

Decoding the locational information in the orb web vibrations of *Araneus*
diadematus* and *Zygiella x-notata

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1 Abstract

2 A spider's web is a multifunctional structure that captures prey and provides an information
3 platform that transmits vibrational information. Many physical factors interact to influence web
4 vibration and information content, from vibration source properties and input location, to web
5 physical properties and geometry. The aim of the study was to test whether orb web vibration
6 contains information about the location of the source of vibration. We used Finite Element Analysis
7 model webs to control and vary major physical factors, investigating webs where spiders use a direct
8 or remote monitoring strategy. When monitoring with eight sensors (legs) at the web centre, a
9 comparison of longitudinal and transverse wave amplitude between the sensors gave sufficient
10 information to determine source direction and distance respectively. These localisation cues were
11 robust to changes in source amplitude, input angle and location, with increased accuracy at lower
12 source amplitudes. When remotely monitoring the web using a single thread connected to the web's
13 hub (a signal thread), we found that locational information was not available when the angle of the
14 source input was unknown. Furthermore, a free sector and a stiff hub were physical mechanisms to
15 aid information transfer, which provides insights for bio-inspired fibre networks for sensing
16 technologies.

1. Introduction

The transfer of information via vibrations through materials and along surfaces is used by a wide range of organisms, from spiders and insects, to elephants and humans [1, 2]. One of the main types of information that organisms can extract from substrate-borne vibrations is the location of the source, which is aided by detection across two or more spatially-separated sensors [3, 4]. There are two parts to the problem of locating a source, firstly determining orientation (or angle) to the source, and secondly determining the distance to the source relative to current body position. Both orientation and distance are needed to pin-point exact location, but the relative importance of each will vary with biological context [4]. Extracting vibration source location is relevant for many biological systems, but can also be important for engineered systems particularly in the context of structural health monitoring and soft robotics [5, 6].

Spider orb webs are excellent model systems in which to study vibration source localisation from both biological and engineering perspectives. Spiders have evolved an almost unique degree of control over information transfer via vibrations as they make their vibration transmission platform, the web, from their own manufactured materials, spider silks [4, 7]. The spiders' active control mechanisms over the vibrational properties of the orb webs include adjusting silk properties during spinning, altering web geometry during web building and active tensioning of the web post-spinning [7-10]. Combined, this control should mitigate physical constraints acting on information transfer [4], including the extraction of information on source localisation. From an engineering perspective, the orb web resembles a soft polymeric sensory network with strategically deployed contact sensors. Bioinspired insights into the transfer of vibrational information through a polymeric network might be useful in applications involving smart multifunctional materials with imbedded sensors, e.g. wearable technologies or soft robotics [11-13].

Spiders detect web vibration via their legs, through slit sensilla sensory organs distributed on their exoskeletons that detect leg displacement [14] as well as, probably, stretch receptors in their

tendons [15]. There are two common strategies for monitoring orb web vibration [16]. The web-dwelling orb weaver *Araneus diadematus* spends most of its time on and around the hub, or web centre. This spider contacts the web with all eight legs in a characteristic stance and thus has eight spatially-separated sources of vibrational information [17, 18]. In contrast, the sector web spider *Zygiella x-notata* monitors web vibration from a near-by retreat using one or two legs contacting a signal thread attached to the hub [18, 19]. In response to items being caught in the web, *Zygiella* moves to the hub, where it will typically pause to orient itself [18].

Vibration sources in the orb web may be abiotic such as wind and branch flutter [20], or biotic such as prey struggle, potential mates, invading conspecifics or predators [21-24]. Biotic sources propagate from a specific location and determining the source location is vital for an appropriate response by the spider. Similarly, detritus caught in the web can be located by the spider for removal during web cleaning [25].

Three types of vibrational waves travel through orb webs: lateral and transverse waves – which comprise motions perpendicular to the fibre, within the plane of the web or perpendicular to the plane respectively – and longitudinal waves, which are parallel [26]. Each kind of wave has a different propagation speed and is subject to different degrees of damping and frequency filtering. This results in differences in arrival time, amplitude and frequency content for each type of wave [26-30], which can potentially be used for localisation information [4].

A range of physical factors affect the information that propagates through an orb web. Firstly, input properties can vary, such as the displacement (amplitude), frequency content and temporal pattern. Secondly, the input position and 3D angle relative to the web plane can vary. Finally, physical properties of the web can differ, such as web geometry, silk tension and stiffness, and the presence of any mass (e.g. spider, prey or a leaf) on the web. Many of these physical factors interact to influence the vibrational information propagating through orb webs [7, 16, 26-28, 30, 31].

This study aims to test the hypothesis that web vibration contains information about the vibration source location, both orientation and distance information. We also test two further specific hypotheses that: i) *Araneus* and *Zygiella* webs differ in the information content on vibration source location; and ii) the linked hypothesis that aspects of web structure under the control of spiders alters the information content on vibration source location. We test these hypotheses using Finite Element Analysis (FEA) computer models, with geometry and material properties based on measurements from real webs, previously validated with experimental data [7, 16]. The advantage of studying webs *in silico* is the ability to inspect the three components of vibrational data at multiple points simultaneously, controlling for variability of relevant physical factors in order to test how they interact to influence localisation information present in web vibration. Whereas previous studies have focussed on the effects of isolated physical factors on the propagation of vibrations in the web [7, 16, 26-28, 30], here we quantify the orientation and distance information present in web vibration and how robust these cues are to changing and interacting physical factors. As outlined above, the interacting physical factors are numerous and complex and we do not aim to investigate all the relevant interactions within this study, although other factors will be discussed. We focus on the major effects of vibration input angle, vibration source amplitude (at small displacements, within the range of struggling prey), vibration source location and *Araneus* versus *Zygiella* webs to test our hypotheses.

2. Methods

2.1 Spiders and webs

Araneus diadematus and *Zygiella x-notata* spiders (N=8 and 12 respectively) were collected within Oxford City and kept in frames (30x30x5 cm) in lab conditions (c. 20 °C, 40 % RH and a 16h:8h light–dark cycle). Spiders had to make at least two webs in a frame for a web to be selected and used for modelling (N=3 for each species [16]). All spiders were handled according to local lab risk assessments and institutional ethical guidelines and as invertebrates, do not currently fall under

regulation by the UK Home Office or EU legislation. Selected webs were photographed and traced digitally to extract the 2D web geometry of the webs that were used in separate computer models (i.e. three models for the three selected webs of each species; no 3D information was extracted or used in the models). Web geometries were extracted from photographs of real webs in all details except for the hub mesh, which was simplified to a stiff spiral. The positions of *Araneus* individuals on their webs were also analysed and multiple spider individuals of both species were weighed to measure their mass.

2.2 Modelling

The finite element models were created using Abaqus/Explicit 6.14-2. The model outputs have previously been compared to and validated by experimentally-measured time-velocity vibration outputs of real webs, where the vibration input stimuli, their locations and the web geometries were the same as in the models [7, 16].

The models were designed to include the main characteristics of real webs: action of aerodynamic drag, pre-tension on the radial threads, 2D geometry taken from real webs and mechanical properties of the different types of silks. The models assumed linear elastic behaviour, which was appropriate for the low strains of the vibration pulse input (radial threads extensions were always <1 %). Therefore viscoelasticity and internal damping were not modelled, although aerodynamic drag forces were [32]. Displacements were prevented at the ends of the anchor threads by pinning at their boundaries. Similar to real webs [9], a pre-tension field was introduced onto the webs. Certain physical factors were kept constant as they were expected to have less relevance for or influence on localisation information in the web, including the vibration input frequency content and temporal pattern, mass of each type of spider on the web and silk material properties. The models used diameters and stiffness values of the different silk types measured from real webs, taken from the literature [9, 10, 33-35]. More details on the model and material properties are given in Mortimer *et al.* [7].

