimer and others 2016), whereas longitudinal waves tend to spread only at stiff spirals via creation of lateral waves (Mortimer and others 2016). In turn, the geometric spreading of waves affects how orb weavers can orientate and locate prey items when comparing sensory inputs into their legs (Landolfi and Barth 1996; Mortimer 2017, Mortimer and others 2019).

2.2 Adjusting silk tension

Orb weavers closely control radial thread tensions during web building, where force scales with spider mass (Eberhard 1981; Wirth and Barth 1992). Across the webs, mooring threads have the greatest forces, then bridging then radial threads, which also scales with a change in the number of fibres so overall cross sectional area (Wirth and Barth 1992). Across radial threads, web tensions vary between upper and lower radials, with higher and lower forces respectively (Wirth and Barth 1992). Experimental manipulation of radial thread tension in cribellate orb webs has been shown to decrease response times of spiders (i.e. more successful prey capture) to small prey (Watanabe 2000). It is currently unknown what cues orb weavers use to inform whether and how radial thread tension is adjusted, for example environmental cues.

Silk tension affects nearly all of silk's sonic properties, but is directly important for the propagation of transverse waves. Based on theory, this is because transverse wavespeed is dependent on the square root of silk tension divided by silk mass per unit length (Frohlich and Buskirk 1982), which has been supported through experimental measurement (Mortimer and others 2014). Silk tension also affects transverse wave amplitude, as supported by FEA modelling data of webs (Mortimer and others 2016). Furthermore, silk tension affects the internal damping of silk, as it directly affects how close the silk fibre is to its yield point, where at deformations higher than the yield point, the silk fibre will increase internal damping and dissipate energy through plastic, or non-recoverable, deformation (Guan and others

2013). Internal damping directly influences the amplitude of both transverse and longitudinal waves as it affects how energy is stored and dissipated during deformation. Finally, silk tension also influences the likelihood of major ampullate silk supercontraction, which is discussed below.

2.3 Adjusting silk stiffness

Orb weavers can adjust silk stiffness using three different mechanisms. During silk spinning, spiders can change the spinning speed, which directly influences silk stiffness, where faster speeds lead to higher stiffnesses due to increased order within the silk protein structure (Vollrath and others 2001). Orb weavers can also adjust silk stiffness after spinning through applying tension to silk threads during building or *ad hoc*, which has been measured through experiments on individual fibres (Guan and others 2012). When static, or fixed, tensions are applied to silk fibres at tensions lower than the breaking load, they undergo a form of permanent deformation where the protein structure becomes more aligned and the stiffness increases (storage modulus up to 28 GPa for *Nephila* major ampullate silk at 1100 MPa load (Guan and others 2012)). The final mechanism to adjust silk stiffness involves a passive process that acts on major ampullate silks called supercontraction. Under high humidity and low tensions, major ampullate fibres will contract up to 50% of their original length (Boutry and Blackledge 2010), the degree of contraction relying on the proportion of proline present (Guan and others 2011; Liu and others 2008). Supercontraction drastically reduces the order within the silk fibre and reduces stiffness down to c. 4 GPa (Liu and others 2008; Pérez-Rigueiro and others 2003). As a passive process, supercontraction can be seen as a way to reset web properties. Importantly, spiders are able to actively respond to control web and silk properties following supercontraction. They can apply tension to supercontracted fibres to increase stiffness, as shown with individual fibres (Guinea and others 2005), allowing the spider to access major ampullate stiffnesses from c. 4 to 28 GPa through active mechanisms (Mortimer and others 2014).

Silk stiffness is particularly important for longitudinal wave propagation through silk. Based on theory, this is because longitudinal wavespeed is dependent on the square root of silk stiffness divided by silk density (Frohlich and Buskirk 1982), which has been supported through experimental measurement (Mortimer and others 2014). Silk stiffness also influences longitudinal wave amplitude, where lower moduli increase the amplitude of longitudinal waves in FEA models of webs (Mortimer and others 2016). Silk stiffness is also important for the mechanical response of orb webs (Boutry and Blackledge 2013), so an ability to adjust silk stiffness provides a mechanism for orb weavers to balance mechanical and sensory functions as conditions change (Mortimer and others 2014). For example, higher stiffness to prevent web deformation in windy conditions, but lower stiffness to increase longitudinal wave amplitude of prey-generated cues.

