

Pitch: the result of physics-guided sensorial optimization

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The ubiquity of periodic signals in nature produced by animals calls for sensors tuned to such information. In the generation of the most basic periodicities by an animal's gait, in the sensing and even in the processing of complex sound environments, simple nonlinear dynamics physics principles play the essential role. A basic analysis in terms of this physics reveals a dramatic reduction in the solution space available for the hearing sensor, such that the apparent cochlear apomorphies between the amniotic lineages can be recast into a scaleable and a non-scaleable arrangement of small signal amplifiers. The scalable solution employed in mammals as the most advanced design, provides a natural context that demands the characterization of complex sounds through pitch.

I. INTRODUCTION

Nature provided our planet with an abundance of species. The question of how this abundance comes about has intrigued humans since early in their existence. In his treatise 'On the Origin of Species', Charles Darwin set forth in 1859 [1] for a scientific explanation, anchoring it in the general principles of competition. Since then, research on evolution has focused mostly on the particular twists and turns the course of natural selection has taken, trying to understand what advantage a specific modification would have given to its bearer.

From this, a sense of irreverence at the ingenuity of the resulting intricate solutions has emerged. Such details, however, seldom shed light on why one particular evolutionary course might have been followed instead of another, apparently equivalent one. It has earlier been observed [2] that a convergent evolution may have directed insect as well as mammalian audition (where this conclusion focused on katydid insect ears). Genetically, mammalian audition is mediated by the same key genes [3], which indicates the close evolutionary relationship. In addition, in mammalian audition, the anion transporter family *prestin* is expressed, whereas audition is mediated in nonmammalian vertebrates and in insects by prestin-homologous proteins [4]. All this points at a strong joint origin and parallel evolution of the hearing system.

Here, we would like to add a fact that has generally been overlooked in this discussion: the extraordinary role of physics as the major guiding force behind specialization that makes these observations understandable from a physics - in contrast to a genetics - point of view. A recent, notable exception in this neglect of the role of physics, is the explanation of the universality in visual cortex organization, where it was shown that simple nonlinear physics principles and not direct genetic blueprinting, guides a self-organized solution in independent evolutionary pathways [5]. In the present

paper dealing again with audition, we argue that if there is a competition advantage solicited by this sense, then physics constrains the potential solution space for sensing devices to an extent that forces the sensory systems to converge to a unified solution: the mammalian cochlea. We will, moreover, show that this cannot be achieved at no cost, and that this naturally leads to pitch sensation. By looking at the hearing sensors from the evolutionary angle, it will become apparent that this sensor is not determined primarily by genetic "bio-engineering", but instead is strongly guided by the "invisible hand" of physics.

II. PERIODICITY FROM NATURAL DYNAMICS

Periodic signals abound in nature; from planetary orbits and rotations down to mechanical vibrations. When extracting information from a complex environment, the most salient properties to be extracted are periodicities relating to data too regular to be of accidental nature. In the auditory world, these signals arrive in terms of pressure waves that in their basic variants are well-understood in terms of mostly linear physics [6]; the further information processing steps by humans then require nonlinear physics principles [7–9]. Clearly, all over in physics we are confronted with harmonic oscillators that naturally entrain wave equations; partly, because Hooke's law is a good approximation to many physical systems.

It seems, however, justified to ask where the origin of this *abundance* of periodic signals generated in the animal world may be? Here we put forward that observed periodicity may often emerge even from a less specialized source: from an underlying chaotic process. In the animal world, the dynamical processes are generally much more complicated and usually nonlinear. A classical example are pattern generators taken in a very general sense. If we take the animal gaits as the illustrative example, we may ignore in this context that their generating frequencies are somewhat low, seen from an auditory angle. As a tendency young animals make strange - as we will interpret it: chaotic - movements. Chaos provides

