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Crista acustica in insect ears modeled by an inhomogenous granular chain

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Insect ears are found on the thorax (in some Hemiptera), the abdomen (in grasshoppers, cicadas and some moths), or the front tibia (in crickets and katydids). *Crista acustica* -also named Siebold's organs- is the sensory organ linked to tympanum when located in forelegs. It is a collection of individually-tuned scolopidia -the most fundamental unit of mechanoreceptor organs in insects- that can discriminate frequencies. A remarkable geometrical property of the arrangement of the soma or cell body of hearing sensing cells -the inner hair cells in the cochlea of mammals and human beings and the scolopidia in the hearing organs of invertebrates- has not yet been explored. We will focus on the arrangement of the cells of the scolopidia of *crista acustica* in the fore tibia of certain Orthoptera (e.g. grasshoppers, crickets, katydids). It consists of a collection of perfectly aligned sensory cells forming a crest on top of a hollow tracheal tube behind the tympanum. The crest can interestingly be modeled as an inhomogeneous granular chain linked to a substrate. The dynamical response in both time and frequency domains of this neurally tunable chain strongly depends on its anatomical arrangement.

1 Introduction

All land arthropods breathe and most of them developed a complex tracheal system for gas exchange. When they exist tympanal membranes cover cavities linked to this network of respiratory tubes running throughout the body.

Many hearing species are found in Orthoptera family, some of them having the ears (the tympanal membranes) located in the tibial part of the forelegs. A sensory organ, *crista acustica* (CA) is found there and its auditory nervous pathway is well described. From behavioral point of view it was proven that these insects hear mating calls but also for some of them echolocation signals emitted by bats.

Crista acustica is a crest made of perfectly aligned scolopidiae (the neural sensory cells) lying on the top of a hollow respiratory tracheal tube linked to tympanal cavities.

From a mechanical point of view it is worth wondering how the chain behaves according to its own parameters and if the alignment itself can produce signal preprocessing.

1.2 Paper organisation

We first define from a bibliographical review a granular chain of interest to model basic anatomical characteristics.

In a second part we introduce the properties of granular media with emphasis on 1D chain of beads linked to a rigid substrate and show through chosen simulation results some remarkable behaviour of each bead and of the chain itself.

In a following part, the response to applied input signals being Gaussian in displacement are compared to applied signals extracted from the simulation of an acoustic network made of narrow tubes and cavities.

A discussion will lead us to a preliminary conclusion.

2 *Crista acustica*

Ears of insects are very diverse which makes it hard to propose a generic sound transducer principle although the whole auditory system is reduced to its simpler form with no outer nor inner ears but nerve fibres being connected in the middle ear to a given set of membranes, septum or tracheal tubes of different type and in various configuration according to the way each specie adapted itself to survive in its own environment: ears were found on insects bodies in at least fifteen different sites and the diversity in their anatomical implementation shows nearly no limit.

Some ears are located on the thorax (e.g. noctuid moths able to escape from echolocating bats), some on the abdomen (e.g. grasshoppers and cicadas but also tree crickets and some moths), some on the tibial parts of the front legs just below the knees (e.g. ground crickets and katydids but also some grasshoppers).

In the latter case, a remarkable geometrical property of the arrangement of the soma and cell bodies of the sensory interface with the nervous system -named scolopidiae in invertebrates- has not yet been explored. Fig. (1) illustrates the perfect alignment of these cells within *crista acustica* as it can be found in some species in the Orthoptera family.



Figure 1: (Left) a dorsal view of the complex tibial organ in the foreleg of a female (armoured) ground cricket illustrates the perfect alignment of cells in the *crista acustica* (scale: 500 μm). The male *Acanthoplus longipes* is shown on right hand side (scale: 1 cm). [1] Reproduced under Creative Commons Attrib. 3.0 license.

2.2 Proposed granular chain model

Our preliminary model of *crista acustica* is based on a 1D chain of granular beads linked to a rigid substrate as illustrated in Fig. (2).

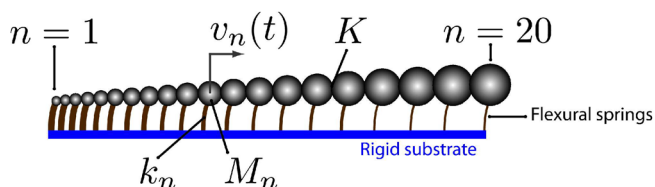


Figure 2: Representation of the *crista acustica* organ modeled as a 1D granular chain. Beads are given a mass M_n and are linked to neighbors and to a rigid substrate by variable spring-like K and k_n couplings.