All models applied a mass on to the web to simulate the effect of spider presence on web vibration. *Araneus* web models used a 20 mg total weight, distributed as eight point masses. The position of the eight points were obtained from photographs of the spiders in their natural positions on real webs (see Figure 2a). *Zygiella* were smaller at 4 mg total weight and from observations we assume that these spiders place only a small amount of their weight on the signal thread. Therefore, a mass of 0.5 mg was added to the web at a single position on the signal thread near the retreat. The positions where mass was applied also formed the output positions of the model, i.e. the spider's leg positions to measure web vibration, and are shown in Figures 2a (given by numbers) and 3a (given by red dot). Model outputs consisted of displacement-time profiles for longitudinal, lateral and transverse waves collected at every mode from the model. The outputs from the positions representing the spiders' legs were gathered at a sampling frequency of 20 kHz. Stresses and strains were also collected at each mode to check the model remained within the elastic region of the silk materials (strain < 1%). The outputs were analysed using a custom-written Matlab code to extract the coordinates of local maxima peaks (minimum separation 0.0001 s), including the amplitude and time of the first significant peak.

The numerical simulation consisted of two steps, where the web structure was given time to reach mechanical equilibrium after imposing an initial pre-tension field, then the radial node was vibrated. The basis of the vibration stimulus input was laser Doppler vibrometer recordings of solenoid motion that were previously used as vibration inputs into real webs [7, 16]. The input was approximately a rectangular pulse of 3 ms duration (maximum displacement 0.34 mm), which contained many frequencies simultaneously. This displacement was chosen to i) keep the elastic model appropriate, as silks would remain in their elastic regions at these displacements, ii) match the input waveform used in experiments of web vibration [7, 16], and iii) be within the range of spider vibration sensors and vibrations generated by struggling prey (displacement is approximately eight times the displacement measured for prey in real webs [31]). The presence of spider mass on the web leads to reflections of the input pulse, leading to multiple amplitude peaks that dampen over time (Figure 1).

The simulations differed in the web type (*Araneus* or *Zygiella*), vibration input location (radial thread and position from hub), vibration input angle (XY and XZ planes, where the X axis is along the radial thread axis) and vibration input amplitude (either 0.34, 3.4 or 6.8 mm), where figure legends specify the combination of parameters used. For the data presented, the polar angle with respect to the Z axis was fixed at 30°, as the effect of polar angle has previously been investigated [7], and an angle of 30° ensures that there is sufficient amplitude of transverse, longitudinal and lateral waves for investigation.

3. Results and Discussion

3.1 Factors affecting longitudinal, lateral and transverse wave amplitude

Understanding the physical factors that affect the detected maximum vibration amplitude are important in order to understand and appreciate the amplitude information available to spiders for determining the location of vibration sources, which is discussed in Sections 3.2 and 3.3.

The angle within the plane of the web (XY) affected the direction and amplitude of longitudinal, lateral and transverse waves on webs with mass on them (Figure 1). A spherical coordinate system was defined with the origin at the input point. The X axis was within the axis of the radial thread, the Y axis was perpendicular to it within the plane of the web (Figure 1b inset) and the Z axis is perpendicular to the web plane. We have previously shown that the polar angle affects wave amplitude [7] (see also Supplementary Figure 1). Taken together, deviation in the input angle in three dimensions altered the amplitude of all three wave types in the web.

In the case of the small amplitude vibration pulse, the detected amplitudes of the three propagating waves are influenced by multiple factors that interact. These include the displacement amplitude of the vibration input, which within a biological context could be due to larger prey [28, 31, 36].

Amplitude is also affected by the input location and web geometry, where vibrations lose energy as they propagate for longer distances through the web mesh [7, 28]. Each wave type also differs in how it dissipates energy, due to a combination of geometric spreading (diluting of vibrational energy

of the web surface), external damping through air drag, and internal damping due to silk properties. Longitudinal waves have been shown to dissipate the least amount of energy, as there is less spreading of vibrational energy to other radials, and less damping due to air drag [7, 26-29]. Longitudinal wave amplitude is also affected by silk stiffness, whereas transverse wave amplitude is affected by silk tension [7]. The presence of mass also introduced reflection points within the web, affecting the amplitude of waveforms over time (Figure 1). In addition, mass decreases peak amplitudes of transverse waves due to inertial effects that also slow down these waves [16]. The addition of prey mass was not included in our models, but is likely to create additional reflection points, alter the tensions present on the web and slow down waves further due to inertial effects. We add to this list the interaction of vibration input angle, meaning that the angle of deformation of the web alters the relative amplitudes and contributions of longitudinal, lateral and transverse waves.

In the real-world, vibrational inputs will vary considerably. When vibration amplitude is higher, reflections will dominate real web vibration, for example as waves reflect off objects caught in the web, such as caught prey [18, 27]. Reflections also lead to standing waves and frequency filtering within the web [4], for example web or spider resonance following impact [30, 37, 38]. Furthermore, vibrations or impacts of higher amplitude are likely to increase internal damping as radial threads yield, which is an effect not tested in our models. Capture threads are also likely to change their response with amplitude – high amplitude lateral waves could lead to tension asymmetry if slack is introduced to these threads. However, the windlass mechanism of the capture spiral [39, 40] may prevent this at slower speeds; this mechanism, however, was not investigated at faster rates.

3.2 Orientation

Orientation to a vibration source requires a detectable gradient that correlates with the direction of a vibration source [4]. Although longitudinal waves show less amplitude spreading in the web [7, 26-28], thus acting as a directional cue, here we quantified the orientation information available within the webs of two spiders that differ in their monitoring strategies: *Araneus* with eight legs at the web hub and *Zygiella* with one leg on the signal thread.

3.2.1 Hub-dwelling spider: *Araneus*

The data we considered for *Araneus diadematus* was the three components of displacement over time at each leg point, modelled as point masses (Figure 2).

Figure 2 shows that for a particular vibration input position and angle, the direction of motion of the three types of waves (radial, tangential and out of plane displacement for longitudinal, lateral and transverse waves respectively) can be grouped into four zones of potential sensory input (Figure 2a). Reversing the input in the radial or tangential directions flips zones 1 and 3 and zones 2 and 4 as both lateral and longitudinal waves change direction simultaneously (Figure 1). The persistence of four zones across different input angles is explained by the structure of the web, which is pulled towards the direction of displacement (Figure 2a) with the web rotating (locally) about the hub, acting as a rotational mesh in response to web vibration.

As expected [7, 27, 28], the amplitude of longitudinal waves provided information on source orientation at the hub (Figure 2b). Within each zone, the amplitude of longitudinal and lateral waves changed across each leg according to the position relative to the input location, but transverse wave amplitude remained relatively constant. When the input location was moved to different radials in the web, the leg with the highest longitudinal wave amplitude was consistently closest to the input location (Figure 2b, dark magenta stars). If these vibrations are used to determine orientation, this would require spiders to be able to separate longitudinal and lateral waves as both reach similar peak amplitudes, but on different legs (Figure 2b). Spider slit sensilla are known to be equally

213 sensitive to lateral and dorso-ventral leg displacement [14], but it is unknown whether spiders can
214 distinguish motion in different directions [7, 27].