3. Silk & vibration sensing

So far we have discussed mechanisms available to the spider that allow a degree of control over vibration propagation in the web, which are likely adaptations to promote vibrational information transfer. Following propagation through the web, the spider must then couple with the vibrating silk, transmitting the vibration to their vibration sensors. Spiders also possess control mechanisms and adaptations that promote transmission of vibratory information from the web to the spider's sensory system, namely control of posture, use of material vibration filters, and using sensory thresholds to control mechanotransduction within their vibration sensors.

Spiders sense substrate-borne vibrations using slit sensilla on each of their legs. Slit sensilla are slits in the spider's exoskeleton, with a membrane spanning the slit and often two sensory cells attached to the membrane at the trough of the slit (Molina and others 2009). The slit sensilla sense deformation of the slit as the spider's exoskeleton is deformed by external or internal forces. A series of slit sensilla are often found grouped together, forming what is known as a lyriform organ due to the geometric arrangement of the slits: often

perpendicular to the leg axis and arranged with longer slits towards the proximal end and smaller slits towards the distal end of the organ (Barth and Geethabali 1982). Slit sensilla and lyriform organs are known to be proprioceptive, allowing the spider to sense the position of its legs and joints, but have also been shown to be sensitive to substrate vibration. In particular the metatarsal lyriform organ, found on the metatarsus near the joint with the tarsus, is sensitive to substrate vibration, as illustrated with ablation experiments and nerve (Liesenfeld 1961; Walcott 1959), extracellular (Barth and Geethabali 1982) and intracellular (Gingl and others 2006) recordings in response to vibrational inputs. In addition, tarsal slits have been found to be sensitive to vibration (Speck and Barth 1982). Other vibration sensors may exist as ablation of the metatarsal organ and the tarsal slits does not prevent spiders from orientating towards prey using substrate borne vibrations (Speck and Barth 1982).

3.1 Coupling: posture & filtering

Orb weavers need to couple with vibrating silk strands in order to transfer the vibrational information from the silk to their slit sensilla embedded in their leg exoskeletons. The steep angle between an orb weaver's tarsus and its silk means it is well suited to couple with longitudinal waves from the web (Landolfi and Barth 1996), but lateral and transverse waves propagate into the spider tarsus as well (Masters 1984a). Amplitude gradients in the web, which provide information on prey location in the web (Mortimer and others 2019), are also maintained after spider coupling (Landolfi and Barth 1996). Coupling between the spider and the web also leads to resonance of the spider's mass, expected at frequencies c. 20 Hz, depending on the mass of the spider, and at higher frequencies for leg segments (Frohlich and Buskirk 1982; Masters 1984a). Modifying the coupling between the spider leg and silk or the addition of mass to the spider tarsus was found to have little to no effect on spider slit sensilla responses (loose coupling resulted in slight lower frequency shift), as recorded through extracellular recordings (Barth and Geethabali 1982). Recent work has shown that spiders adjust their coupling with webs through actively adjusting their posture,

thus modifying propagation through the legs via changing the physical properties of the legs (Mhatre and others 2018).

In addition to coupling, the material properties of the exoskeleton of the leg also alter and filter vibrational information before it reaches the metatarsal lyriform organ. In particular, spiders have a metatarsal pad that is distal to the metatarsal organ (Morley and others 2016), which has been extensively studied in *Cupiennius salei* (Erko and others 2015; McConney and others 2007; Young and others 2014). Detailed examination of the metatarsal pad revealed it acts as a high pass filter for vibrations, i.e. low frequencies are damped and higher frequencies are transmitted with low damping (McConney and others 2007). This can be explained by the viscoelasticity of the pad – indeed any polymer is expected to have stiffnesses that change with rate of deformation and/or temperature due to their polymeric structure, which can be quantified by the glass transition temperature of the polymer, which has been investigated for the metatarsal pad (McConney and others 2007; Young and others 2014). Structural features of the pad also give it a protective function for the lyriform organ – at low frequencies and high deformations, the highly hydrated distal part of the pad will deform and reduce the displacement transferred to the organ, protecting the sensitive organ from high amplitude vibrations that may cause damage and/or change in function or speed of response (Erko and others 2015). Spiders also have a lateral furrow to focus vibrations from the tarsus to the metatarsal organ (Barth and Geethabali 1982).