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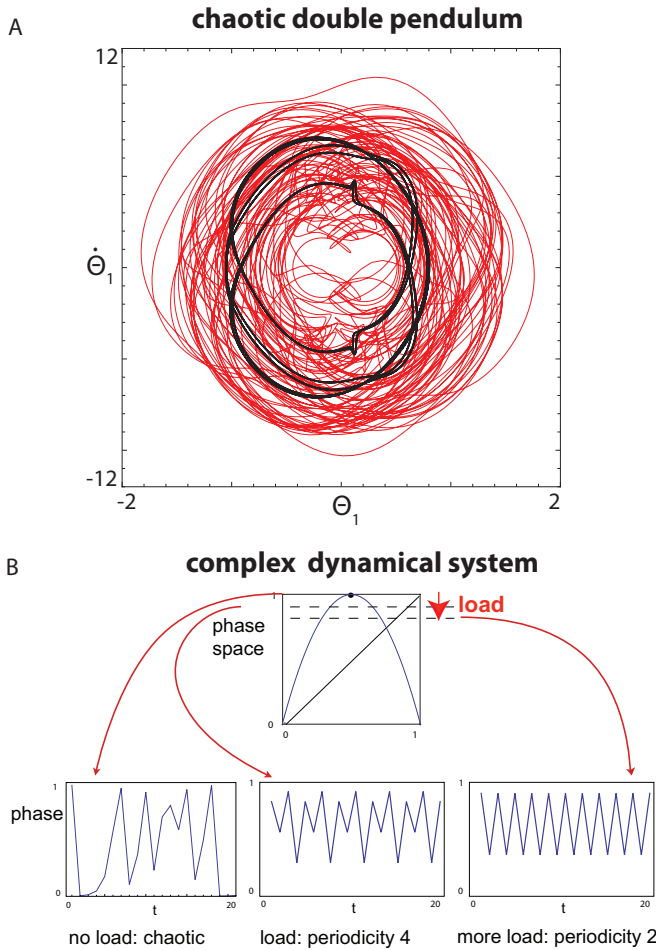


FIG. 1: A. Free (red) vs. soft limiter-controlled (black) orbit of a chaotic double pendulum model of a double-joint limb. Limiter by a spring that becomes active whenever in one of the joints, an angle exceeds a threshold. B. Explanatory example: Fully chaotic iterated parabola with limiters at different heights (dashed), leading to periodic motion.

the basic basin from which partial motions are selected, offering a great richness of choices to the system [10, 11]. Influence of living conditions or conditions arising from the survival paradigm then constrains the selection in an easy to grasp manner to simpler, less costly behavior, by acting as limiting conditions that change chaotic into periodic behaviors, a paradigm known under the name of limiter control [12–15]. It can moreover be inferred that the energy spent in a limiter-controlled periodic state is minimal [16]. For animals, load, weight or speed may act as such limiters; seen for instance in the transition from walk (period 4) to trot (period 2) ‘gaits’ in quadrupeds under the constraint of increasing speed or by the weight paradigm illustrated in a more abstract way in Fig. 1. As a result, periodic signals are not restricted to simple physical oscillators, they are also the most basic sound signatures of more complex systems from the animal world. Here, we illustrate this by taking, similarly to Ref. [12], two joints that would move chaotically, if not limited by

elastic forces active as soon as one has crossed a certain threshold. Without loss of generality, we may restrict the control to the upper joint, where we introduce a spring-type energy $V = \frac{1}{2}k[\theta_1 - \text{sign}(\theta_1)\theta_0]^2$ that only becomes active for $|\theta_1| > |\theta_0|$. The addition to Hamilton’s equations $\propto k[\theta_1 - \text{sign}(\theta_1)\theta_0]$, for $|\theta_1| > |\theta_0|$ offers, by a choice of θ_0 to force the system onto a desired periodic orbit.

III. SMALL POWER FREQUENCY SENSING

Hearing a weak sound first among competitors is a substantial evolutionary advantage, for spotting a predator, or a conspecific for reproduction. In the simplest case, a single frequency may be sufficient for the identification of conspecifics. This is a well-studied case in insect hearing, where the small wing surface is generally insufficient to generate pressure waves efficiently at its frequency. For spotting the female, the male mosquito *Aedes aegypti* therefore performs ‘near-field’ hearing, sensing the bulk movement of air molecules (rather than far-field pressure waves) with a sensor that is tuned to the wingbeat frequency of females that display different bodyweight and wing size distributions [17]. To pick up this faint and variable information, mechanical excitable systems are used. The functional basis of most insect hearing, is the chordotonal organ [18]. This includes Johnston’s Organ of the mosquito or of *Drosophila*. Although seemingly very different at first view, genetically and physiologically the human cochlear hair cells that later on we will centrally deal with follow exactly the same building principle [19].

For detection and perception, very faint input level sounds first need to be amplified actively (i.e., by using energy added from outside), which then will enable the processing of this information as for fully developed inputs. Here, again a quite general physical principle is used: that of small signal amplifiers [20, 21]. This paradigm consists of the observation that physical systems generally undergo bifurcations, if their system parameters or physical properties are changed. Upon crossing a bifurcation point, the nature of solution (trajectory, behavior, etc.) of the system changes, in many cases by going from rest into an oscillatory state. Very close to bifurcation, dynamical systems lose stability (they cannot decide which behavior they should pick). The natural consequence is that small inputs have huge effects in the response; this provides their small-signal amplifier property.