215 Since this method to orientate relies on the amplitude of longitudinal waves, it was important to test
216 the robustness of this mechanism concerning other factors that would also affect longitudinal wave
217 amplitude. Input angle influenced the direction and amplitude of longitudinal waves (Figures 1, 2,
218 Supplementary Figure 1), but did not alter the gradient present across the eight legs when source
219 location and amplitude were kept constant. The exception was that legs at 0° and 180° degrees
220 relative to the source (leg 1 and leg 4) became more similar as input angle approached wholly within
221 the fibre axis away from the hub (Figure 3a-c). Our models predicted that orthogonal inputs relative
222 to the radial thread within the web plane are harder for the spider to localise as longitudinal wave
223 amplitudes tend to decrease towards zero (Figure 1). This was partly due to the small amplitudes
224 used here, as larger transverse wave amplitude leads to higher longitudinal wave amplitude [41], so
225 more directional information will be available as vibration amplitude increases [7].

226 Distance and source amplitude also affect longitudinal wave amplitude. In our model experiments,
227 distance to the source did not mask orientation information at small amplitudes (Supplementary
228 Figure 2a) as this did not change the longitudinal wave amplitude gradient present across the eight
229 legs at the hub. The structure of the hub exaggerated orientation information at low source
230 amplitudes. The stiff spirals present at the hub introduced a damping gradient onto longitudinal
231 waves which meant that there was a detectable difference in amplitude between legs
232 (Supplementary Figure 2a, as shown by the amplitude ratios of less than 1 relative to the closest leg,
233 i.e. all legs had lower amplitude), which would aid orientation. However, at higher source
234 amplitudes, similar to the effect of input angle, legs that were c. 0° and c. 180° relative to the source
235 became more similar and some of the latter had higher longitudinal wave amplitude than the closest
236 leg (Supplementary Figure 2b, c, as shown by amplitude ratios closer or higher than 1 relative to the
237 closest leg). There was also an interaction with distance (Supplementary Figure 2b, c), with higher

amplitudes at input locations closer to the web frame (i.e. further from hub) due to higher energy transfer into the stiff framing threads [7]. Therefore, other orientation gradients would be needed at higher source amplitudes and some input angles to solve between high longitudinal wave amplitude on legs c. 0° or c. 180° relative to the source, which could be lateral or transverse wave amplitude (Figure 2, Figure 5, Supplementary Figure 2e, f).

3.2.2 Retreat-dwelling spider: *Zygiella*

To further probe available information on source direction in the web, we assessed the directional information available to a spider that uses a signal thread, such as *Zygiella x-notata* (Figure 4). For a given set of vibration input angles, there were four zones of direction of movement for longitudinal, lateral and transverse waves as input location moved around the web (Figure 4a). In theory, the ratios of the three waves could be used to provide information on input direction (Figure 4b).

However, as input angle also affected the ratios of the three wave types, the spider cannot solve for vibration input direction when the input angle is unknown. As before, changes in input angle in the radial or tangential directions will flip zones 1/3 and 2/4 meaning that the direction of motion of the signal thread cannot be used to determine zone of vibration source location on the web when input angle is unknown. We therefore postulate that *Zygiella*, and other spiders that use a signal thread [42], cannot orientate to a vibration source using signal thread vibration and must move to the hub and orientate there using eight legs similar to *Araneus*. This is supported by observations that *Zygiella* always goes from the retreat to the hub initially and, upon arrival, often actively plucks radial threads to locate caught prey [18]. This, obviously, has implications for overall speed of prey localisation.

Aside from the lack of directional information, there were some other notable mechanistic comparisons between the two strategies of web vibration monitoring. Unlike the *Araneus* web system, the use of the signal thread meant that *Zygiella* measured the movement of the hub, rather than the rotation of the web mesh. The directions of longitudinal and lateral waves were out of

phase with the input due to the missing sector – the hub followed the direction that most of the surrounding web mesh was rotating towards. As the hub is at the rotational centre for longitudinal and lateral waves, within a complete orb web (Figure 2) the centre of the hub does not move much within the plane of the web, as movements of the surrounding web mesh are approximately equal and opposite. In contrast, the missing sector creates an imbalance of web mesh movement caused by the web asymmetry. The missing sector therefore caused the hub to move more within the lateral and longitudinal axes, acting to amplify the vibrations that were measured with a signal thread.

3.3 Locating distance

Whereas orientation to a vibration source requires a detectable gradient that correlates with vibration source direction, determining the distance to a vibration source requires a gradient that correlates with distance to the source. This could be time of arrival or amplitude difference between two or more legs for two separate wave types [4]. However, if we assume the spider has information on source direction, only one other time or amplitude difference across different wave types or legs is required for determining the distance, as long as this correlates with distance to the source, is robust to range of input parameters and provides a time or amplitude difference that can be detected by the spider. Frequency content or resonant modes could possibly also be used for locating the source, but will vary considerably in reality as web geometry, silk properties and spectral content of the source differs. An alternative method to detect distance could be the use of web plucking [18], which is used to detect presence and possibly distance to a caught object in their web. The mechanism that spiders use to detect and locate objects in their web using plucking is unknown, but time lag is unlikely as the waves will be too fast to detect [16]. This active method is not always used by the spider, and it takes longer to locate items than the ‘passive’ detection of propagating vibrations through the web [18].

287 As *Zygiella* had neither an orientation cue from the signal thread, nor a comparison between
288 spatially-separated legs, we predict that *Zygiella* will be unable to determine distance to the source
289 from signal thread vibrational motion. We can therefore conclude that *Araneus* and *Zygiella* webs
290 differ in the information content on vibration source location.

291 3.3.1 Time difference

292 Both longitudinal and transverse waves have such high wave speeds that the propagation time
293 through webs without mass is under the minimum time difference that spiders can detect (2-4 ms)
294 [3, 16, 29, 43], meaning that time of arrival between legs would not be useable information by the
295 spider [28]. When mass is present on the web, transverse waves are slowed down sufficiently that
296 difference in peak time of transverse and longitudinal waves are within a detectable range and vary
297 with vibration source location [16].

298 We tested whether peak time difference between: (i) transverse waves across different legs, and (ii)
299 transverse and longitudinal/lateral waves on an *Araneus* web with mass could be used to determine
300 source distance. We used three input amplitudes over four propagation distances to look for a
301 correlation with propagation distance but no correlation with input amplitude. Here we found that
302 differences in peak times in both scenarios were consistently over 4 ms, which suggests that spiders
303 may detect the waves as separate arrival events (Supplementary Figures 3 and 4).

304 Comparing transverse peak time between legs, we found that legs at c. 0° and c. 180° relative to the
305 source were most dissimilar (leg 1 versus 5 in Figure 2) and the ratio in transverse peak time
306 correlated with distance to the source. However, the proposed distance estimation mechanism was
307 not robust to source amplitude as it could not discriminate between close and small sources versus
308 bigger and further away (Supplementary Figure 3).

309 Comparing the difference in peak time between transverse and longitudinal/lateral waves, we found
310 there were no consistent trends with propagation distance, regardless of source amplitude, for

either the peak time differences or the ratio in peak time differences between the legs relative to the leg closest to the source (Supplementary Figure 4). This meant information on source location was not available. However, the leg closest to the source also had a consistently smaller difference in peak time between transverse and longitudinal waves, providing another possible orientation gradient for the spider (Supplementary Figure 4a).

An added level of complexity is given by the observation that transverse wave speeds are highly variable in the web being a function of thread tension as well as being influenced by thread diameter and radial number [28, 29]. This means any mechanism involving transverse wave time will have to be robust to considerable variability [28].