The effect of coupling and the physical properties of the spider is a promising research area for future exploration – in theory spiders should differ in how vibrational information is transferred from the web to their vibration sensors according to their mass, leg morphology and angles, joint stiffnesses, leg stiffnesses and the types of vibrational inputs. Open questions are to what extent spider morphology might be tuned to receive vibrational inputs, or whether they can actively adjust their physical properties on demand to promote vibrational information transfer.

3.2 Sensing: Tuning curve & biological inputs

We have so far considered propagation through the extended phenotype of the web, then coupling between the web and spider, and then propagation through the spider leg to the embedded slit sensilla sensors. Whereas these previous stages can be considered to act on vibrational information within the external environment, sensory transduction translates the mechanical vibration to physiological information within the cells of the spider. The sensory transduction process, here mechanotransduction, also acts as a filter on vibrational information – certain thresholds are in place to ensure that nerves only fire under certain conditions. This allows relevant biological information to be detected, but prevents too many false positives by filtering out mechanical vibrations that contain little relevant information.

The sensory thresholds can be quantified and visualised using a tuning curve. Figure 3 uses data collected by Barth and Geethabali (1982) and Liesenfeld (1961), showing the tuning curves of the slit sensilla of three spider species. On the whole, across a frequency range of 0.1 Hz to 5000 Hz, the overall sensory thresholds between these three spider species are similar: high displacements at c. 10-100 μm are required at low frequencies below c. 20 Hz, but the required displacement decreases down to c. 1-10 nm at frequencies up to 5000 Hz. Differences in the tuning curves between spiders do exist (Figure 3), which may indicate adaptations of spiders to detect vibrations on substrates with vastly different properties and so vibratory environments (i.e. different noise levels, frequency filtering, frequencies of biological information). Since not much data exist on the tuning curves of spider slit sensilla beyond the detailed study of *Cupiennius salei*, more research is needed to determine if tuning curves have functional significance for spiders of different ecologies.

The overall shapes of tuning curves have been supported with more recent intracellular recordings, which have confirmed the presence of two sensory cells per slit that differ in physiological characteristics (Gingl and others 2006; Molina and others 2009). Behavioural evidence also supports these trends (Hoffmaster 1982; Klärner and Barth 1982; Liesenfeld

1956; Masters 1984b), although the tuning curves suggest spiders are sensitive to lower amplitudes than those found to release predatory behaviour in spiders (by 40-60 dB) (Klärner and Barth 1982). This can be explained by the mechanics of the metatarsal pad, which acts to reduce the displacement amplitude transmitted to the sensory organ at high amplitudes, creating resilience to high amplitude inputs (Erko and others 2015).

Assuming the tuning curve of *Zygiella* is representative of orb weavers, the question is raised about whether the curve can be explained by the vibratory environment of the orb web – is the available tuning curve of spiders suited to extracting biological information from vibrating orb webs? Put another way, is the available orb weaver sensory tuning curve likely to be an adaptation to promote vibrational information transfer from the orb web?