Many of the known biological small-signal amplifying systems operate below the bifurcation point to oscillation, but spontaneously may even cross it. In the context we are considering here, such spontaneous oscillations make generally no particular sense. However, since the bifurcation happens upon a smooth change of some parameter, very similar physical mechanisms hold on either side of the bifurcation point (the same equations

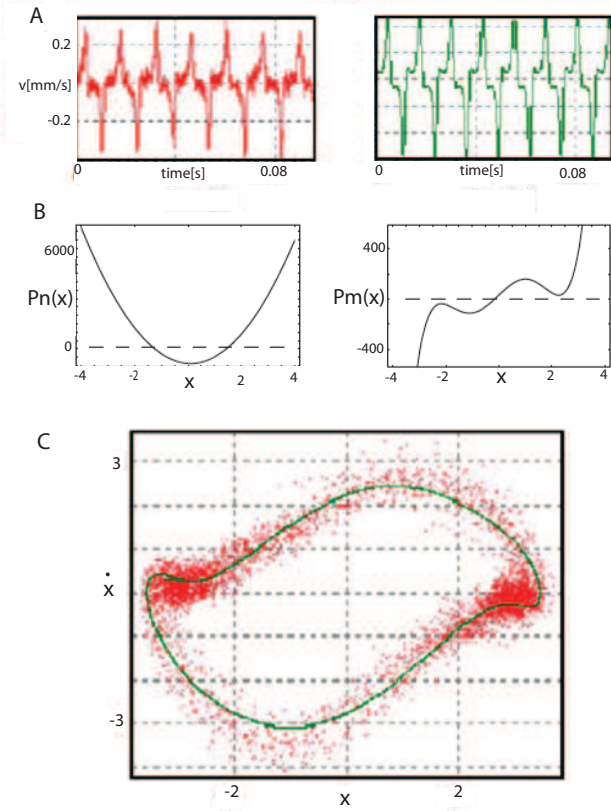


FIG. 2: Fully developed self-sustained receiver oscillations (SO) of *Drosophila*, 20 min after DMSO injection (after Ref. [22]): A) Red: Data, green: simulations. B) Best data-based polynomial approximation of SO $\ddot{x} + Pn(x)\dot{x} + Pm(x) = 0$, with $n = 2$ and $m = 5$, displaying a Hopf bifurcation (the classical equation $\ddot{x} - \mu(1 - x^2)\dot{x}$ has a Hopf bifurcation at Hopf parameter $\mu = 0$). C) Data (red) and reconstructed SO (green).

with changed external parameters apply). Thus the behavior beyond bifurcation can be used to infer the deeper nature of the active amplification process. This approach has been followed in the example of the *Drosophila* antenna [22], where the injection of biochemical dimethyl sulfoxide (DMSO) leads to a crossing of the bifurcation point. From the observed velocity time series of the antenna oscillations, an underlying generalized van der Pol system could be identified which operates in the close vicinity of a Hopf bifurcation [22] (see Fig. 2).

At a more detailed level, enlightening understanding of the amplification dynamics can be gained from the behavior around zero displacement position $x = 0$, where the nonlinear damping term $Pn(x)$ attains negative values for small displacements x (Fig. 3B). $Pn(x) < 0$ implies that energy is injected into the system, indicating the presence of an active amplification process. Around $x = 0$, the nonlinear restoring force $Pm(x)$, together with its first and second derivatives, are relatively small. This implies that for small receiver displacements, virtually

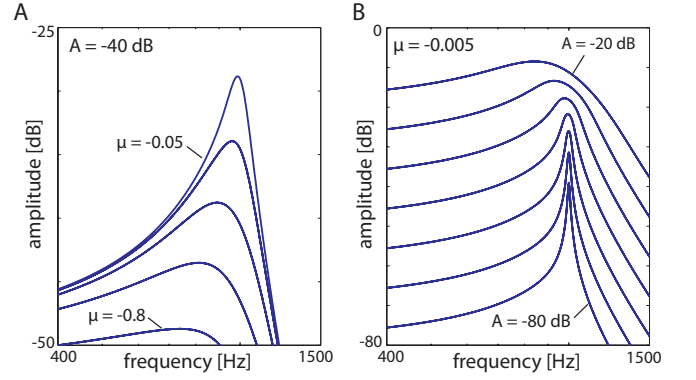


FIG. 3: Active amplification by a single Hopf amplifier [23] conditioned on the passive behavior in the cochlea (leading to the asymmetry if compared to [20, 21]). The description mimicks the behavior of outer hair cells with a preferred frequency CF embedded into the basilar membrane: A) Response amplitude vs. signal detuning frequency for different distances $\mu \in \{-0.05, -0.1, -0.2, -0.4, -0.8\}$ from bifurcation point, B) for different signal strengths (increase in steps of 10 dB).

no restoring force is present. By means of the negative damping term, the system is thus easily driven out to large amplitudes. The comparison between data and obtained trajectories reveals the close correspondence between the data and the model (Fig. 2). When run below the bifurcation point to self-sustained receiver oscillations, the system has all the amplification properties shown in Fig. 3.