3.3.2 Amplitude difference

An amplitude difference can also be used in theory to determine a vibration source location. As set out in Figure 1, longitudinal and lateral wave amplitude change as a function of input angle. This means that amplitude ratios between wave types cannot be used for distance estimation, as input angle will be unknown and will confound any correlations between amplitude ratios and distance. The remaining options are a comparison of equivalent wave types across legs, which were investigated for each of the wave types across four vibration input locations on a radial thread using three vibration input amplitudes. Again, we looked for a correlation with distance and a lack of correlation with source amplitude.

Both longitudinal and lateral waves showed inconsistent trends over distance between pairs of legs (Supplementary Figure 2). However, peak transverse amplitude gave information on distance from the source (Figure 5). Comparing the ratio between legs; legs that were c. 0° and c. $90/270^\circ$ relative to the source increased in ratio with increasing distance, which was robust over different source amplitudes (Figure 5a). If legs were more similar in peak amplitude, i.e. a ratio closer to 1, this indicated that the source was further away, whereas if legs were less similar in peak amplitude, then the source was closer. Our models indicated that this mechanism would be more accurate with

decreasing source amplitude, as shown by the more linear relationship between distance and ratio at the lowest source amplitude level. Ratios between other legs were not as useful or consistent for determining source distance.

The transverse peak amplitude also gave information on source amplitude (Figure 5b). A higher transverse peak amplitude was more likely to represent a larger source amplitude, although the gradient over distance showed some ambiguity between close and small sources versus bigger and further away (Figure 5b). However, this ambiguity decreased as source amplitude decreased (as shown by the flatter relationship between distance and amplitude), which is in part due to decreased aerodynamic drag when source velocity is lower. Using transverse wave amplitude as a cue for vibration input amplitude would be useful for the spider for discrimination between vibration sources, to ensure spider responses are suitable for vibration sender identity, e.g. responding immediately to the capture of suitable prey [22, 28, 31] versus avoiding bats caught in the web, where identifying bats would allow the spider to avoid potential harm [44].

Transverse peak amplitude will also be sensitive to input angle, mass, silk tension, and web geometry, which affects the propagation path of transverse waves. The proposed distance determination mechanism would therefore be less accurate when any of these factors vary over different parts of the web, altering the transverse amplitude ratio between the legs. However, only input angle is not under some degree of control by the spider. Input angle did not alter transverse wave amplitude between legs, meaning input angle did not alter the ratio between legs by more than 4%, which is within the error due to source amplitude (Figure 3d-f, where input location was 82.6 mm from hub). In terms of mass, an uneven distribution of spider mass on the web is likely [9, 17], but due to the characteristic stance of spiders, the distribution is likely to be taken into account according to the legs involved (e.g. higher inertia on front legs which face down, which are also more sensitive [3]). Prey mass will cause a localised effect that should correlate with distance to the prey, so may aid with prey distance estimation.

Spiders will actively search for and remove masses from their webs [18, 25, 45]. Importantly, spiders actively control, adjust and monitor web tensions during and after web building [7, 9, 46] while all aspects of web architecture/geometry is controlled by the spider during web construction [47]. Details of the web hub geometry, including asymmetry, will be particularly important for controlling the ratios between legs as it will directly influence both transverse wave damping and how transverse wave amplitude spreads over the web as it passes through the hub [7]. This may be one factor influencing why spiders remove the proto-hub and replace it during the final stages of web construction [47]. Overall, the proposed distance determination mechanism seems robust to the major physical factors investigated here, so is a relevant model of the vibrations propagating from struggling prey [28, 36]. In addition, control mechanisms are in place to allow the spider to learn from any errors in determining distance to maximise future fitness.

3.4 Use during information transfer

We have outlined how the time and amplitude information contained within *Araneus* web vibration can be used to determine direction and distance. The question arises whether this information can be detected by the spider in its biological context? Furthermore, do spiders use this information to inform responses to vibrations? Starting with information detection: in theory, comparing amplitudes across legs should be a relatively simple process, and wandering spiders use it for orientation [3]. It does not require any memory and it makes no assumptions of the time pattern, frequency content or absolute amplitude of the source. It does assume that the spider can compare transverse motion across legs – i.e. up-down motion of tarsi, which remains to be tested in orb weavers. Noise, such as from wind [20], will make it harder for the spider to detect the localisation information, as the signal to noise ratio drops [20]. Other environmental factors out of the spiders' control, such as humidity will also affect web tension and stiffness [7], although gradients across the web are not predicted to be affected.

Further studies will wish to test how these mechanisms work as other relevant physical factors change. The frequency content of the source, location and magnitude of masses on the webs and the details of the geometry of the web that might arise through plasticity within and between individuals [8, 9] are expected to affect the web system resonant modes [30] and frequency filtering within the web which may provide further source location cues. Furthermore, the effect of prey mass, silk decorations or other debris will alter web tensions, inertial effects and reflection points, which we predict will provide orientation cues towards these objects and increase the vibration amplitude differences between legs that we propose can be used to estimate distance to the object, which remains to be investigated further.

Concerning whether the spiders use this information: orb weavers are certainly able to quickly orientate towards prey-generated vibrations [18], but whether they make use of distance cues is less clear. In some cases, behaviour is modulated as a function of distance [21], but in other cases a direction would be sufficient as they will determine prey location through tactile sensors. More studies are required to test whether spiders can be tricked into thinking prey are at different locations in their web based on the vibrational information given to them.

We believe that our study provides novel and important insights for bioinspired technologies that make use of filament networks (of a quasi-viscoelastic nature) for sensing and information transfer. We have shown that aspects of web structure under the control of spiders alters the information content on vibration source location. In particular, the use of free sectors to create asymmetry in filament networks can be used to focus information propagation to particular locations (as the webs do towards the signal thread). Spatially-separated sensors in specific locations surrounding an area where vibrations are damped (seen at the web hub) are also important to extract sufficient information for decoding the vibration source location.

4. Data accessibility

Electronic supplementary material supporting this article is available through download. This includes Supplementary Figures 1 to 4. Raw data, diagram of input and output locations and matlab analysis codes have been uploaded open source to Dryad: doi:10.5061/dryad.7rm572m.

5. Competing interests statement

The authors declare no competing interests.

6. Author contributions

BM conceived the research. AS developed the web model, set up the simulations and ran the analysis code. BM interpreted the model data. All authors contributed to article preparation and editing.