Biological information propagates from prey in the orb web and courtship vibrations of potential mates. Prey vibrations cover a large frequency range c. 5-1000 Hz, which varies according to the size and behaviour of the prey (Landolfi and Barth 1996; Masters 1984b). Larger prey, such as *Calliphora* have lower peak frequencies and higher amplitudes, whereas smaller prey such as *Drosophila* have higher peak frequencies and lower amplitudes, although there is lots of frequency overlap (Landolfi and Barth 1996). Prey that is caught and struggling in the web tends to be lower in frequency at c. 5-50 Hz, whereas prey that is buzzing using its flight motor will have a higher frequency range c. 100-1000 Hz, although amplitudes are in a comparable range (Landolfi and Barth 1996; Masters 1984b). Few recordings of courtship signals of orb weavers have been published, but frequencies seem to range between 16 and 180 Hz and differ with behaviour, e.g. *Argiope keyserlingi* 'abdominal wagging' versus 'shudder' have peak frequencies between 58 to 178 Hz and 16 to 49 Hz respectively (Wignall and Herberstein 2013).

Aside from biological information, noise can also dominate at certain frequency ranges. Under 10 Hz, noise in the web is prevalent (Landolfi and Barth 1996; Masters 1984b), from natural sources such as wind and the resonance of the spider on the web (which varies with

mass) (Frohlich and Buskirk 1982), as well as disturbance of the plant material that webs may be connected to via mooring threads (Wu and Elias 2014). The prevalence of noise likely acts to decrease spider vibration sensitivity in this low frequency range.

Given these data, the prediction for an adaptive tuning curve to promote biological information transfer would be that spider tuning curves would be most sensitive to 30-1000 Hz, where prey and courtship cues/signals will dominate and noise is lower. This is supported to a certain extent, *Zygiella* reaches its maximum sensitivity at 300 Hz, at a lower frequency than *Tegenaria* or *Cupiennius* (Figure 3). Yet the lower than expected sensitivity below 300 Hz and the higher than expected sensitivity above 1000 Hz needs to be explained.

Below 300 Hz, physical constraints are likely to be shaping the tuning curve. The material properties of the metatarsal pad impose physical constraints as they act as high pass filters (McConney and others 2007). The presence of the filter will be unavoidable given the viscoelastic properties of the pad and the function to increase sensory organ resilience (Erko and others 2015), but you might expect the frequency range on which the filter acts could be tunable, as supported by the species differences seen in Figure 3. The inevitable constraint of background noise becomes increasingly dominant at lower frequencies, which may shape the frequency range of the high pass filter. There will be a trade-off between desiring to filter out irrelevant noise to limit triggering of predatory behaviour when no prey is present, thus limiting energy loss (i.e. avoid false triggering), and respond to prey-generated vibrations (i.e. limit no triggering when prey is present). Increased sensitivity to higher frequency ranges where signal to noise ratio is higher should reduce the trade-off towards successful prey capture (Masters 1984b).

Above 1000 Hz, and indeed between 600-1000 Hz where prey generated vibrations will be less common and restricted to buzzing (Landolfi and Barth 1996; Masters 1984b), there is not sufficient data to explain the sustained high sensitivity of the slit sensilla tuning curve. I

hypothesise that this could be an adaptation to allow the spider to detect silk vibration resonance in their web, which gives useful biological information on where objects are present in their web.

Orb weavers are known to locate and remove objects from their web, whether finding immobile prey or removing detritus from the web (Cloudsley-Thompson 1995; Pasquet and others 2007). They find these objects through a form of echolocation – they send out vibrations into the web through a plucking or bouncing behaviour and are able to accurately locate objects following this behaviour (Klärner and Barth 1982). The mechanism of how this is achieved is currently unknown, although it is thought to be due to the ‘echo’ returning to the spider (Klärner and Barth 1982).

Objects in the web are known to create vibrational resonances as they set up reflection points of waves due to a mismatch in impedance (Landolfi and Barth 1996). An object caught in the capture area of an orb web will therefore reflect vibrations back to the spider, but also create standing waves of a particular frequency only on the radial thread where the object is. Due to the wavespeeds of silks, a difference in time between sending then receiving the vibration will be too short to determine object location (Landolfi and Barth 1996; Mortimer and others 2018). Equally, detecting an amplitude difference is also unlikely to be used to determine object location due to the fast propagation speeds and short propagation distances involved. However, the standing wave frequency will be proportional to the distance to the object. For example, fundamental frequency of transverse standing wave with a spider-object distance of 50 and 100 mm would be 1033 and 516 Hz respectively (assuming tensions of 100 μN and mass per unit length of $9.36 \times 10^{-9} \text{ kg m}^{-1}$ (Mortimer and others 2014; Wirth and Barth 1992)). I therefore propose that orb weavers use the high frequencies of standing waves on silk fibres to locate objects caught in their web, which would explain the sensitivity to high frequency vibrations at low amplitude.