The human hearing system copes with similar constraints. The moderate decay of sound pressure with distance implies that the sound pickup system has naturally to deal with large dynamic signal ranges. In fact, the physics of the environment force us to deal with sounds from a 120 dB sound pressure range. This is tantamount to an instrument measuring, interchangeably without adjustment, voltages on a computer motherboard as well as those of a high-voltage power line. For local systems to bifurcate from steady state into an oscillatory state, essentially two bifurcations are known: saddle-node (tangent) bifurcation of equilibrium points (in the neuronal Morris Lécar equations) or by a subcritical Hopf bifurcation (in the neuronal Hodgkin-Huxley equations). While the different bifurcations can both serve as small signal amplifiers, the particular bifurcation delivers a specific fingerprint onto the amplification law [23]. In the case of the human hearing system, it is the electromotile outer hair cells in the vicinity of a Hopf bifurcation that provide this nonlinear amplification. Their describing time-continuous dynamical Hopf system is below the threshold, but would start to oscillate at its characteristic frequency ω_0 if stimulated by an incoming signal of frequency ω somewhere in the vicinity of ω_0 . This system has the response shown in Fig. 3, which embraces all the required amplification properties. It is worth noting

that these amplification profiles are of fundamental importance; we will show that their properties are preserved the whole way up the auditory pathway. From them, the main properties of the Mammalian hearing sensor can be reproduced and understood ([24], in particular the supplemental materials).

IV. MANY-FREQUENCY CHALLENGE

Beyond the task of identifying a weak characteristic frequency of a conspecific, several frequencies may be of interest. Procreation and survival may necessitate the distinction of sounds emitted by the mate, the predator, and the prey. Some birds, for example, use a complex language for warning the flock specifically about specific predators [25]. For species that interact more intricately with the world around, a whole range of perceivable frequencies is required to understand and interpret the environment. The hair cells in today's cochleae that act as the small signal amplifiers in the mammalian case, emerged very early in evolutionary history, before even the split of the stem reptiles from which the amniotes evolved, approximately 400 million years ago [30]. For a scheme to evolve to amplify and distinguish a broad suite of frequencies, these hair cells must somehow embody a tuning mechanism. The simplest solution on first view would be a construction scheme by which each sensor would inherently react to one particular frequency.

There is, however, one complication not taken account of by this view, which is that the nonlinear amplification property of the sensors comes at a price: the superposition principle does not hold for nonlinear amplifiers. Together with the desired frequencies, undesired families of interaction products among the amplifiers emerge (this is a very general observation that holds basically for all such sensors). To suppress their emergence, the sensors would need to be ‘well-separated’, e.g. by placing them at a large distance. Since this also implies large distances of the wiring, such systems are only preferable in the case of relatively few frequencies to be dealt with and animals of small local extensions, such as insects. In fact, the chordotonal organs upon which insect hearing is based, are found all over the insect body (Fig. 4). From these separated sensors, a huge variety of more specialized “hearing” organs has developed in different parts of the anatomy for different species [18]. A distributed hearing system implemented similarly for higher animals such as mammals, would increase the expense and complexity of connection and integration, and, moreover, would involve a difficulty of signal interpretation. Indeed, even in the insect case, the majority of adaptive behavior appears to be elicited by the sounds detected by the localized, specialized hearing organs, which show simple, narrow frequency tuning [18].

To circumvent this problem, the family of amniotes inherited from the stem reptiles a particular kind of local amplifier organization: they put the sensors responding