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10. Figures

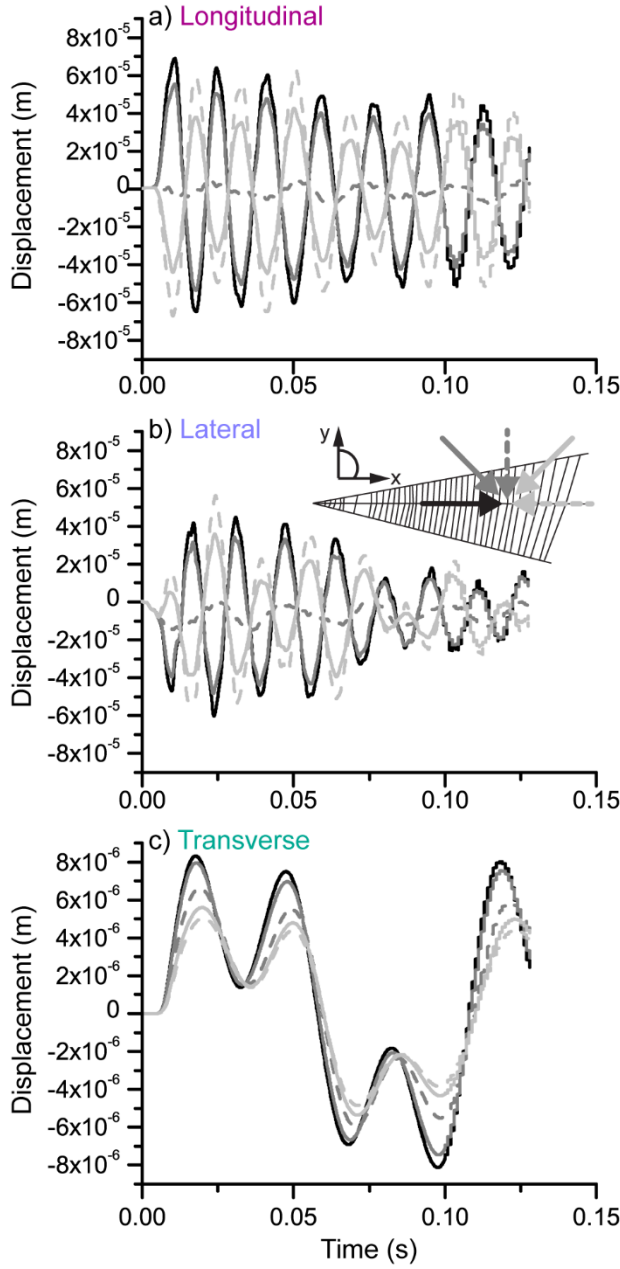


Figure 1. Effect of input azimuthal (within the web plane) angle on a) longitudinal, b) lateral and c) transverse waves. The azimuthal angles were: 0° (along radial fibre axis away from hub) given by solid black, 45° given by solid dark grey, 90° by dashed dark grey (orthogonal to radial fibre), 135° by solid light grey and 180° (along radial fibre towards hub) by dashed light grey. There was also a 30° input polar angle with respect to the Z axis (axis perpendicular to the web plane) for a-c. Inset on panel b illustrates the azimuthal angle within the web plane, i.e. a 2D representation ignoring the constant Z-axis angle which comes out of the plane of the web. Note different axes in panel c. Data are shown for a model *Araneus* web with mass with an input amplitude of 0.34 mm.

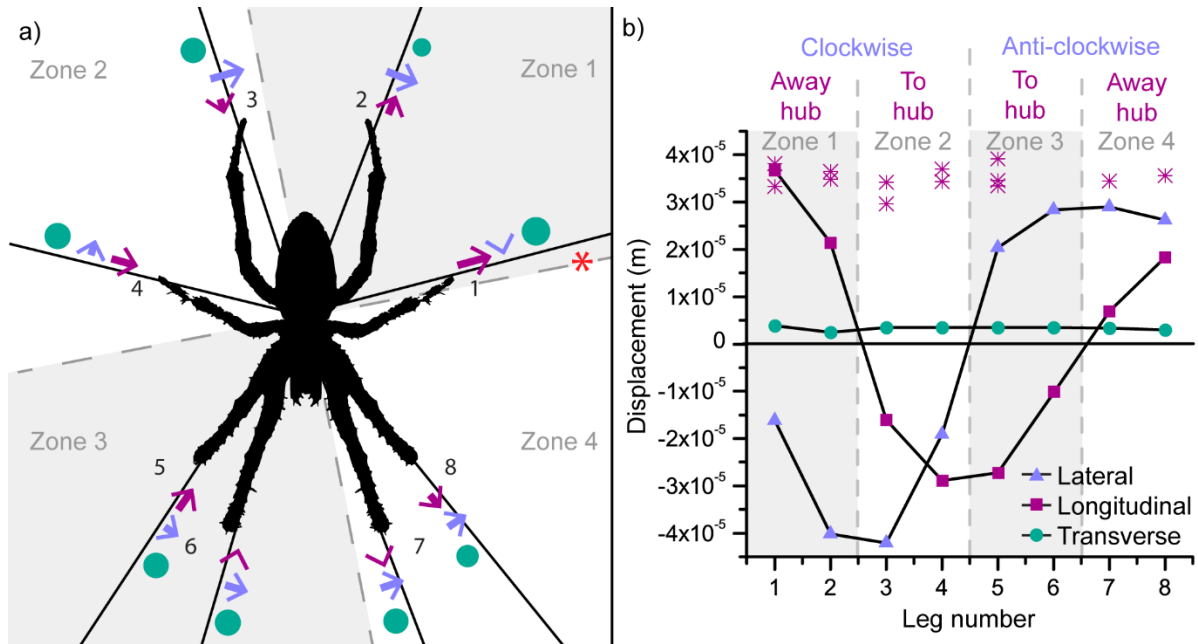


Figure 2. Orientation information for a hub-dwelling spider, such as *Araneus diadematus*. a) Single input location (red asterisk gives radial thread, input is 83.6 mm from hub) and eight output locations at each leg based on the characteristic stance of *Araneus* at the hub for longitudinal (dark magenta), lateral (lilac) and transverse (dark teal) waves. Direction and relative amplitude of first peak are given by arrow direction and line length. The directions of the three types of waves break the web up into four zones, going anticlockwise from vibration source, indicating a rotational mesh mechanism. These zones are correct for an input polar angle of 30° with respect to the Z axis – i.e. 30° bias away from hub measured from the Z axis (perpendicular to web plane). b) Longitudinal (dark magenta squares), lateral (lilac triangles) and transverse (dark teal circles) first peak amplitude varies over the eight legs at the hub for the applied input position and angle, and longitudinal first peak amplitude remains an indicator of vibration source direction as input location moves around the web (dark magenta stars), where distance to the hub is kept constant.