Why, then, is *Cupiennius* most sensitive at 1000 Hz, given that it does not use silk to detect prey-generated vibrations? Physical constraints could be acting. There may simply be a lack of physical mechanism to damp vibrations at high frequencies – a high pass filter may have evolved due to the viscoelasticity of the pad, but a low pass filter has not in spiders.

Evolutionary constraints could be also be acting. There is conflicting evidence about whether silk-based vibration sensing was an ancestral state – the majority of diverse spiders in the Infraorder Araneomorphae (c. 38000 species) have previously been thought to evolve from an orb weaving ancestor (Bond and others 2014; Garrison and others 2016), but more recent evidence suggests that the common ancestor had no foraging web (Fernandez and others 2018). However, relatives in the sister group Mygalomorphae also use silk for sensory transmission (e.g. trap door spiders (Coyle and Icenogle 1994)) and irregular ground sheets are the most likely ancestral state of the entire Araneae Order (Fernandez and others 2018). More study is needed to explore the sensory ecology of spider vibration sense using modern techniques and comparable experimental conditions between spider species, to infer how it has evolved and whether sensory adaptations exist to promote vibrational information transfer across species.

4. Future directions

In conclusion, many unanswered questions remain on the adaptations of spiders to promote vibrational information transfer. Studies are needed on whether and when orb weavers use their proposed control mechanisms to alter web vibration transmission properties, in response to various biotic and abiotic cues. Beyond orb weavers, a systematic study focussing on the webs of the Orbiculariae (orb weavers, sheet web spiders, cob web spiders) could reveal how adaptations to promote vibrational information transfer through webs varies with web types. Coupling between the spider and web has been shown to affect the vibration that enters spider vibration sensors, and more research is required on how different spiders' physical properties and active mechanisms alter coupling to their vibration transmission platform and filtering before sensory transduction. Furthermore, additional

research is required on vibration sensing from a range of different spider species to understand the evolutionary ecology of one of the spiders' major senses, the ability to detect surface vibrations.

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References

- Barth FG, Geethabali. 1982. Spider vibration receptors - threshold curves of individual slits in the metatarsal lyriform organ. *Journal of Comparative Physiology* 148(2):175-185.
- Bond JE, Garrison NL, Hamilton CA, Godwin RL, Hedin M, Agnarsson I. 2014. Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. *Current Biology* 24(15):1765-1771.
- Boutry C, Blackledge TA. 2010. Evolution of supercontraction in spider silk: structure-function relationship from tarantulas to orb-weavers. *Journal of Experimental Biology* 213(20):3505-3514.
- Boutry C, Blackledge TA. 2013. Wet webs work better: humidity, supercontraction and the performance of spider orb webs. *Journal of Experimental Biology* 216(19):3606-3610.