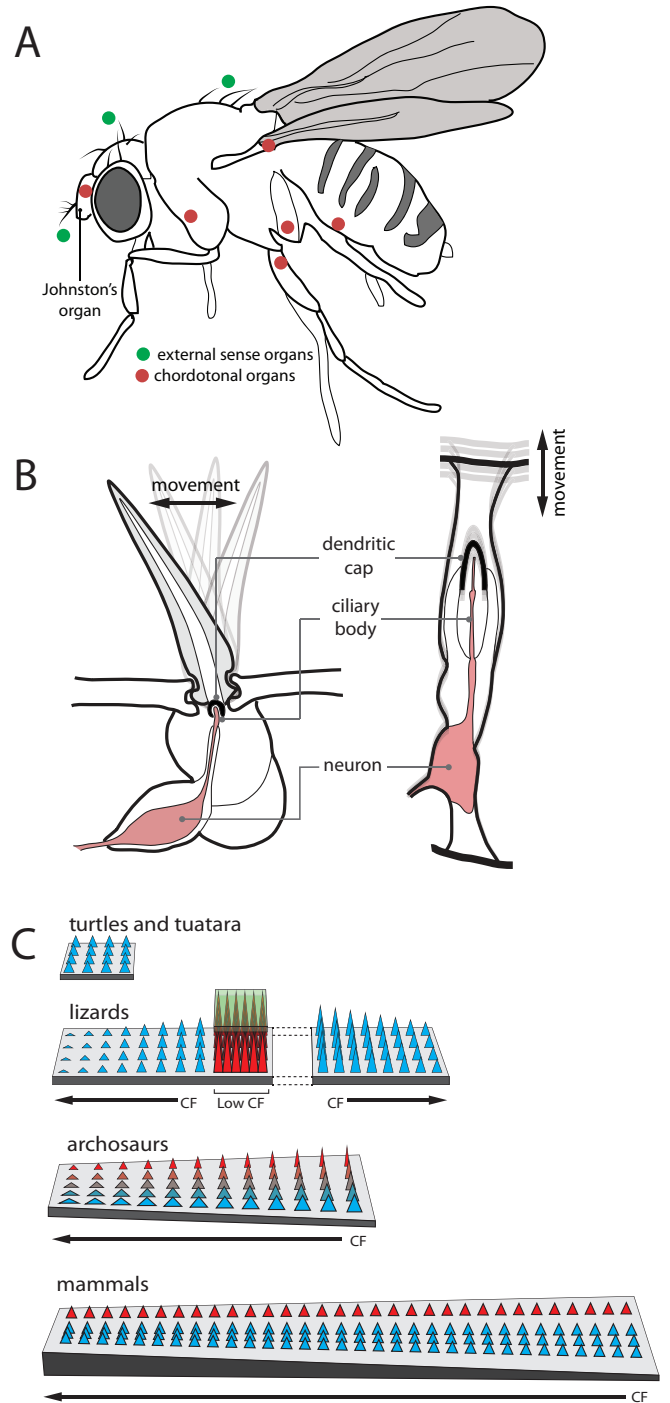


FIG. 4: Sensory hair cells and chordotonal organs. A) Location of sensory hair cells and chordotonal organs in *Drosophila*. B) Insect variant of inner and outer hair cells (arista and chordotonal organs), based on common genetic origins [4]. C) Schematic arrangement of amniotic frequency sensitivity (where only a representative example of the many variations in lizards is shown).

to different frequencies locally centralized onto a membrane tissue area: the prototype of the ear was born. A number of tuning “parameters” are cited in the literature that control the frequency sensitivity of different hair cells. They distinguish broad scale and localized changes in the mechanical properties of the basilar papilla and/or tectorial membrane (macro- and micro-mechanical tuning), as well as local modifications to the properties of the hair cells themselves (micro-mechanical and electrical tuning) [30]. In the localized arrangement, the amplifiers are doomed to interact. This renders the above divisions far less stringent than they appear at first sight, and has far-reaching consequences.

When building a localized hearing sensor designed to aid survival, the sensor should be encoded, constructed, and connected in the most efficient manner, while maximizing interpretability of the output. Tonally, this implies some broad structural arrangement of the characteristic (preferred) frequencies across the device (whether encoded in the sensors, via the substrate, or in combination). This might be implemented, broadly speaking, in one or two dimensions (the hair cells which form the basis of the sensor require a surface on which to attach, so any three dimensional arrangement would necessarily consist in stacking of sheets of sensors, i.e. a collection of two dimensional arrangements). Frequencies require only one dimension for definition, so higher dimensional placements (such as concentric rows on a circular membrane) would result in inefficient spacing or excessive wiring: the former has obvious problems with scalability, while the optimization of the latter was the driving organizational principle of Cortex [34]. We suggest that tonotopic placement in broadly one dimension can be considered a priori as the starting point for efficient sensor design. Also from the point of view of wiring simplicity, the easiest arrangement is one with a single tonotopic gradient. This can be seen as the case in both birds and mammals, but not in the lizards, which show an enormous variety of partial tonotopic arrangements (Fig. 4). For lizards, it is not difficult to imagine that pure tones can still be interpreted directly with ease. An increase in complexity of the input, however, will generate irregularity by combination tone emergence, that becomes hard to imagine manageable, and generates a significant cognitive burden that must be overcome higher up in the auditory pathway. Since the evolutionary process is not easily reversed (but rather reset, through extinction) the great variety of hearing sensors exhibited by the lizards can be seen as examples of local minima available to an optimization process that has already converged to a segmented, modular sensor solution, and is not required to achieve a global optimum. In fact, the Turtles and Tuatara show a far simpler sensor arrangement, with a very limited range of frequency sensitivity, thereby minimizing the effect of the interaction products between sensors of different characteristic frequency at a price of a much reduced hearing capability. Moreover, they generally seem not so much to base their living on auditory information compared