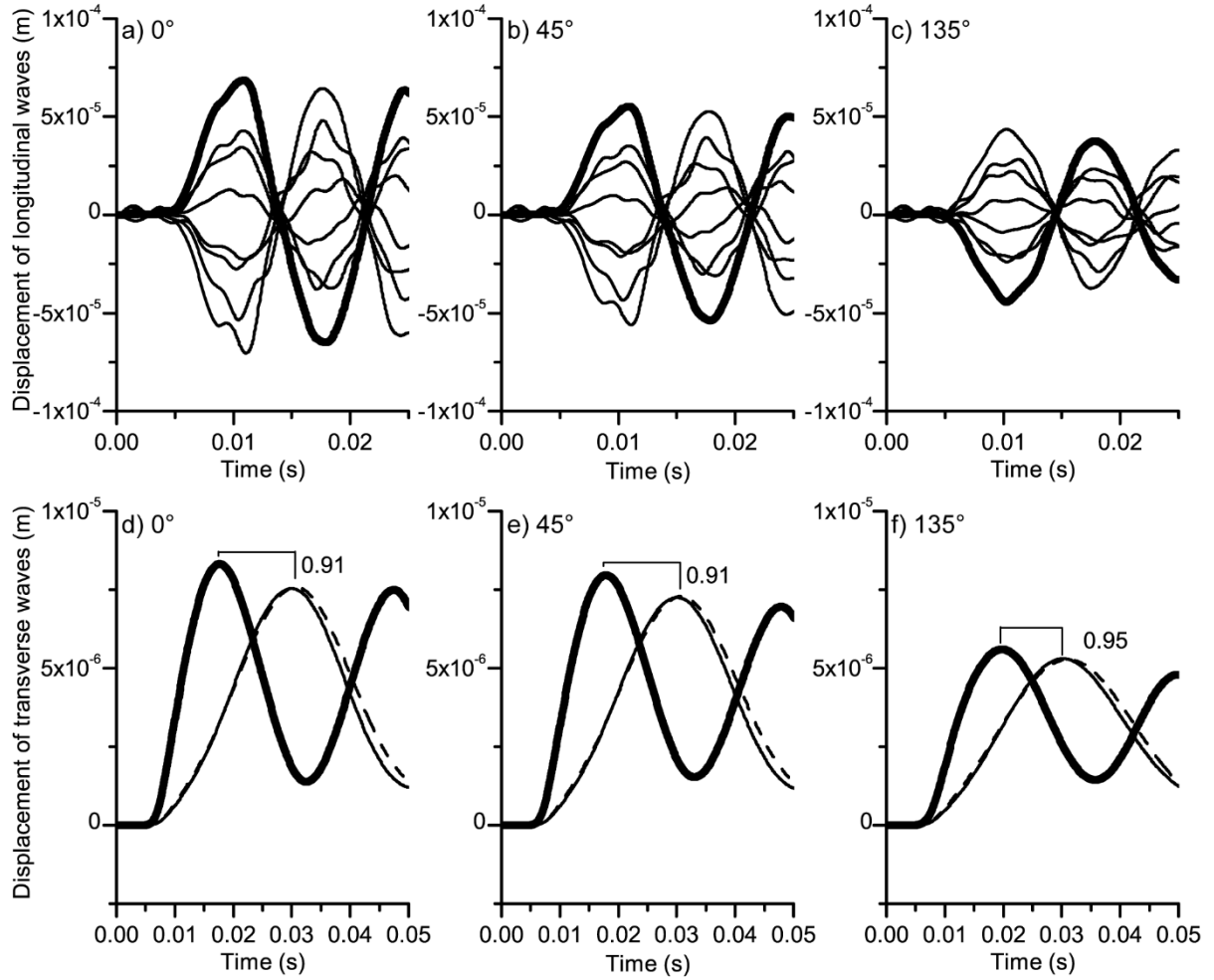


Figure 3. Effect of input azimuthal angle on: a-c) longitudinal waves across all 8 legs, d-f) transverse waves across legs 1, 3, and 7 when input location was stationary 83.6 mm from hub (see Figure 2 for labels of leg and input radial). Leg 1 is denoted by thicker black line, and in d-f, solid thin line gives leg 3 and dashed line gives leg 7. The input azimuthal angle varied in within the plane of the web (see Figure 1): 0° for a and d, 45° for b and e and 135° for c and f. There was also a 30° input polar angle relative to the Z axis (perpendicular to web plane). Data are shown for a model *Araneus* web without mass with an input amplitude of 0.34 mm. The ratio between the first transverse peaks is given on panels d-f.

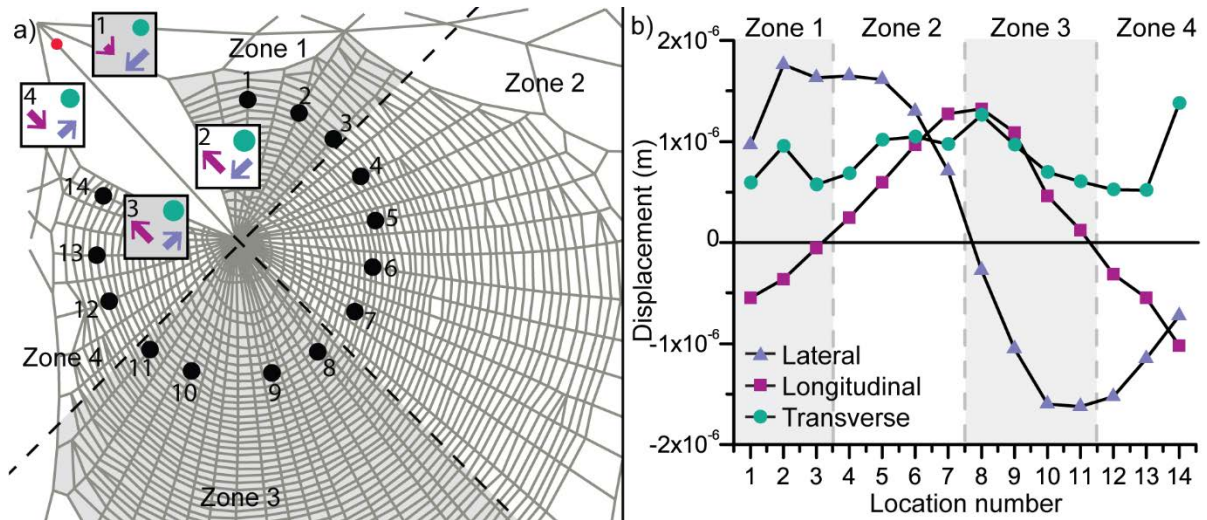


Figure 4. Orientation was not possible for a retreat-dwelling spider, such as *Zygiella x-notata* when input azimuthal angle was not known. a) Input location (black numbered circles) and one output location on the signal thread for longitudinal (dark magenta), lateral (lilac) and transverse (dark teal) waves. Direction and relative first peak amplitude on the signal thread are given by arrow direction and line length. The directions of the three types of waves broke the web up into four zones relative to the signal thread, indicating the signal thread matched hub movement. These zones were correct for an input polar angle of 30° relative to the Z axis—i.e. 30° bias away from hub measured from the Z axis (perpendicular to web plane). b) Longitudinal (dark magenta squares), lateral (lilac triangles) and transverse (dark teal circles) first peak amplitude varied over the 14 input locations when measured at the signal thread, but the first peak amplitudes of all three waves change with input azimuthal angle, meaning no directional information is present when input angle is unknown.