- Cloudsley-Thompson JL. 1995. A review of the anti-predator devices of spiders. *Bulletin of the British Arachnological Society* 10(3):81-96.
- Coyle FA, Icenogle WR. 1994. Natural history of the Californian trapdoor spider Genus *Aliatypus* (Araneae, Antrodiaetidae). *Journal of Arachnology* 22(3):225-255.
- Davranoglou LR, Cicirello A, Taylor GK, Mortimer B. 2019. Planthopper bugs use a fast, cyclic elastic recoil mechanism for effective vibrational communication at small body size. *PLoS Biology* 17(3):e3000155.
- Devetak D, Mencinger-Vračko B, Devetak M, Marhl M, Špernjak A. 2007. Sand as a medium for transmission of vibratory signals of prey in antlions *Euroleon nostras* (Neuroptera: Myrmeleontidae). *Physiological Entomology* 32(3):268-274.
- Eberhard WG. 1981. Construction behaviour and the distribution of tensions in orb webs. *Bulletin of the British Arachnological Society* 5(5):189-204.
- Eberhard WG. 2019. Adaptive flexibility in cues guiding spider web construction and its possible implications for spider cognition. *Behaviour* 156(3-4):331-362.
- Eletto H, Neukirch S, Vollrath F, Antkowiak A. 2016. In-drop capillary spooling of spider capture thread inspires hybrid fibers with mixed solid-liquid mechanical properties. *Proceedings of the National Academy of Sciences of the United States of America* 113(22):6143-6147.
- Endo J, Takanashi T, Mukai H, Numata H. 2019. Egg-cracking vibration as a cue for stink bug siblings to synchronize hatching. *Current Biology* 29(1):143-148.
- Erko M, Younes-Metzler O, Rack A, Zaslansky P, Young SL, Milliron G, Chyasnachyus M, Barth FG, Fratzl P, Tsukruk V et al. . 2015. Micro- and nano-structural details of a spider's filter for substrate vibrations: relevance for low-frequency signal transmission. *Journal of the Royal Society Interface* 12(104):13.
- Fernandez R, Kallal RJ, Dimitrov D, Ballesteros JA, Arnedo MA, Giribet G, Hormiga G. 2018. Phylogenomics, diversification dynamics, and comparative transcriptomics across the spider tree of life. *Current Biology* 28(9):1489-1497.

- Frohlich C, Buskirk RE. 1982. Transmission and attenuation of vibration in orb spider webs. *Journal of Theoretical Biology* 95(1):13-36.
- Garrison NL, Rodriguez J, Agnarsson I, Coddington JA, Griswold CE, Hamilton CA, Hedin M, Kocot KM, Ledford JM, Bond JE. 2016. Spider phylogenomics: untangling the spider tree of life. *Peerj* 4:e1719.
- Gingl E, Burger AM, Barth FG. 2006. Intracellular recording from a spider vibration receptor. *Journal of Comparative Physiology A* 192(5):551-558.
- Guan J, Porter D, Vollrath F. 2012. Silks cope with stress by tuning their mechanical properties under load. *Polymer* 53(13):2717-2726.
- Guan J, Porter D, Vollrath F. 2013. Thermally induced changes in dynamic mechanical properties of native silks. *Biomacromolecules* 14(3):930-937.
- Guan J, Vollrath F, Porter D. 2011. Two mechanisms for supercontraction in *Nephila* spider dragline silk. *Biomacromolecules* 12(11):4030-4035.
- Guinea GV, Elices M, Pérez-Rigueiro J, Plaza GR. 2005. Stretching of supercontracted fibers: a link between spinning and the variability of spider silk. *Journal of Experimental Biology* 208(1):25-30.
- Hill PSM. 2008. *Vibrational Communication in Animals*. Cambridge, MA: Harvard University Press.
- Hill PSM. 2009. How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften* 96(12):1355-1371.
- Hill PSM, Wessel A. 2016. Biotremology. *Current Biology* 26(5):R187-R191.
- Hoffmaster DK. 1982. Responses of the spider *Argiope aurantia* to low frequency phasic and continuous vibrations. *Animal Behaviour* 30(1):123-127.
- Holbrook RI, Mortimer B. 2018. Vibration sensitivity found in *Caenorhabditis elegans*. *Journal of Experimental Biology* 221(15):jeb178947.
- Klärner D, Barth FG. 1982. Vibratory signals and prey capture in orb-weaving spiders (*Zygiella x-notata*, *Nephila clavipes*, Araneidae). *Journal of Comparative Physiology* 148(4):445-455.