The scolopidiae in *crista acustica* have not yet been studied under such an hypothesis and the detailed biomechanical datas are missing thus parameter values were adjusted in order to demonstrate some behaviour of interest.

3 Granular media

An unconsolidated model granular media is an ordered or disordered arrangement of spherical elastic particles in non-cohesive contacts (e.g. packings of mm in diameter

glass beads) and acoustic methods are the only one able to probe the elasticity of such three-dimensional media [2].

Crista acustica can be modeled as an inhomogeneous granular chain linked to a substrate where each bead is given a different set of parameters. The simulated configuration of the 1D chain shown in Fig. 2 is as follows:

- In some species the body cells are aligned in CA according to a strong gradient in their size. It was hypothesized that the mass of the beads will follow the size rule if cell density is considered constant. An example of gradient is given in [3] with a factor of 1 to nearly 4 in diameter and thus a factor of 1 to less than 64 in mass was chosen.
- The number of body cells vary according to species (typical values were found between more than 10 and less than 30) and a mean value of 22 beads is chosen to illustrate possible behavior of the chain.
- The stiffness k_n of the springs between each bead and the rigid substrate can slowly vary according to the position of the bead in the chain since it is observed in some species that the length of the link between the body and the soma cells are spatially dependant on position. A factor of 2 to 1 is chosen.
- Body cells are described as being in contact with each others allowing the transfer of a signal that is input at one end of the chain. Although inter-bead spring stiffness K could also vary with its position in the chain the parameter is kept constant
- A viscous dissipation driven by the speed of each bead $v_n(t)$ is introduced to take account of the biological nature of the beads and to prevent any occurrence of a pure resonance within the chain.

The input signal is a Gaussian in displacement applied to the first bead except in the last simulation results.

3.2 Simulation results

The chain is modeled as a collection of coupled oscillators being repeated modules of the same electrical equivalent circuit with a different set of parameters given to each bead. A no force condition is applied on the last bead.

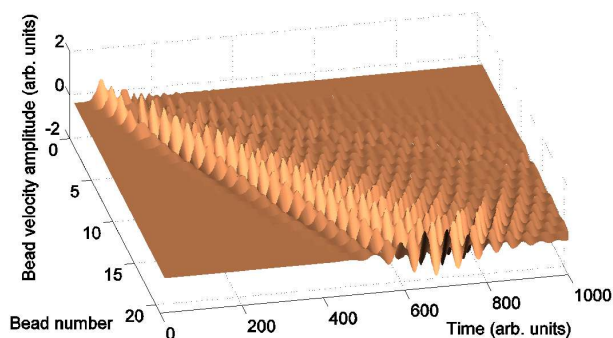


Figure 3: Simulated behavior of the cells within crista acustica modeled as a 1D granular chain of 22 beads. Bead velocities are displayed as a function of time and bead position. A Gaussian displacement signal that had been input on the 1st bead can slowly propagate and recombine due to coupling with neighbors and substrate.

The implementation has been performed in a Spice-like tool but could be further studied in the Tactyle Software suite developed by Asygn [4]. The simulated behavior of the chain is shown in Fig. (3) and one can guess that the temporal results will strongly depend on any change in the chain configuration, the input signal being Gaussian.

Fig.(4) and Fig.(5) demonstrate that additional signal processing feature can be introduced in frequency and time domains due to the chain itself thus the dynamical response of a chain constituted of independent and neurally tunable individual sensory cells can in return depend on any dynamic variation of the parameters of any cell within the chain in response to coupling interaction with its neighbors.

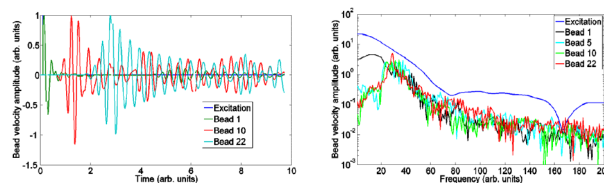


Figure 4: Simulated bead velocities as a function of time (left) and frequency (right) under a high level of viscous dissipation and no gradient in the coupling to the substrate nor mass values (homogeneous chain): the movement of beads has been spread in time. Arbitrary units are used: dissipation is 5, inter-bead stiffness is 2000, coupling stiffness to substrate is 10^{-6} and mass is 1