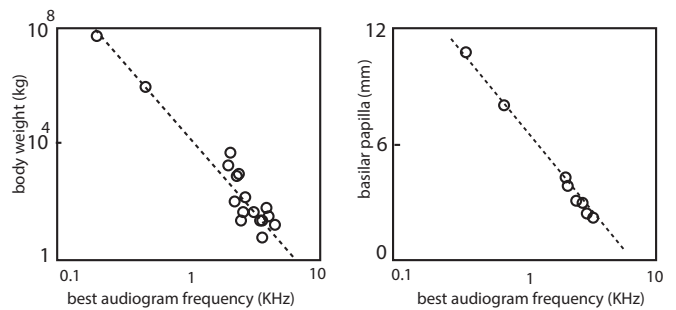


FIG. 5: Body weight and basilar papilla length vs. best hearing frequency. The two highest data points in each plot are extrapolations for extinct dinosaurs, by Dooling [33].

to mammals and birds. From an evolutionary optimization viewpoint, their solution is similar to the frequency tuned hearing organs of insects, by which much of the complexity in the auditory environment is, in large part, not sensed. The tokay gecko, instead, who is an excellent listener, developed two types of hair cells similar in character to the mammalian inner and outer hair cells [26].

V. SCALING THE DESIGN

The essentially one-dimensional tonotopic placement of the hearing sensors where frequency and distance space collapse on a logarithmic scale, taken by the Archosaurs and eventually mammals, offers a second, potentially even more important advantage. Such an arrangement may be implemented without detailing specifically the frequency properties of each sensor individually, but by using essentially the same construction making it frequency-specificity by the biological environment (i.e.: the membrane) on which it is placed. The scalable construction process offered by the elongation of the basilar papilla (and thereby extension of frequency range and accuracy) is limited in the Archosaurs by the existence of frequency tuning in the hair cells themselves (electrical tuning) [30], which is absent in the mammals.

By removing this diversification of hair cells, with the frequency sensitivity of receptors essentially defined by the membrane substrate, the mammalian hearing sensor finally achieves a fully scalable solution. Indeed, investigations of the mammalian outer hair cells have revealed that a single hair cell is likely to be broadly tuned in isolation [31]; its frequency specificity is mostly obtained from its embedding into the basilar membrane as the carrier. The frequency specificity is obtained by the exponential decreasing of the basilar membrane stiffness and the associated modification of the surface tensions [23, 32]. The independence between the individual receptor structure and the frequency to which it responds, combined with mechanical differences in the surrounding structure which are able to be defined by a single growth

process, permits the immense increase in length seen in these hearing sensors. It is the final step in this process of sensor elongation, the spiraling (for space and innervation efficiency), that gives the mammalian cochlea its name.

Scalability of the hearing sensor is, moreover, important in the context of evolution of the species within a single family, where scalability of the hearing organs is reflected in the emergence of approximate natural scaling laws between the properties of the originator of a sound and the sound itself, which can be easily verified. We observe, for instance that the relationship between the weight of an animal, and the frequency it hears best can be approximated by a power law (Fig. 5). Moreover, the frequency of best hearing is correlated with the high-frequency limit of hearing: small species with a short basilar papilla hear higher frequencies, compared to larger species with a longer basilar papilla [33]. In Archosaurs, the correlation between body mass and the length of the basilar papilla indicates not only the flexibility of this type of solution, but also indicates the deeper nature of the relationship between relevant periodicities and the underlying physics. Finally, it is arguably the most efficient way of overcoming the general wiring constraints with which the cortex is confronted. Earlier [34], we showed that the doubly fractal network architecture of the cortex minimizes the networks total wiring length required to generate a coherent information wavefront at any given speed of information transfer. It seems not too far-stretched to assume that the construction of the cochlea serves the same constraint principle regarding its interfacing with the cortex. Recent modeling experiments using quite arbitrary stimuli to cochlea have in fact, indicated the very stable scale-free structure of the network of ‘excited nodes’ (c.f. Fig. 6 [35]).

VI. COPING WITH COMPLEX EXCITATION

A strong point of support for our thesis of physics guiding the evolution of the hearing sensor, is that among the mammals, the sensor construction is quite uniform. The human cochlea, e.g., is extremely similar to that of a squirrel, cat, dog, or a guinea pig. In all these cases, the nonlinear interactions of the small-signal amplifiers produce interaction products (combination tones). As the sound travels down the basilar membrane, these combination tones become ever more dominant (Fig. 6 and Ref. [24]) and generate very complex responses.