- Krink T, Vollrath F. 1997. Analysing spider web-building behaviour with rule-based simulations and genetic algorithms. *Journal of Theoretical Biology* 185(3):321-331.
- Landolf MA, Barth FG. 1996. Vibrations in the orb web of the spider *Nephila clavipes*: cues for discrimination and orientation. *Journal of Comparative Physiology A* 179(4):493-508.
- Liesenfeld FJ. 1956. Untersuchungen am netz und über den erschütterungssinn von *Zygiella x-notata* (CL) (Araneidae). *Zeitschrift Fur Vergleichende Physiologie* 38(6):563-592.
- Liesenfeld FJ. 1961. Über leistung und sitz des erschütterungssinnes von netzspinnen. *Biologisches Zentralblatt* 80:465-475.
- Liu Y, Sponner A, Porter D, Vollrath F. 2008. Proline and processing of spider silks. *Biomacromolecules* 9(1):116-121.
- Masters WM. 1984a. Vibrations in the orbwebs of *Nuctenea sclopetaria* (Araneidae). 1. Transmission through the web. *Behavioral Ecology and Sociobiology* 15(3):207-215.
- Masters WM. 1984b. Vibrations in the orbwebs of *Nuctenea sclopetaria* (Araneidae). 2. Prey and wind signals and the spiders response threshold. *Behavioral Ecology and Sociobiology* 15(3):217-223.
- McConney ME, Schaber CF, Julian MD, Barth FG, Tsukruk VV. 2007. Viscoelastic nanoscale properties of cuticle contribute to the high-pass properties of spider vibration receptor (*Cupiennius salei* Keys). *Journal of the Royal Society Interface* 4(17):1135-1143.
- Mhatre N, Sivalingham S, Mason AC. Posture controls mechanical tuning in the black widow spider mechanosensory system. *bioRxiv* doi:10.1101/484238.
- Molina J, Schaber CF, Barth FG. 2009. In search of differences between the two types of sensory cells innervating spider slit sensilla (*Cupiennius salei* Keys.). *Journal of Comparative Physiology A* 195(11):1031-1041.
- Morley EL, Sivalingham S, Mason AC. 2016. Developmental morphology of a lyriform organ in the Western black widow (*Latrodectus hesperus*). *Zoomorphology* 135(4):433-440.

- Mortimer B. 2017. Biotremology: Do physical constraints limit the propagation of vibrational information? *Animal Behaviour* 130:165-174.
- Mortimer B, Gordon SD, Siviour CR, Holland C, Vollrath F, Windmill JFC. 2014. The speed of sound in silk: linking material performance to biological function. *Advanced Materials* 26(30):5179-5183.
- Mortimer B, Soler A, Siviour CR, Vollrath F. 2018. Remote monitoring of vibrational information in spider webs. *The Science of Nature* 105:37.
- Mortimer B, Soler A, Siviour CR, Zaera R, Vollrath F. 2016. Tuning the instrument: sonic properties in the spider's web. *Journal of the Royal Society Interface* 13(122):20160341.
- Mortimer B, Soler A, Wilkins, L, Vollrath F. 2019. Decoding the locational information in the orb web vibrations of *Araneus diadematus* and *Zygiella x-notata*. *Journal of the Royal Society Interface*. In press (20190201).
- Naftilan SA. 1999. Transmission of vibrations in funnel and sheet spider webs. *International Journal of Biological Macromolecules* 24(2-3):289-293.
- Nakata K. 2012. Plasticity in an extended phenotype and reversed up-down asymmetry of spider orb webs. *Animal Behaviour* 83(3):821-826.
- O'Connell-Rodwell CE, Arnason B, Hart LA. 2000. Exploring the possibility of low-frequency seismic communication in elephants and other large mammals. *American Zoologist* 40(6):1154-1155.
- Pasquet A, Cardot J, Leborgne R. 2007. Wasp attacks and spider defence in the orb weaving species *Zygiella x-notata*. *Journal of Insect Behavior* 20(6):553-564.
- Pérez-Rigueiro J, Elices M, Guinea G. 2003. Controlled supercontraction tailors the tensile behaviour of spider silk. *Polymer* 44(13):3733-3736.
- Singer F, Riechert SE, Xu HF, Morris AW, Becker E, Hale JA, Nouredine MA. 2000. Analysis of courtship success in the funnel-web spider *Agelenopsis aperta*. *Behaviour* 137:93-117.