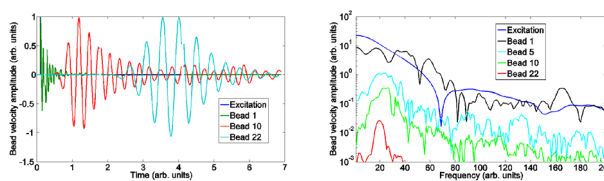


Figure 5: Same as previous except the introduction of a gradient in mass values (inhomogeneous chain): the spreading in time is increased and a filtering effect is introduced in the frequency domain. Arbitrary units are used: dissipation is 5, inter-bead stiffness is 2000, Stiffness to substrate is 2000, masses are 1,3,5,...43

3.3 Discussion

Fundamentals of the transducing of physical signals into spiking neurons is still a wide open field and among them hearing -the transducing of acoustical signals- can bring some interesting new features. The alignment of cells in crista acustica goes in pair with a strong reduction of the number of sensory cells [5] especially in the case of singing species where it could be linked to crista acustica (Table 1).

Moreover recent works demonstrate that membrane of cells can be sensitive to mechanical stimuli:

- Specialized transmembrane receptors associated with the cytoskeleton can serve as local anchors, linking cells to their neighbours or to the extracellular matrix (ECM), in a way that supports some long-range assembly with specific structural and mechanical properties [6] that allows us to model crista acustica as a granular chain.
- A scolopidia is composed of three cells: a cap cell, a scolopale cell (body cell) and a bipolar sensory

nerve cell. The shape of body cells within crista acustica made us model them as beads in our simplified granular chain. This hypothesis is supported by recent experimental results [7]. With a minimalistic tissue model consisting of a linear array of three cells the authors demonstrated that the traction forces exerted by the outer cells are not balanced such that the inner cell experiences similar force levels to the cells on the periphery.

- In response to externally applied forces, cells actively rearrange the organization and contractile activity of the cytoskeleton and redistribute their intracellular forces. In an in-vitro set-up under small deflections [8], they behave like simple springs so that their deflections are directly proportional to the local forces applied by the attached cell. Thus using linear springs is justified.
- Finally the hypothesis of a contribution of a substrate is also supported by findings in the literature although it might not be realistic enough to describe it as a rigid beam: the collective motion that is seen in the movement of epithelial cells is influenced by the balance between cell traction against a surface and the tension between cells modulated by its cell-cell contacts [9].

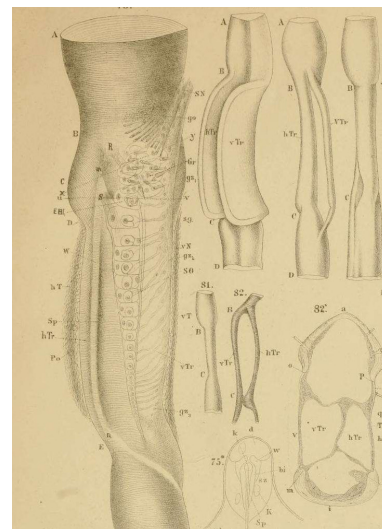


Figure 6: Vitus Graber [11] produced in 1875 a description of the medial membrane on the top of which is located CA (cross section view -right bottom-) vTr and hTr being two tympanal cavities and the tubes being part of the through the body distributed respiratory system.

Table 1: Number of sensory receptors according to a spatial arrangement. See [5].

Insect species	Specific spatial arrangement	Number of auditory receptors
Bushcricket	alignment	20 - 60
Cricket		50 - 70
Grasshopper		30 - 80
Grasshopper	no alignment	2000
Cicadas		600 - 2100

4 Crista acustica is embedded in a network of acoustical tracheae

In each foreleg crista acustica is located on the top of a hollow tracheal tube which means that it is not only located behind tympanal membranes but it is also embedded in a respiratory network made of acoustical tracheae.

The role of such an acousto-mechanical system remains unexplained although its related distributed nervous system has recently been studied by several research teams (e.g. [10] describes the nervous pathway arising from crista acustica in a giant specie of a tree insect -a weta-). The anatomical complexity of the intricate configuration is the main difficulty although it has been known for centuries [11] as shown in Fig. (6). The diversity of each anatomical implementation among species makes the effort reward-less without the finding of a generic and commonly shared basic physical effect or analog signal preprocessing principle.