Pulling the strongly nonlinear sensors onto one area and arranging it in a tonotopic fashion thus leaves the animal required to cope with the emergent interaction complexity. Astonishingly, the mammalian auditory system does not make any noticeable effort to correct for the (seen from the the classical signal processing dogma) undesired information gathered at the level of the cochlea. Whereas filtering out at least some of the ‘artificial’ components would certainly have been possible, this is

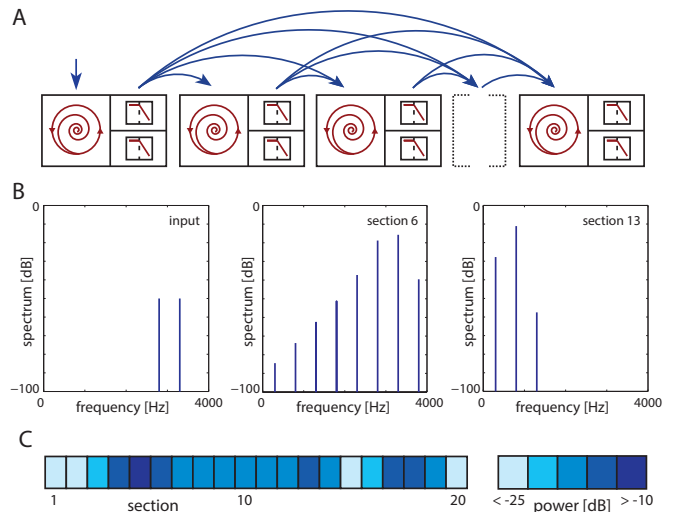


FIG. 6: Two-tone stimulation, -50 dB each tone, of the Hopf cochlea (7.04 - 0.22 kHz, 20 sections all tuned to $\mu = -0.1$). A) Interactions in the discretized cochlea model. B) Signal change along a discretized cochlea [38–40], showing the emergence of complex excitation patterns by the emergence of combination tones further down the cochlear duct. C) Generated cochlear excitation pattern.

just not how the mammalian hearing system works [28]. Biologically detailed simulations of the auditory pathway demonstrate [36] that all the data collected at the cochlear level (including all sensory interactions!) are as faithfully as possible transported along the pathway (c.f. Fig. 7), despite undergoing a whole astonishing variety of transformations and transductions on this way. This supports the insight that pitch is present at the cochlear level and not primarily a cortical product [9, 24, 36]. In fact, we explicitly showed in [36] that pitch extracted from the continuous physics at cochlear level [9] fully coincides with the pitch extracted at the end of the auditory nerve from discrete spikes [36, 37].

We know from other fields of physics that a common recipe to get a grip on emergent complexity is to attach to it an overall characterization; a fractal dimension or a Lyapunov exponent describing the complexity generated by a chaotic process confined to a strange attractor are examples thereof. We put forward that the deeper nature of pitch could arguably be seen as such a strategy. In the simple case of stimulations by pure tones, pitch sensation coincides with the physical properties of the stimulator. For only slightly more complicated stimulations, the pitch, however, develops a profile of its own and substantially departs from the physical characterization of the stimulating signal, due to physical properties of stimulated response that is rooted in the interaction among the nonlinear sensors. Such is the origin of the celebrated second pitch shift (Fig. 8) investigated by Smoorenburg in particular. Motivated by the *missing fundamental* paradigm, Smoorenburg performed psychoacoustical

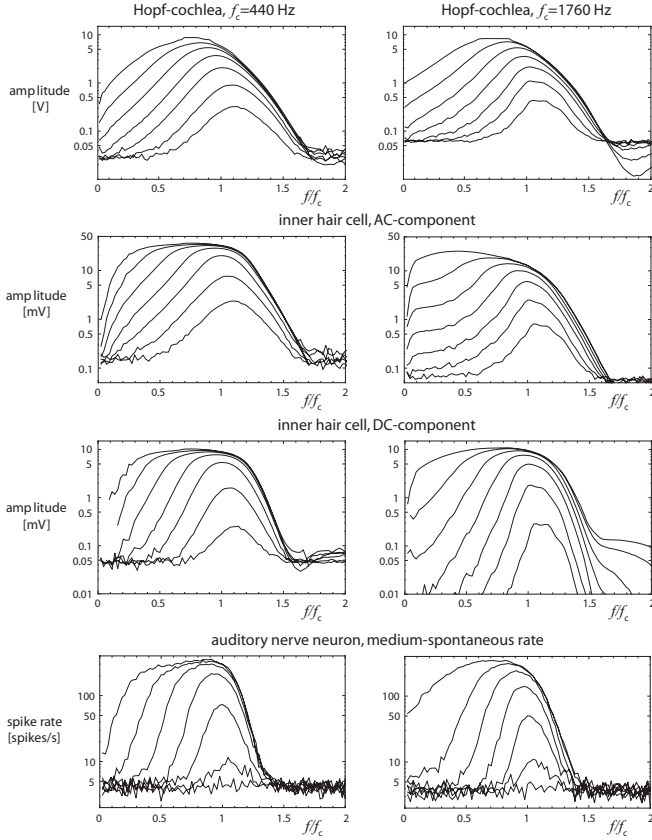


FIG. 7: Mammalian hearing along the auditory pathway, two frequency ‘channels’. Lines refer to equal input levels. Vertical direction: amplification characteristics, horizontal direction: frequency-tuning. At the end of the pathway, the cochlear sound information is practically unchanged [36] (analog cochlea implementation [38–40]).