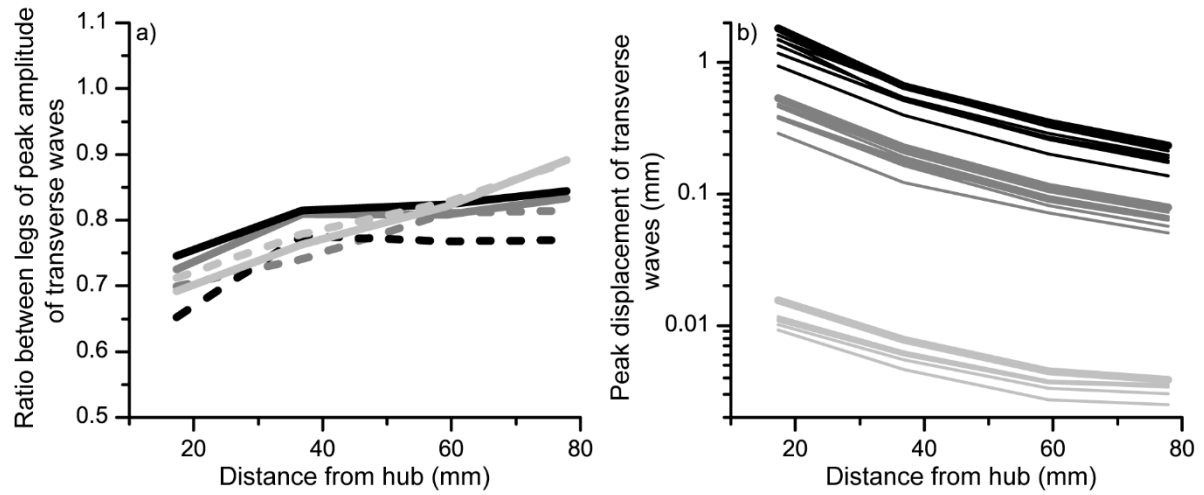
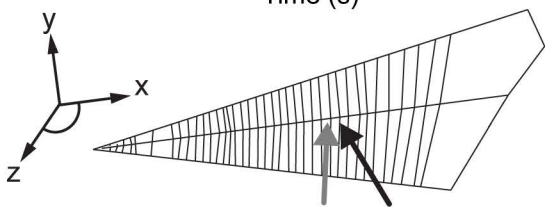
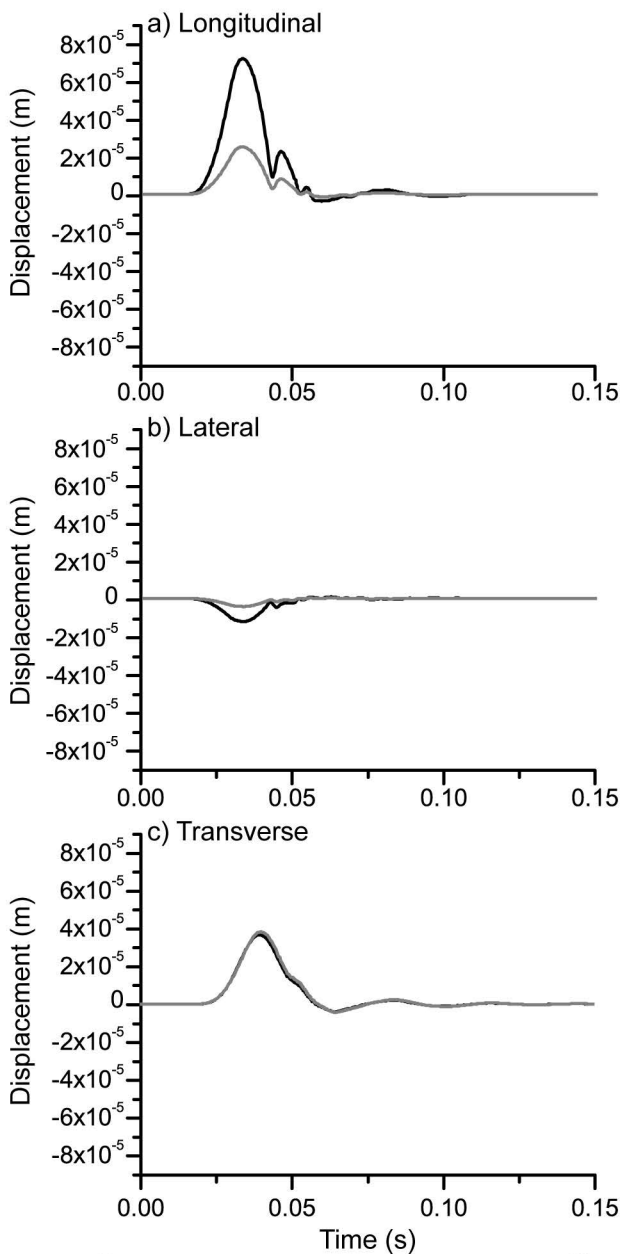
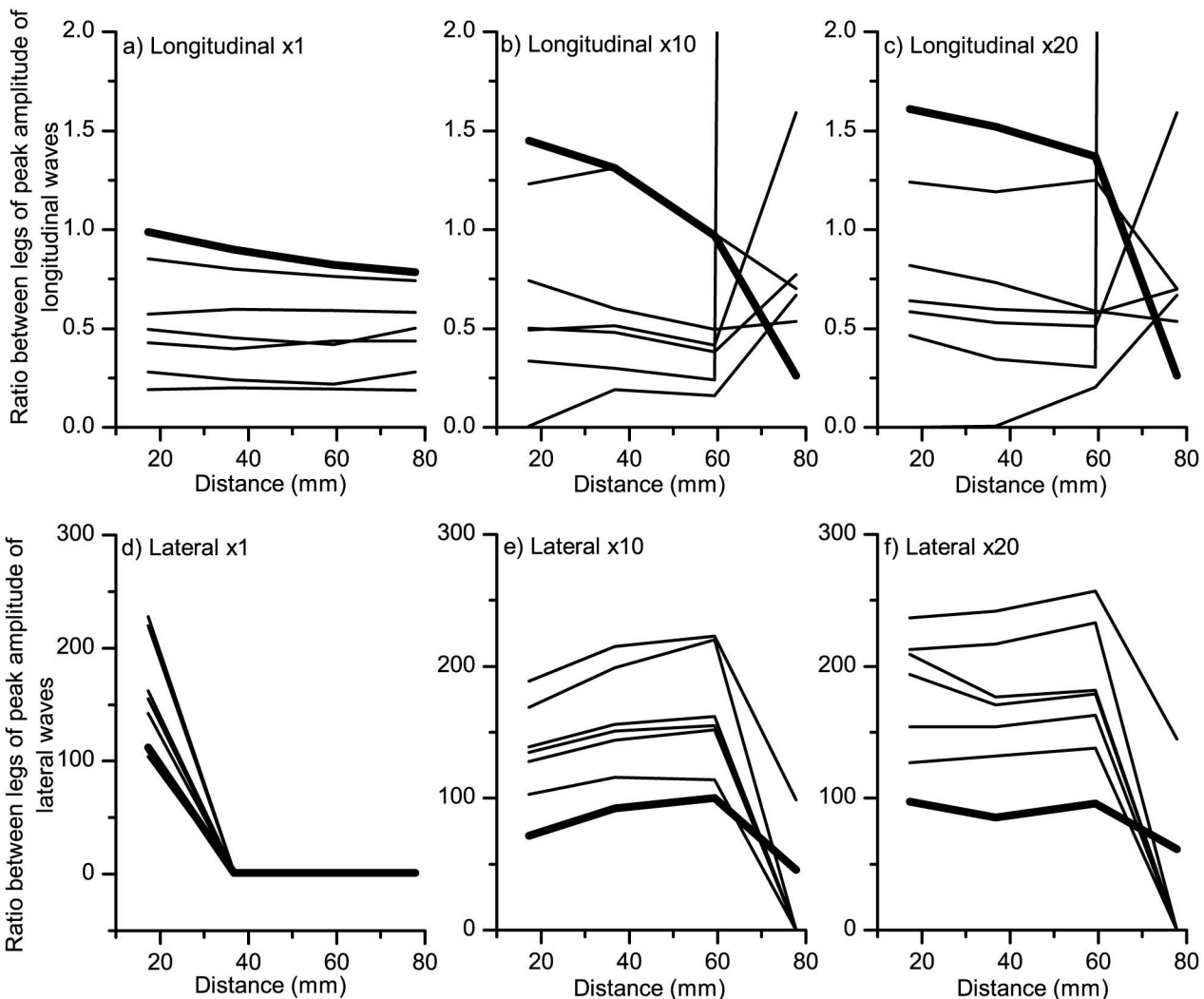