The tibial tracheal tubes are connected to a network which finally opens to the outside through conical-shaped holes called spiracles spread along the body. In many species the spiracles can be opened and closed by valves. Although insects with a passive respiratory system keep valves mainly opened, some of the larger insects actively ventilate their tracheal systems by contraction of muscles located in the valves.

4.2 Non gaussian input signal

At this stage it is worth checking what kind of rough change in the simulated behaviour of the chain could be brought by a more realistic input signal.

Here we check the influence of a signal that is shaped by the response of an acoustical network. The impulse response of the basic network of tracheal tubes in cricket has been independently simulated in [4] (this conference proceeding). Although it does not represent the exact acoustical configuration requested here the impulse response has been changed into a force applied on a 1mm² surface as shown in Fig. (7) and then into a displacement of the first bead calculated in our arbitrary unit system.

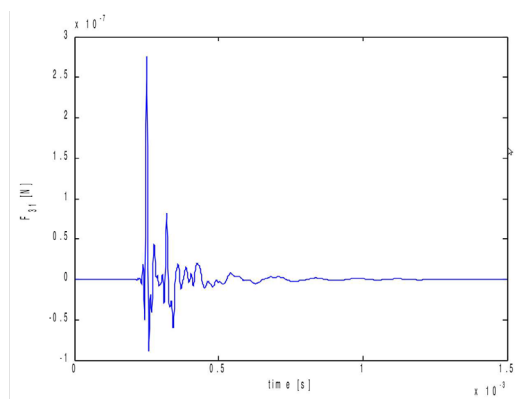


Figure 7: The impulse response of the network of tracheal tubes in cricket resulting from [4] expressed as a force applied on a 1mm² surface.

The simulated behavior of the beads within the chain is shown in Fig. (8) and Fig. (9). The parameters have been modified to provide a suitable cutoff frequency. Basically the response of the chain is kept unchanged: in the time domain the first beads movement keep being strongly influenced by the excitation signal while the distal bead movements last under the influence of the whole chain.

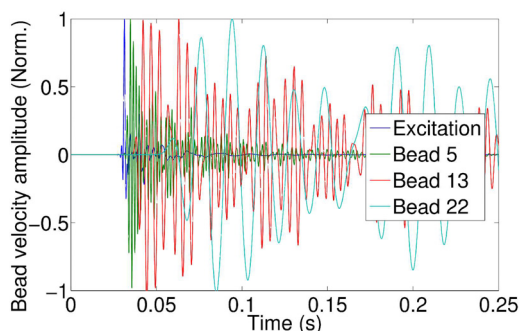


Figure 8: Simulated bead velocities as a function of time under a high level of viscous dissipation and no gradient in the coupling to the substrate. The cutoff frequency has been adjusted according to a new input signal (a displacement of the 1st bead shaped as shown in Fig. (7)).

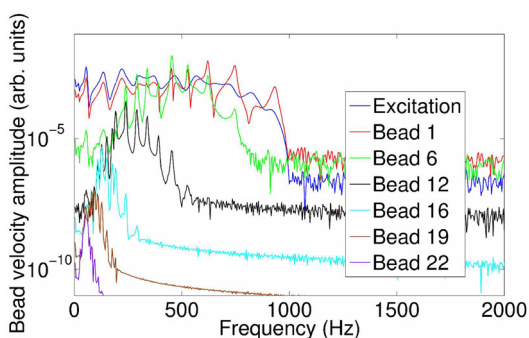


Figure 9: Simulated bead velocities as a function of frequency under same condition as Fig.(8). The cutoff frequency has been adjusted according to a new input signal (displacement of bead 1 shaped as shown in Fig. (7)).

In the frequency domain the effect of filtering is still clearly seen together with an effect that is best expressed on the first beads now less dependent on the sole input signal.

5 Conclusion

In insects the auditory nervous pathway is connected directly to the vibro-acoustical membranes within middle ears. Although no outer nor inner ears are found, a direct mechanical or indirect acoustical or fluidic coupling mean is often found at anatomical level between the middle ears.

Crista acustica embedded in such an environment can be modeled thanks to a 1D inhomogeneous granular chain and it is permitted to imagine that some active system within the cells can help get rid of a strong signal attenuation and would be able to help induce coda-type waves [12] from which it might be easier to extract relevant information.

Given the through the body-distributed nervous system together with the small size of insects it might not be surprising that microscale physical phenomena might be mandatory to small animals to perform highly specific analog preprocessing right at the interfaces that sense the

physical world in order to reduce the neural processing needs and to speed up on purpose best escape behaviors.

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