two-tone pitch-shift experiments where the response signal to an input of the form $F_1 e^{2\pi i f_1 t} + F_2 e^{2\pi i (f_1 + 200)t}$ was evaluated by well-trained subjects, and compared to what the then known physical theories would predict. The human result was found to, first, depart from what would have been expected from a ‘lowest order’ stipulated ‘fundamental frequency’ (first pitch shift effect), and, second, even from a more evolved -somewhat hand-waving physical theory (de Boers’s formula [41]), taking account of nonlinearities by including the emergence of combination tones (second pitch shift effect). The emergence of complex patterns of excitations then leads to a multivalued perceived pitch, manifested by up to three different perceived pitches for the same experiment. In what pitch is actually heard, the efferent connections to the cochlea may play a significant role and, along with this, earlier perceived sound [42]. The detailed modalities of this readout are described in Ref. [9]. When the pitch was read out from a detailed model of the cochlea taking into account Smoorenburg’s psychoacoustic and biophysical observations, the perceived pitch f_p could be computed from the dominant peaks of the signal’s au-

tocorrelation function and was found to fully agree with the psychophysical evaluations (the two- or even three-fold ambiguity of pitch is a coherent observation in all these experiments [9, 36]). The second pitch shift could then be attributed to the fact that the sound waves are transmitted by the cochlear fluid, a fact that previous theories of the perceived pitch disregarded.

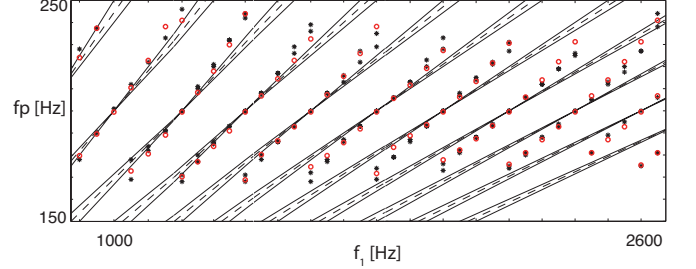


FIG. 8: Perceived pitch f_p . For two-tone stimuli ($f_2 = f_1 + 200$), Smoorenburg showed by his psychoacoustic experiments that the classically predicted pitch-shift of $\delta f / (k + 1/2)$ does not emerge (‘second pitch shift’: black dots (partial sound levels 40 dB sound pressure level, two subjects) vs. black lines). Red dots: Pitch extracted from a Hopf cochlea [9].

To cope with the generated complexity and to render a ‘purification’ of the signal unnecessary, the ‘pitch sensation’ tool seems to have been created very early in evolution. This might have been found to work much better than what more classical signal processing methods would be able to offer. The pitch sensation as defined jointly in terms of physics and physiology [9] permits the auditory system to identify or tag even an inharmonic sound by condensed information as a “fundamental frequency”, even though the latter may be absent in the physical stimulus. This embracing property of pitch has recently been used as the main guiding principle in an approach [42] for extracting elements of the auditory scene, which is at the heart of the cocktail party problem. Our physical understanding of the compound hearing sensor, the cochlea, also put forward how such a tuning in to a desired sound could be achieved by means of the efferent connections that exist from diverse levels of the auditory pathway to the cochlea. By assigning to these connections the task of tuning the amplifiers away from being effective (i.e., by moving the Hopf parameter further away from bifurcation) for undesired signals, using the pitch of the desired signal as the guiding feature, we can show how it is possible in a computationally cheap manner to extract desired and suppress undesired sounds, even if they partially overlap [42]. In real-world applications, such a guidance may be based on past experience (we know what an instrument/speaker will sound like), exploit particular information acquired at the beginning of the listening process, or be a self-enhancing process. We often invest considerable efforts for “tuning in” to a target sound, before we are finally able to follow it. Finally, we would like to point out that the study of the evolutionarily very old hearing sensory system might also

shed light on one fundamentally important question that currently science is trying to answer: What is the best computational network structure for processing complex

neural information? Here, the cochlear amplifier network provides an at least partial answer that will be discussed in a forthcoming work [35].

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