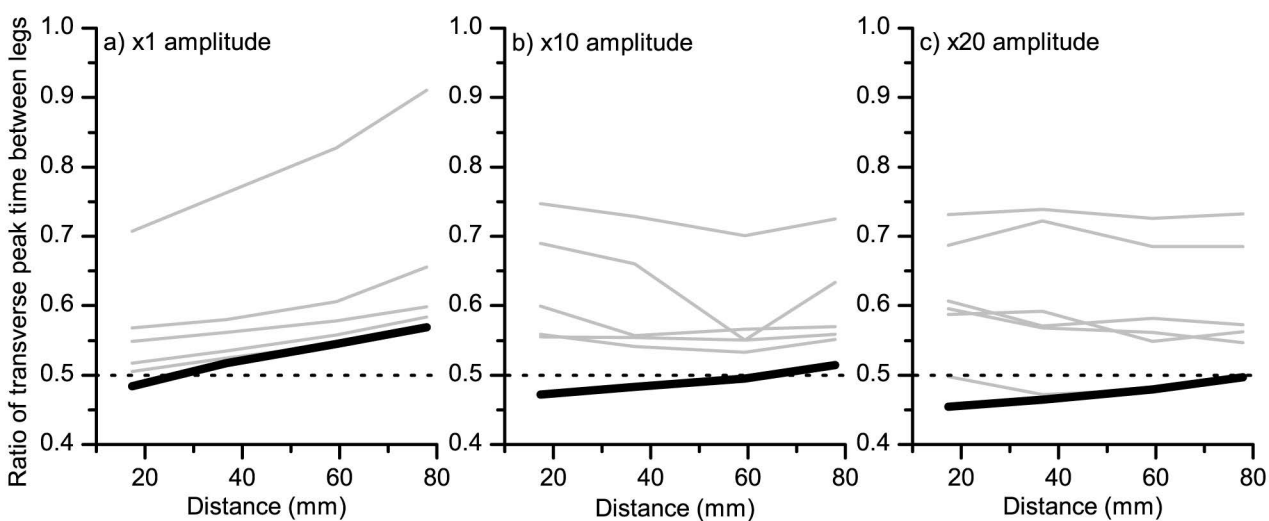
Figure 5. Transverse first peak amplitude gave information on source amplitude and distance from the hub to the source for *Araneus* at the hub. Light grey, dark grey and black denote x1 (0.34 mm), x10 (3.4 mm) and x20 (6.8 mm) input amplitudes respectively. a) Ratio of first peak amplitude of transverse waves relative to leg 1, where leg 3 (c. 90° to source) is given by solid line and leg 7 (c. 270° to source) is given by dashed line, b) First peak amplitude of transverse waves, where leg 1 is given by thicker lines. Input radial and leg output locations are indicated in Figure 2a. Input polar angle was 30° relative to the Z axis (perpendicular to web plane) – i.e. 30° bias away from hub measured from the Z axis.



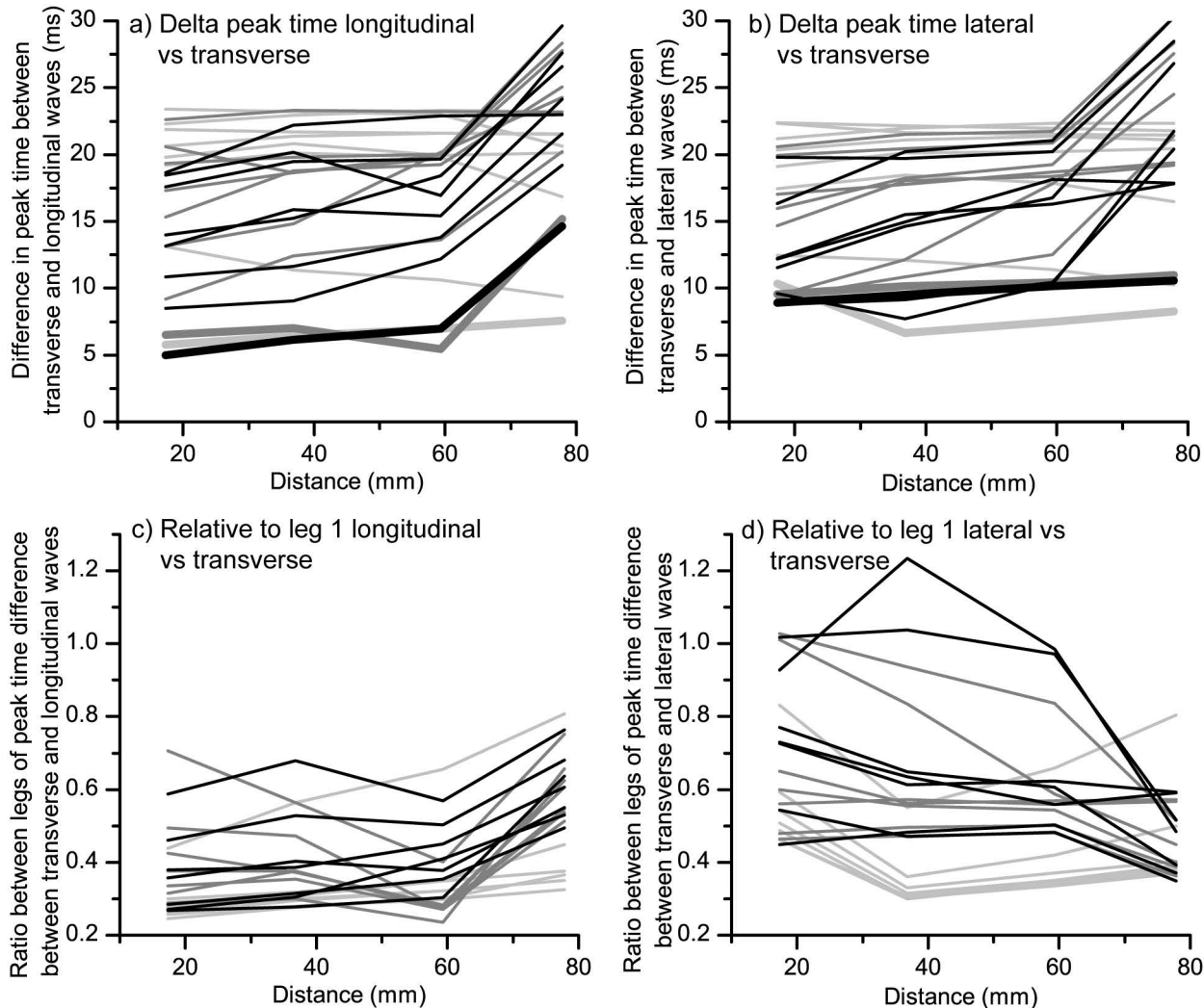
Supplementary Figure 1. Effect of input polar angle on: a) longitudinal, b) lateral and c) transverse waves when input and output locations were stationary (see Figure 2 – asterisk for input and leg 1 for output locations). The input polar angle varied in the Z axis: the angle was either 10° given by solid black or 30° given by solid dark grey. Data are shown for a model *Araneus* web without mass with an input amplitude of 0.34 mm.



Supplementary Figure 2. Ratio in first peak amplitude between leg 1 and other legs versus distance between hub and source for a-c) longitudinal and d-f) lateral waves. Panels a and d show x1 source amplitude (0.34 mm), b and e x10 (3.4 mm) and c and f x20 (6.8 mm), where thicker lines give the values for leg 4 versus leg 1. Input radial and leg output locations are indicated in Figure 2a. Input polar angle was 30° relative to the Z axis – i.e. 30° bias away from hub measured from the Z axis.



Supplementary Figure 3. Ratio of first peak times of transverse waves across legs relative to leg 1, which was closest to the source versus distance from the source to the hub. a) x1 (0.34 mm) amplitude, b) x10 (3.4 mm) amplitude and c) x20 (6.8 mm) amplitude. Black lines give the ratio for leg 5 versus leg 1 and grey lines give the ratios of other legs. Input radial and leg output locations are indicated in Figure 2a. Input polar angle was 30° relative to the Z axis – i.e. 30° bias away from hub measured from the Z axis. Dashed line indicates that for a ratio value, both close and small sources had the same value as bigger and further.



Supplementary Figure 4. Difference in first peak time between transverse and a) longitudinal and b) lateral waves over distance from source to the hub. Light grey, dark grey and black denote x1 (0.34 mm), x10 (3.4 mm) and x20 (6.8 mm) input amplitude respectively, where thicker lines give the values for leg 1. Ratio between leg 1 and other legs in first peak time difference between transverse and c) longitudinal and d) lateral waves versus distance from source to the hub. Input radial and leg output locations are indicated in Figure 2a. Input polar angle was 30° relative to the Z axis – i.e. 30° bias away from hub measured from the Z axis.