- Snarr KA. 2005. Seismic activity response as observed in mantled howlers (*Alouatta palliata*), Cuero y Salado Wildlife Refuge, Honduras. *Primates* 46(4):281-285.
- Speck J, Barth FG. 1982. Vibration sensitivity of pretarsal slit sensilla in the spider leg. *Journal of Comparative Physiology* 148(2):187-194.
- Vibert S, Scott C, Gries G. 2016. Vibration transmission through sheet webs of hobo spiders (*Eratigena agrestis*) and tangle webs of western black widow spiders (*Latrodectus hesperus*). *Journal of Comparative Physiology A* 202(11):749-758.
- Vollrath F, Downes M, Krackow S. 1997. Design variability in web geometry of an orb-weaving spider. *Physiology & Behavior* 62(4):735-743.
- Vollrath F, Madsen B, Shao ZZ. 2001. The effect of spinning conditions on the mechanics of a spider's dragline silk. *Proceedings of the Royal Society B* 268(1483):2339-2346.
- Walcott C. 1959. Behavior and vibration sensitivity in the spider. *Anatomical Record* 134(3):650-651.
- Watanabe T. 2000. Web tuning of an orb-web spider, *Octonoba sybotides*, regulates prey-catching behaviour. *Proceedings of the Royal Society B* 267(1443):565-569.
- Wignall AE, Herberstein ME. 2013. The influence of vibratory courtship on female mating behaviour in orb-web spiders (*Argiope keyserlingi*, Karsch 1878). *PLoS One* 8(1):e53057.
- Wirth E, Barth FG. 1992. Forces in the spider orb web. *Journal of Comparative Physiology A* 171:359-371.
- Wirth M, Wolff JO, Appel E, Gorb SN. 2019. Ultrastructure of spider thread anchorages. *Journal of Morphology* 280(4):534-543.
- Wu CH, Elias DO. 2014. Vibratory noise in anthropogenic habitats and its effect on prey detection in a web-building spider. *Animal Behaviour* 90:47-56.
- Young SL, Chyasnachyus M, Erko M, Barth FG, Fratzl P, Zlotnikov I, Politi Y, Tsukruk VV. 2014. A spider's biological vibration filter: Micromechanical characteristics of a biomaterial surface. *Acta Biomaterialia* 10(11):4832-4842.

Zschokke S, Vollrath F. 1995a. Unfreezing the behaviour of two orb spiders. *Physiology and Behavior* 58(6):1167-1173.

Zschokke S, Vollrath F. 1995b. Web construction patterns in a range of orb-weaving spiders (Araneae). *European Journal of Entomology* 92(3):523-541.

Figure legends

Figure 1. Diagram of the orb web of *Araneus diadematus*. The radial, bridging and mooring threads are made from major amplullate (MA) silk, whereas the capture spiral is made from flagelliform and aggregate (FL, AG) silk. Adhesive disks made from piriform (PI) silk keep the web structure and an auxiliary spiral made from minor amplullate (MiA) silk is used during web building but subsequently removed in this species.

Figure 2. Links between spider control mechanism, material and sonic properties of silks, and their biological relevance. Numbers give the reference: 1 Mortimer and others (2016), 2 Landolfi and Barth (1996), 3 Wirth and Barth (1992), 4 Mortimer and others (2014), 5 Boutry and Blackledge (2010), 6 Guan and others (2012), 7 Guan and others (2013), 8 Liu and others (2008). Adapted from Figure 5 in Mortimer and others (2016).

Figure 3. Tuning curves of slit sensilla in three spider species of different ecologies.

For *Cupiennius*, extracellular recordings of individual slits were made (Barth and Geethabali 1982), for *Zygiella* and *Tegenaria*, leg nerve recordings were made (Liesenfeld 1961).

Adapted from Figure 8 in Barth and Geethabali (1982) (Barth and Geethabali 1982), reproduced with permission from the publisher Springer Nature.